

Impacts of climate change on intertidal habitats

Nova Mieszkowska ^a, Louise Firth ^b and Matt Bentley ^c

^a *The Marine Biological Association, Plymouth, PL1 2PB, UK*

^b *Ryan Institute, National University of Ireland Galway, Galway, Ireland*

^c *Dove Marine Laboratory, Newcastle University, Newcastle-upon-Tyne, NE1 7RU, UK*

EXECUTIVE SUMMARY

The extent of intertidal habitat has not declined over the past few years. Whilst evidence for faunal changes in soft sediment communities remains scarce, there is clear evidence for an increase in the extent of the invasive oyster *Crassostrea gigas* beds, particularly in Southern England. For intertidal seagrass beds, insufficient information on bed extent and thermal tolerance and pH sensitivity mean that at present these drivers seem to be exerting both negative and positive impacts respectively. The synergistic impact is not currently known.

Range shifts in warm and coldwater species are continuing to occur. Warmwater species inhabiting rocky shores have not shown any adverse effects despite the colder winters of 2009/10 and 2010/11 with similar levels of recruitment and no mass mortality of adults for warmwater species in populations monitored annually around the UK.

The need to understand climate change impacts within the real-world context of multiple stressors is especially important for intertidal habitats which are subject to pressures from many human activities, and is coming to the fore of research priorities.

1. WHAT IS ALREADY HAPPENING?

The UK and Ireland have 32,086 km of coastline distributed within seven of the eight UK regional seas areas (Atlantic North-West Approaches, Rockall Trough and Faeroe/Shetland regional sea not containing any intertidal habitat) (Austen *et al.* 2011). Intertidal habitats exist at the margin of the terrestrial and marine realms, and species occupying these ecosystems are subject to environmental challenges posed by both regimes. Semidiurnal tidal cycles and seasonal fluctuations in sea and air temperature mean that intertidal organisms are subject to thermal extremes: fluctuations in environmental temperature in the order of 25°C can be experienced over a single tidal cycle (Helmuth, 1999). Additional stressors such as desiccation, current and wave forces, rapid fluctuations in salinity, oxygen availability and nutrient levels mean that organisms are often living close to their physiological tolerance limits, and are thus sensitive to further changes in aerial and aquatic regimes driven by climate change.

Climate has a pervasive influence at all levels of organisation in biotic systems because of temperature-dependent processes occurring from the molecular through to ecosystem scales (Cain, 1944; Atkinson *et al.*, 1987; Stenseth *et al.*, 2002). Marine ectotherms respond faster than terrestrial species to environmental change as the typically short lifespans and

sessile or sedentary nature of the adult and juvenile stages prevent escape from changing environmental regimes (Carr *et al.*, 2003; Helmuth and Denny, 2003). Intertidal invertebrates and macroalgae occupy low trophic levels and are responding quicker to alterations in climate than species at higher trophic levels (e.g. Smith, 1985; Barlow *et al.*, 1988; Jenouvrier *et al.*, 2003). They often show the first response in a cascade of effects up the food chain and are therefore important sentinels of climate change impacts (Johnson *et al.*, 2011). In addition to temperature, several other climate-related drivers are also impacting, or are highly likely to have adverse effects upon coastal habitats including sea-level rise, increases in relative wave height and storminess, and the associated secondary effects arising from adaptation and mitigation activities in coastal regions. The evidence base for these is far less than for temperature-related impacts to date, but increasing research and monitoring efforts are demonstrating that intertidal habitats are already being impacted by several aspects of global environmental change.

The potential impacts of ocean acidification (OA), also caused by human emissions of carbon dioxide (CO₂) into the atmosphere and subsequent uptake into the world's oceans are now beginning to become apparent. Increasing CO₂ uptake causes the chemistry of seawater to change towards more acidic conditions. This is of particular concern

to animals and plants that form calcium carbonate shells, skeletons or other structural components. Exposure time will be a key parameter determining the calcification response of organisms to OA, as long-lived species may have physiological mechanisms that allow them to cope with relatively short perturbations (Widdicombe *et al.*, 2010). However, OA conditions will be chronic, affecting organisms in intertidal habitats for the entire period that they are immersed.

Emergent research shows that in some cases organisms such as the Boreal barnacle *Semibalanus balanoides* cannot maintain larval development (Findlay *et al.*, 2009), shell formation rates can drop below normal levels and shells can become weakened and start to dissolve, immune systems can be impaired and essential physiological processes such as respiration and metabolism can change (e.g. the blue mussel *Mytilus edulis* (Berge *et al.*, 2006; Beesley *et al.*, 2008; Thomsen *et al.*, 2010). For algae, OA may have a positive effect by increasing photosynthetic productivity, although for algae such as the pink corallines found in rockpools, negative effects of impaired calcium carbonate skeleton production may also be a problem (Porzio *et al.*, 2011).

1.1 Intertidal mudflats

Intertidal mudflats are predominantly located in the middle reaches of estuaries but also occur in other sheltered coastal areas. They are widespread being found in over 1000 estuaries and shallow bays/inlets in the UK. They are closely interlinked with saltmarsh habitats, which often form the border at the upper limit, and dissipate wave energy, reducing erosion risk for these sensitive habitats. Intertidal mudflats are listed as an Annex 1 habitat in the Habitats Directive, are a UKBAP Priority Habitat and are nominated for the OSPAR List of Threatened and Endangered Species and Habitats (European Commission 1992, OSPAR 2008a, <http://www.ukbap.org.uk/PriorityHabitats.aspx>). They are created by deposition of fine particulate sediments such as silts and clays (less than 0.063mm diameter) up to sandy gravels in low energy environments.

Climatic drivers are changing the geomorphology of open coast sediment systems via increasing wave height and storm surge and increased water depth (Lowe *et al.*, 2009). The morphodynamic state of beaches is being altered by increases in storm frequency and greater wave energy. This can cause steepening of the beach slope and a change in the sediment particle composition towards coarser particles, and allows modelling of storm effects using historical data (Reeve *et al.*, 2008; Karunarathna *et al.*, 2012). In Charting Progress 2, the southern North Sea, Eastern Channel, Western Channel and Celtic and Irish Seas are all currently assessed as having large areas of intertidal sediments negatively affected by anthropogenic impacts (Benjamins *et al.*, 2010). Climate change sensitivity assessments for Welsh marine habitats based on published data available for habitat extent, quality and ecosystem function and adaptive capacity scored intertidal mudflats as being highly sensitive to the main drivers of climate change; sea surface and bed temperature, sea-level rise, storminess, precipitation, salinity, pH and suspended sediment (Gubay *et al.*, 2010; Jones *et al.*,

2011). Climate is a contributing factor, altering the biological composition and integrity of such habitats may change over time, even though the sediment environment upon which such broad-level habitats are described may remain the same (Jones *et al.*, 2011). Existing data from monitoring surveys cannot, however, accurately separate the various effects of climate, such as temperature and sea-level rise from other factors such as damage from dredge fishing gear and bait digging.

1.2 Estuarine soft sediment habitats

Intertidal soft sediment shores form part of a range of coastal marine ecosystems which are highly productive (Fitch and Crowe, 2011). Regions of soft sediment habitat currently situated around the outer regions of estuaries such as the Humber, in the northern North Sea support high macrobenthic biomass (Fujii, 2007) but low diversity and few rare species. Soft sediment intertidal habitats are dynamic in nature, and are structured by a combination of factors including wave action, local hydrodynamics, wind direction and sediment transportation. Within an estuary, soft sediment benthic intertidal systems can be very variable in species composition, biomass, density and productivity, which can be driven by salinity, tidal range and sediment type (e.g. McLusky, 1989; Ysebaert *et al.*, 2003). Estuarine soft sediment shores are also amongst those that are most at risk from anthropogenic stressors. These stressors, coupled with the effects of climate change, on these highly vulnerable ecosystems may bring about changes in community structure of infaunal and surface dwelling flora and fauna (see for example Lenihan *et al.*, 2003; Krause-Jensen, 2007). Recent research has yielded valuable information about the interactive effects of climate-related and other pressures. In studies of intertidal soft sediments the combined effects of increased temperature, inorganic nutrients and organic matter were additive, rather than antagonistic or synergistic (Fitch and Crowe, 2011, O'Gorman *et al.*, 2012). This highlights the need for future studies to consider cumulative rather than individual effects of climate and other stressors.

There have been few clear indications of the effects of climate change on soft sediment communities in the UK to date, but this is due in part to the inherent difficulty in making observations in these habitats as opposed to, for example, the intertidal rocky shore. Many species remain hidden in the sediment and quantifying changes in distribution and abundance is relatively difficult and it is not at present possible to provide a comprehensive review of regional differences in climate impacts. Models of future climate impacts are being developed based on historical alterations in estuarine structure and subsequent erosion and increasing coarseness of grain size due to local geomorphological changes and mesocosm approaches are yielding predictions on impacts of climate change variables (temperature; atmospheric CO₂) on biodiversity-ecosystem functioning (Bulling *et al.*, 2010). These indicate that increasing temperature and atmospheric CO₂ reduce nutrient levels and have a negative effect on marine invertebrate biodiversity, although the interactions between various drivers are complex. There are some obvious recent changes though, in relation to the spread and extent



Figure 1: Extensive *Crassostrea gigas* beds covering soft sediments in the Yealm, Devon (photo Keith Hiscock)..

of the Pacific Oyster *Crassostrea gigas*. This species was first introduced to the UK in 1890, it was the reintroduction in 1962 under licence from MAFF for aquaculture that resulted in the successful invasion of natural rocky and soft sediment intertidal habitat in the UK by this species (Walne, 1971; Herbert *et al.*, 2012). Whilst this species attaches to hard substrata on the rocky shore, it is now found in dense beds associated with soft sediment in estuaries, including the River Thames estuary as is the invasive clam *Venerupis philippinarum* (Worsfold, pers. comm.). Settlement in *Crassostrea* species is facilitated by a conspecific chemical cue (Pawlik, 1994) and it is likely that the establishment of a few pioneers leads rapidly to further settlement and colonisation. Climate projections are thought likely to result in *C. gigas* successfully recruiting annually in southwest England, Wales and Northern Ireland by 2040 in response to continually warming marine environmental temperatures (Figure 1; Maggs *et al.*, 2010).

1.3 Estuarine rocky habitats

Rocky habitat is relatively uncommon in UK estuaries, being mainly found in the Celtic and Irish Seas and north-west Scotland. It is located in low wave energy environments with reduced salinity, increased turbidity and siltation compared to open coast reefs. The coldwater macroalga *Pelvetia canaliculata* is found on the highshore of both estuarine and coastal rocky habitats. Abundances of *P. canaliculata* have shown a slight decline in the past few years on shores close to the mouths of estuaries in the Western English Channel (MarClim dataset). In contrast, abundances of *Halidrys siliquosa*, another brown alga, also found in Boreal waters but with a wider distribution south to Morocco, appear to have increased over a similar period (S. Marsham, pers. comm.)

1.4 Rocky intertidal

The majority of recent climate-driven impacts on rocky habitats have been observed at the individual species level, with northern range limits of some warmwater species

extending northwards and coldwater species range limits retreating. The topshell *Phorcus (osilinus) lineatus* continues to colonise shores along the rocky coastline of North Wales beyond recent range limits where it has not previously been recorded (Mieszowska, 2012) and numbers are increasing at the new north-eastern range edge population at Kimmeridge on the Dorset coastline of south England. Similar patterns have been observed in the warmwater topshell *Gibbula umbilicalis* along the far eastern English Channel and around into the southern North Sea (Mieszowska *et al.*, 2012). Numbers of individuals continue to increase within populations around the Welsh and English coastlines each year throughout the 2010s. The warmwater limpet *Patella depressa* was recorded at Aberdaron, North Wales, for the first time in 2012, whereas the previous northern range limit had remained at Porth Neigwll, 3km away, during the 2000s (Mieszowska, 2013b).

The trend of decreases in the relative abundances of cold, and increases in warmwater species of barnacles and limpets at long-term survey sites has continued during the past five years (Mieszowska, 2009, 2010a; Mieszowska *et al.*, 2012; Mieszowska and Hawkins, unpublished data¹). Despite the 2009/10 and 2010/11 being cooler than average for the 21st Century, no range retractions or reductions in abundance of warmwater species have been recorded on UK rocky intertidal shores, and the high densities of spring recruitment of the coldwater barnacle *Semibalanus balanoides* recorded throughout England and Wales in 2010 after the colder winter did not result in increased abundances in these populations, as the majority of recruits had died by the summer of 2010 (Mieszowska, 2011; Mieszowska *et al.*, 2012; MarClim dataset). In 2010, the warmwater limpet *Patella depressa* was recorded by the MarClim project for the first time on the Isle of Man (Hawkins *et al.*, 2012). The first record of *P. depressa* from annual MarClim surveys on artificial sea defences at Elmer in West Sussex was also confirmed in 2012 (Hawkins, pers. obs.). Annual studies throughout the 2000s and historical data stretching back to the 1960s confirm that the northern limit has remained static within the Irish Sea for over a decade despite populations increasing in abundance and becoming dominant over the coldwater *Patella vulgata* throughout southern England and Wales (MarClim time-series dataset 2012). Shifts in distribution and abundance of *P. depressa* may have a negative impact on *P. vulgata* (Firth *et al.*, 2009). In a study using a predictive framework to assess the potential impact of the expansion in range of *P. depressa* on *P. vulgata* and *P. ulyssiponensis*, Firth *et al.* (2009) found that *P. depressa* lowered the growth of *P. vulgata*, but only when it co-occurred with *P. ulyssiponensis* in rockpools. There was no effect of *P. depressa* on either *P. vulgata* or *P. ulyssiponensis* on their own. The coldwater limpet *Testudinalia testudinalis* was quite common on rocky shores on the Isle of Man in the 1970s, but has not been found in recent years. (Hawkins, *et al.*, 2012) Its current recorded southern limit in Europe is

¹References to unpublished data represent new data collected during 2010-2012. These data have been QA'd and analysed but are not yet published in peer-review manuscripts or grey literature reports. All such data referenced here has been collected by the author or collaborating researchers and we are confident that they accurately reflect current and ongoing changes within coastal habitats.

north Scotland and it is highly likely that the distribution of this limpet has shifted northwards due to warming coastal temperatures (Mieszkowska *et al.*, 2006).

Multidecadal cycles in relative abundances of the coldwater barnacle *Semibalanus balanoides* and warmwater *Chthamalus* spp. are strongly correlated with both local sea surface temperatures and show strong links to the basin-scale Atlantic Multidecadal Oscillation (AMO) which reflects long-term fluctuations in the marine climate (Mieszkowska *et al.*, 2012). The distribution and abundance of interacting chthamalid and *Semibalanus* barnacle species on Irish and UK coasts is strongly controlled by abiotic factors, most likely temperature and desiccation (Power *et al.*, 2011). For example, there is an increase in the proportion of *C. montagui* in the barnacle guild as habitats become hotter and drier at very small scales affected by microclimate (cm), medium scales of wave exposure (10s km) and at latitudinal scales governed by macroclimate (200 km). *C. montagui*, which we know from previous research prefers dryer environmental regimes with low precipitation rates, dominates all vertical areas of the intertidal in warmer climate zones such as Portugal (O’Riordan *et al.*, 2004). The Marine Biological Association’s 60-year time-series shows higher abundances of warmwater chthamalids follow warm local SST years and also track the annual AMO. In contrast, higher densities of the coldwater species *S. balanoides* occur during colder SST periods (Mieszkowska *et al.*, 2012; MarClim database). The shorter lifecycle of *S. balanoides* compared to the chthamalids and the increase in spring and summer temperatures to which newly settled *S. balanoides* recruits have been exposed during the last decade are likely mechanisms by which barnacle densities are responding to low-frequency temperature variability expressed in the AMO (Mieszkowska *et al.*, 2012).

Phenological shifts are occurring in warmwater gastropods in populations close to northern distributional limits in the UK. Reproductive cycles of the topshells *Phorcus lineatus* and *Gibbula umbilicalis* have shifted earlier in the year by 3 months during the last 2 decades (Underwood, 1973; Garwood and Kendall, 1985; de Francisco Mora, 2010). Gonad development in the southern limpet *Patella depressa* now commences 19 days earlier in the 2000s than during the 1940s (Moore *et al.*, 2010). Annual studies throughout the 2000s demonstrated that *G. umbilicalis* also switched reproductive strategies from a single to double reproductive peak (bivoltine) in northern populations for the first time in 2008. By 2011 females contained ripe gonads throughout the year. This is characteristic of southern populations inhabiting warmwaters at lower latitudes (Bode *et al.*, 1986) and may be indicative of the plastic nature of reproductive processes in response to changes in temperature. In contrast, the limpet *Patella vulgata*, which has a biogeographic range centred in cooler, more northerly latitudes has shown an increase in annual frequency of reproductive failure and a delay in onset of gonad production between the 1940s and 2000s (Moore *et al.*, 2010).

These findings must be taken into consideration in the wider context of rocky shore communities. The majority of rocky

shore species monitored annually around the UK show stable population abundances and no changes to the distributional limits of many macroalgae and sessile invertebrates since the start of intensive annual sustained observations in the 2000s, with little change from the historical data from the 1950s and 1960s (Crisp and Southward, 1958; Lewis, 1972; Mieszkowska *et al.*, 2006; 2012). The thermal limits of algae are well documented and mortality or cessation of reproductive activity occurs above and below critical temperatures (Lüning, 1990). Predictions of thermal limits of invertebrates are more complicated due to acclimation and evolutionary adaptation, meaning that what constitutes an upper lethal limit for a species in the middle of the distributional range is likely to be different for individuals at range limits. Currently, the marine climate around the UK is not warm enough to cause mortality or severe impairment of many coldwater species, although these thresholds are likely to be exceeded in the current decades (UKCIP, 2009). Changes in climate may also induce trophic cascades in rocky intertidal ecosystems as demonstrated in field experiments in Loch Hyne, Ireland. Reduction in predator body size, as predicted with climate warming was simulated in the common shore crab *Carcinus maenas*. This triggered a four level trophic cascade, with a resultant increase in abundance of the next trophic layer down the foodweb and thus a decrease in meiofaunal grazers and subsequently an increase in standing stock of biofilm (Jochum *et al.*, 2012).

Invasive Non-Native Species (INNS) are dealt with in a separate chapter of the MCCIP Report, with a brief overview of the main changes related to intertidal habitats presented here. Artificial man-made habitats can often support higher densities of INNS than natural rocky shores due to reduced competition from established native species, more vacant habitat and year-round settlement allowing opportunistic colonisation of vacant space (Mineur *et al.*, 2012). The invasive sea squirt *Corella eumyota* has been previously restricted to artificial habitats in the south and south-east coast of Ireland and south England. In 2012 MarClim annual surveys around north Wales found *C. eumyota* for the first time at four of these long-term monitoring sites on natural rocky shores www.marclim.co.uk (Figure 2). It is not known at present whether this is climate related, but this outbreak will be tracked in future annual surveys to determine whether these individuals form sustained populations or whether the outbreak was ephemeral and organisms are unable to survive in these natural habitats under current climatic conditions (Mieszkowska, 2013a).

The Pacific oyster, *Crassostrea gigas* has been farmed in estuaries around the UK since the 1960s. As recently as 2002, waters were still considered to be too cold for it to reproduce and therefore present a substantial risk of invasion to natural systems (Herbert, 2012). In recent years, *C. gigas* has settled on natural habitat outside of farms and spread around the UK coastline as warmer temperatures have facilitated survival and reproduction in wild populations (Campbell, 2012). The worst affected area is in the eastern English Channel, where dense beds of *C. gigas* now occur. An intensive study of a wild population in south Devon confirms that the population is



Figure 2: The invasive tunicate *Corella eumyota* on the rocky intertidal reef at Holyhead, Anglesey. (photo Heather Sugden).



Figure 3: *Sargassum muticum* acting as a host for *Colpomenia peregrina*. (photo Nova Mieszkowska).

reproductively active and self-sustaining (Campbell, 2012). Natural estuarine and open coast colonisation has increased over the last 2 years in the vicinity of oyster farms in the western English Channel and Scotland. Evidence suggests that the risk to biodiversity from wild settlement of Pacific oysters relates not so much to local changes in species diversity per se but to the extent of habitat transformation (Herbert *et al.*, 2012).

The invasive brown alga *Sargassum muticum* has been present in the UK and Ireland for several decades and is now found around most of the coastlines (Baer and Stengel, 2010). This species arrived on the Isle of Man from Ireland sometime in the mid-2000s and has become much more common in the last 3 years or so (Hawkins *et al.*, 2012). Surveys on the Isle of Wight found it acting as a biogenic host for the epiphytic invasive alga *Colpomenia peregrina* (Figure 3), whereas *C. peregrina* in this area was not found on natural substrate or growing on native species demonstrating how proliferation of one invasive may also promote the establishment and spread of other invasive species (Mieszkowska *et al.*, 2013b).

1.5 Intertidal chalk habitats

Intertidal chalk is classified as a UKBAP Priority Habitat, and is listed in Annex I of the EC Habitats Directive and the OSPAR list of Threatened and/or Declining Species and Habitats (OSPAR, 2008a). Intertidal chalk systems include sea caves and littoral fringe cliffs and platforms, which host micro-habitats of biological importance. Such habitats are rare in Europe, with those occurring in the southern North Sea and Eastern English Channel regional seas accounting for 57% of all chalk habitats in Europe (ICES, 2003).

Climate warming is likely to be enhancing colonisation of intertidal chalk by INNS including the invasive brown alga *Sargassum muticum*, *Codium fragile* and *Colpomenia peregrina* on the Isle of Wight and Eastern English Channel, as increases in abundance across the 2000s correlate with increases in sea and air temperature. These species are increasing in abundance and are a threat to native species which are restricted to this limited habitat (Mieszkowska *et al.*, 2013b). The non-native Pacific oyster *Crassostrea gigas*

has colonised chalk platforms along the eastern section of the Eastern Channel and Southern North Sea, including Ramsgate, Margate, Forelands and the Thanet coast in the last few years (Herbert *et al.*, 2012).

1.6 Seagrass beds

Seagrass beds occur in soft sediments within sheltered intertidal and shallow subtidal areas where there is protection from wave action. Seagrass plants stabilise sediment and provide a three-dimensional habitat for epifauna and flora and a sheltered environment for juvenile fish and cephalopods. They provide a major food resource for waterbirds, and the dead plant matter is a large organic source for intertidal benthic systems (Barnes and Hughes, 1982). Three species, *Zostera marina*, *Zostera marina* var. *angustifolia* and *Zostera noltii* occur in UK regional seas. Breeding populations of spiny and short-nosed seahorses, two species of pipefish, *Entelurus aequoraeus* and *Sygnathus typhle* are almost totally restricted to seagrass beds (OSPAR, 2008b). They play an important role in wave attenuation, buffering intertidal habitats from exposure to wave forces (Paul and Amos, 2011). Seagrasses can produce up to 2g carbon per square metre per day during the temperate growing season (OSPAR, 2008b) with high biomass of up to 5kg per m² (Barnes and Hughes, 1982). *Zostera* beds are therefore important habitats that support biodiverse communities, including nationally rare species, and are an important source of carbon to intertidal and subtidal coastal systems (Fourqurean *et al.*, 2012).

Intertidal seagrass beds, predominantly comprising of *Zostera noltii* and *Z. angustifolia* are under threat from multiple anthropogenic pressures. They are individually classified as scarce (<http://www.ukbap.org.uk/PriorityHabitats.aspx>), and the overall status of seagrass beds in the UK is considered to be degraded (Wilding *et al.*, 2009). Loss and fragmentation of seagrass beds via nutrient loading and turbidity are the main drivers of decline globally (Short and Neckles, 1999). Pressures from activities such as land claim, coastal development and localised activities including recreational boat mooring and bait digging are a major cause of physical disturbance and damage to seagrass beds in UK regional

seas (Wilding *et al.*, 2009). Physical disturbance and removal of seagrass habitat decreases the diversity and biomass of associated epifauna (Reed and Hovel, 2006). *Zostera* beds of even small spatial extent support much higher biodiversity than the surrounding sediment that they are still classified as being of conservation importance (Hirst and Attrill, 2008). Intertidal *Z. noltii* beds in Wales have been scored as being highly sensitive to the main drivers of climate change; sea surface and bed temperature, sea-level rise, storminess, precipitation, salinity, pH and suspended sediment (Jones *et al.*, 2011). The extent of *Z. noltii* and *Z. angustifolia* in the Lothians area of Scotland has increased in recent years (Smith *et al.*, 2002). There is no published evidence for climate-driven changes to UK or Irish seagrass habitats. Molecular research on *Z. noltii* from the southern end of its range in Portugal showed that genes responsible for photosynthesis were generally under-expressed in heat-shocked plants (Massa *et al.*, 2011). Given existing knowledge of lethal thermal limits and physiological performance under raised marine temperatures outlined above is not unreasonable to expect that seagrass distribution and condition will be influenced by climate related changes in sea temperature, increased storm activity, changes in prevailing wind conditions and also by ocean acidification, shown to be important in other countries (Borum *et al.*, 2004; Bjork *et al.*, 2008). Direct evidence of the impact of increasing temperature on the distribution and physiological performance of seagrasses in UK coastal waters is lacking and highlighted as a key knowledge gap.

Regional differences

The current status of individual seagrass beds shows mixed trends around the UK. Within the Solent Estuary, seagrass extent does not seem to have greatly changed over the last two decades (Lefebvre *et al.*, 2009). A huge reduction in bed size of *Z. noltii* at Bembridge Ledges on the Isle of Wight in 2012 may be due to recent sedimentation in the area, possibly combined with a warming climate (Mieszowska *et al.*, 2013b; Herbert, pers. comm.) The number of *Zostera* beds has increased in Wales and Scotland during the 2000s. Post 2007 estimates are of an increase of approximately 27.8 ha, roughly 4.9% for Wales (Boyes *et al.*, 2009; Howsen, 2009; Mercer 2009; CCW, unpublished data) but an exact amount is hard to calculate for Lothian seagrass beds due to a lack of time-series data (Smith *et al.*, 2002). The exact dynamics of change cannot be pinpointed as there are gaps of several years between surveys at some sites. *Zostera noltii* does better in a low salinity environment for germination and increased freshwater runoff in recent years may have been the driver for the increased success of this species in Welsh seagrass beds.

1.7 Biogenic reefs

The honeycomb worm *Sabellaria alveolata* is a warmwater sedentary tube-dwelling polychaete that constructs tubes from suspended sediment and shell fragments (Wilson, 1971). *S. alveolata* colonies form bio-constructions (Figure 4): veneers, adhering to rocks in the midshore of the intertidal zone (Wilson, 1971); and reefs which are generally found at lowshore on exposed coast (Gruet, 1982; Cunningham *et al.*, 1984). Reef-forming *S. alveolata* provides important habitat for a wide range of other species and is considered priority

habitat within the UK Biodiversity Action Plan (BAP) and is covered by Annex 1 of the EC Habitats Directive. *S. alveolata* is one of the most important biogenic reef forming species in inshore British Waters (Holt *et al.*, 1998).

The northern range limit of *S. alveolata* has been extending into higher latitudes in Scotland during the 2000s, and abundances have increased or remained stable at established sites in the Western English Channel and Irish Sea regional seas (Frost *et al.*, 2004, Burrows, Mieszowska and Hawkins, unpublished data). These changes are thought to be a direct response to less severe winter temperatures in recent decades (with the exception of the cooler winters of 2009/10 and 2010/11). The *S. alveolata* reef in Pen Llyn ar Sarnau SAC in north Wales has shown deterioration in the last few years, reversing the trend seen in the early 2000s. Long- and onshore sediment transport related to storminess is likely to be affecting the status of the reef, but is highly variable both within and between locations (Boyes and Allen, 2008, Brazier, unpublished data). Winter 2009/2010 was the coldest of the 2000s and low temperatures may have negatively affected northern populations of *S. alveolata*. Preliminary evidence from a 2012 survey (Firth, pers. obs.) did not record any obvious mortality but sustained monitoring is necessary to detect future changes. There is evidence to suggest that the proliferation of artificial coastal defence structures along this coastline may provide "stepping-stones" to dispersal across stretches of unsuitable habitat (Frost *et al.*, 2004).

Blue mussels can form high-density beds which function as a biogenic habitat for a wide range of epifaunal and infaunal species (O'Connor and Crowe, 2007), and are an important food source for seabirds. Blue mussels are boreal (*Mytilus edulis*) and cosmopolitan (*Mytilus galloprovincialis*) in origin. Neither species is exposed to environmental temperature regimes close to their thermal tolerance limits in the UK and Ireland and rising temperatures are not considered to be a major threat to these species over the coming years. Mussels are shell-forming organisms and ocean acidification represents a potential threat to shell-formation and other physiological processes. In a short mesocosm experiment, Beesley *et al.* (2008) found that CO₂-acidified water reduced the health of *Mytilus edulis* through elevated levels of calcium



Figure 4: Example of veneer formation of *S. alveolata* at Bude, north Cornwall. (photo: Louise Firth).

ions (Ca^{2+}) in the haemolymph, but had no impact on tissue structures. The authors concluded that *M. edulis* possesses strong physiological mechanisms by which it is able to protect body tissues against short-term exposure to highly acidified seawater. The OSPAR Assessment process has identified mussel beds in the Western and Eastern English Channel areas as 'under threat' from eutrophication and associated phytoplankton blooms, which are changing in frequency and intensity due to climate warming (OSPAR, 2008b).

Populations of the native oyster *Ostrea edulis* have declined throughout Britain over the last few decades due to a range of factors including overfishing, substratum loss, smothering, introduction of pathogens and synthetic compound contamination (Jackson *et al.*, 2008). *O. edulis* is listed in the OSPAR List of Threatened and/or Endangered Species and Habitats (OSPAR, 2008a). No direct impacts of climate change have been attributed to the decline of *O. edulis* in UK waters. The introduction of the warmwater non-native species of oyster, *Crassostrea gigas*, the slipper limpet *Crepidula fornicata* and the American oyster drill *Urosalpinx cinerea*, are thought to exert negative impacts to natural *O. edulis* beds via competition, pathogenic transfer, reduction in sediment bed quality and predation (Hancock, 1954; Minchin *et al.*, 1993; Miossec *et al.*, 2009). Their future impacts may increase, aided by a warming climate more suitable to their physiological niches. Limited research has been carried out to date to test these theories, but within estuaries in the Western Channel area, *C. gigas* appears to be breeding and settling on natural rock, outcompeting *O. edulis* within the intertidal zone (Mieszkowska, 2009). Extensive reefs of Pacific oysters could also facilitate aquatic macrophytes (Reise and van Beusekom, 2008).

1.8 Artificial structures

The threat of sea-level rise, flooding and coastal erosion has led to a growing need to defend our coasts. Efforts largely comprise the use of hard-substrate defence structures which are fast-becoming ubiquitous features of coastal landscapes in intertidal and shallow subtidal environments (Figure 5) (Airoldi *et al.*, 2005; Moschella *et al.*, 2005). These structures can take many forms including seawalls, jetties, breakwaters, groynes and dykes and are generally built at the expense of natural habitats (Airoldi *et al.*, 2005; Chapman and Underwood, 2011). A significant proportion of the UK coastline now has defence structures installed to prevent or reduce coastal erosion and flooding of adjacent land, in addition to stabilising and retaining beaches and reclaimed land (Table 1).

These structures are typically built in locations that are dominated by sedimentary habitats and have the potential to provide habitat for a wide range of hard-bottom marine species. It has been suggested that the structure and functioning of colonising assemblages are analogous to those living on natural rocky shores and that the artificial structures can sometimes function as surrogates or stepping stones between areas of natural rocky habitats (Thompson *et al.*, 2002; Martin *et al.*, 2005; Branch *et al.*, 2008). However, there is mounting evidence that epibiota and fish assemblages associated with artificial structures differ from those on



Figure 5: Coastal defence structure at Westshore, near Llandudno, North Wales. (photo: Louise Firth).

natural reefs (Moschella *et al.*, 2005; Perkol-Finkel *et al.*, 2005; Firth *et al.*, 2013).

In the UK, artificial coastal defence structures are becoming increasingly common along the south coast of England where Portland Bill, Dorset and St. Catherine's Point on the Isle of Wight represent natural barriers to dispersal (Crisp and Southward, 1958). Many southern warm-adapted invertebrate species (*Perforatus perforatus*, *Gibbula umbilicalis*, *Patella ulyssiponensis* and *Melaraphe neritoides*) have managed to breach these hydrographic barriers reaching natural rocky shores to the east of the Isle of Wight (Herbert *et al.*, 2003, 2007; Mieszkowska *et al.*, 2005, 2006; Keith *et al.*, 2011). It has been suggested that artificial coastal defence structures and marinas have acted as stepping-stones, facilitating these extensions in areas where species' range limits would naturally be prevented from extending in areas of permanently unsuitable habitat (Moschella *et al.*, 2005; Hawkins *et al.*, 2008). In 2011 and 2012 a population of the warmwater limpet *Patella depressa* has been found at Elmer, West Sussex 45km east of previous limits at Southsea, Hampshire. These individuals are thought to have settled within the last three years and have not been seen in previous annual surveys dating back throughout the 2000s (Hawkins, pers. obs.). Furthermore, artificial coastal defence structures are proliferating in North Wales between Llandudno and the Wirral. It is thought that these structures have facilitated the colonisation of *Sabellaria alveolata* along this stretch of coastline (Frost *et al.*, 2004) following the catastrophic effects of the cold winter 1962/63 which obliterated *S. alveolata* populations (Crisp, 1964).

2. WHAT COULD HAPPEN?

2.1 Intertidal mudflats

Mudflats are known to be sensitive habitats with respect to erosion, bait digging, coastal development and climate change, but there is insufficient information to be able to currently determine what impacts climate drivers such as increased temperature, decreasing pH, increased wave fetch, altered precipitation and salinity will have on these ecosystems.

Table 1: Overview of exposure of UK and Ireland coastal regions to erosion and coastal protection (relative proportions are given in brackets). Figures from EuroSION (2004).

Region	Coast length (km)	Coast length that is eroding (km)	Coast length with defence works and artificial beaches (km)
Scotland	11,154	1,298 (11.6%)	733 (6.6%)
Wales	1,498	346 (23.1%)	415 (27.7%)
England	4,273	1,275 (29.8%)	1,947 (45.6%)
Northern Ireland	456	89 (19.5%)	90 (19.7%)
Ireland	4,577	912 (19.0%)	475 (10.0%)

2.2 Estuarine soft sediment habitats

There have been few clear indications of the effects of climate change on soft sediment communities in the UK to date, but this is likely to be due in part to the inherent difficulty in making observations in these habitats. Models of future climate impacts are being developed based on historical alterations in estuarine structure and subsequent erosion and increasing coarseness of grain size due to local geomorphological changes. Experimental work on brittlestars and clams suggest that rising temperatures will have more of an impact on survival, physiological performance and reproduction than reduced pH (Godbold and Solan pers. comm).

2.3 Estuarine rocky habitats

Low wave energy estuarine rocky habitats which currently support high biomasses of macroalgae may undergo structural changes once thermal regimes exceed those of the most sensitive lifestages, usually the propagules which play a vital role in dispersal and maintenance of populations. As most estuarine rocky reef occurs in the north of the UK and Ireland, given the predicted rate of temperature increases due to climate change such restructuring of estuarine habitats is likely to be decades away at predicted emissions scenarios currently used for model scenarios (UKCIP09).

2.4 Rocky intertidal

Both warmwater species of topshell are continuing to increase in abundance in populations throughout the UK and Ireland, with northern range limits extending north in the Celtic, Irish Seas and Northeast Atlantic and north-east along the English Channel and North Sea (MarClim dataset). In 2012 the warmwater limpet *Patella depressa* showed an increase in northern limits in North Wales and north-eastern limits in South England for the first time in two decades of annual monitoring in 2012 after a continuing increase in abundance and dominance in densities compared to the coldwater *Patella vulgata* at shores around south-west and south England. Many species have not shown changes in distribution and/or abundance throughout the 2000s and 2010s as they are not yet exposed to temperatures approaching those deleterious to performance and survival for the most sensitive life stages. Whilst these are difficult to predict for some invertebrates, upper thermal limits are known for most macroalgae and therefore loss of coldwater species from

habitats close to their southern distributional limits could be modelled. Novel dynamic species distribution models developed for the topshells are able to predict persistence and population abundance at specific long-term study sites around the UK in response to predicted future SST and wave exposure using MarClim time-series categorical abundance data (Mieszkowska, 2013a).

2.5 Intertidal chalk habitats

A lack of data for intertidal chalk reef and sea caves prevents quantitative assessments of recent and future impacts of climate change, however, those species common to hard rocky reef will show similar changes on chalk habitat. Increased wave exposure will increase erosion rates and thus loss of chalk reef habitat. Sea caves are showing erosion of the internal back walls and so they may increase in volume with increased wave action (Irving *et al.*, 2006; Mieszkowska, *et al.*, 2013b).

2.6 Seagrass beds

As per intertidal mudflats, intertidal *Zostera* beds are thought to be sensitive to several climate drivers and emergent research suggests that whilst ocean acidification may increase photosynthesis, warming temperatures may reduce photosynthesis (Echevarria-Heras *et al.*, 2006), therefore individual and synergistic impacts of climate change are still unable to be quantified.

2.7 Biogenic reefs

The warmwater *Sabellaria alveolata* is likely to increase in abundance and the distribution of this reef-forming polychaete is likely to extend further around Scotland. The lifecycle of *S. alveolata* which extends over several years with periods of senescence may complicate any distributional changes driven by warming temperatures.

Neither the Boreal blue mussel *Mytilus edulis* and cosmopolitan *M. galloprovincialis* is exposed to environmental temperature regimes close to their thermal tolerance limits in the UK and Ireland and are not at risk of a reduction in densities in the next decade. Negative effects of ocean acidification may impair physiological performance and shell calcification but again not until pH levels drop to those predicted towards the end of the 21st century.

2.8 Artificial structures

The construction of artificial coastal defences as adaptational measures for climate-driven increases in wave height, storminess and flooding, as well as increased coastal development in future years will provide more hard artificial habitat in areas of soft sediment currently unsuitable for rocky intertidal species. This is likely to exacerbate the observed 'stepping stone' effects in the Eastern English Channel and the North Wales coast and may also enhance the spread of warmwater species in soft sediment-dominated areas such as the Wirral and Cumbria regions.

3. KNOWLEDGE GAPS

a. Gaps in data coverage

Sustained monitoring and observations on intertidal soft sediment habitats is still lacking at the regional and national level, making changes to intertidal species and communities difficult to detect and attribute to specific stressors.

Rocky shore monitoring has not been carried out at the national scale in Scotland since 2005 and therefore range shifts detected in the early 2000s have not been tracked.

b. Intertidal mudflats, seagrass beds and chalk substrate

These habitats are known to be sensitive habitats with respect to erosion, bait digging, coastal development and climate change, but there is insufficient information to be able to currently determine what impacts climate drivers such as increased temperature, decreasing pH, increased wave fetch, altered precipitation and salinity will have on these ecosystems.

c. Multiple stressors

The impacts of multiple stressors on marine systems and species is becoming increasingly apparent, although to date there have been few experimental and monitoring programmes with the ability to separate out the effects of individual stressors or determine whether impacts are additive or synergistic (Firth and Williams, 2009; Fitch and Crowe, 2012). For intertidal systems, especially those in or near estuaries and semi-enclosed water bodies, climate change is likely to be affecting species and communities in combination with eutrophication, heavy metal and synthetic contaminant exposure, marine litter and reduction in extent and condition of natural habitat due to coastal development and construction of sea defences.

d. Invasive non-native species

Reports of new sightings of INNS are increasing in artificial marine habitats and natural systems but it is not known how much of this increase in species is due to an increase in research and monitoring effort and reporting. Separating out the effect of climate change from the natural invasive dynamics of a species has not been achieved with intertidal species to date and requires further targeted effort.

4. SOCIO-ECONOMIC IMPACTS

The National Ecosystem Assessment for the UK, carried out in 2011 identified the wide range of ecosystem goods, services

and benefits that marine systems offer of significant value to UK society: food including fish and shellfish, reduction of climate stress by regulating carbon and other biogases; genetic resources for aquaculture; industrial inputs for blue biotechnology such as biocatalysts, natural medicines; fertiliser (seaweed); coastal protection; waste breakdown and detoxification leading to pollution control, waste removal and waste degradation; disease and pest control; tourism, leisure and recreation opportunities; a focus for engagement with the natural environment; physical and mental health benefits; and cultural heritage and learning experiences. Energy provision is likely to be an increasingly important marine ecosystem service (Austen *et al.*, 2011).

Approximately 3,000–4,000 tonnes (wet weight) per year of the seaweed *Ascophyllum nodosum* are harvested annually in the Uists and three commercial seaweed harvesting companies were identified in Northern Ireland, although small-scale collection is also seasonally customary (McLaughlin *et al.*, 2006). Twelve species of seaweed are commercially harvested as fresh vegetation or drift, beachcast seaweed. Although a global value of £3.6 billion annually has been calculated for harvested seaweed (McLaughlin *et al.*, 2006), no value has been calculated for the UK and Irish markets to date (Austen *et al.*, 2011).

Bait collection or provision activity is rarely recorded or declared, but market surveys indicate that some 500–700 tonnes of bait worms are dug for personal use and 300–500 tonnes of worms from commercial (including 'black economy') sources enter the retail trade (Austen *et al.*, 2011). Bait worms entering the retail market are derived from wild-dug and farmed sources in the UK. The commercial value of the main bait species (e.g. ragworms (*Neanthes (Nereis) virens*, *Hediste (Nereis) diversicolor*, *Nephtys species*), lugworms (*Arenicola marina*, *A. defodiens*) and peeler crabs (*Carcinus maenas*)) in the UK is between £25–£30 million per annum (Fowler, 1999).

The National Ecosystem Assessment concluded that marine ecosystem services are at present poorly quantified and highlighted the need for increased research and monitoring in order to understand and measure the links between marine biodiversity, ecosystem function and provision of ecosystem goods and services, and the effects of human impacts on these links. Although recent national assessments (e.g. Charting Progress 2, State of Scotland's Seas) have gathered a lot of evidence, extensive data gaps remain. Such knowledge would support more effective marine planning and licensing of activity in UK waters for the sustainable use of Marine habitats and the maintenance of clean, healthy, productive and biologically diverse seas.

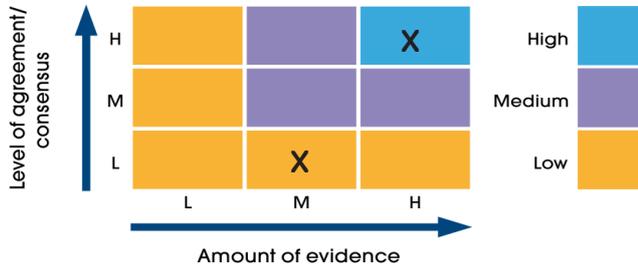
5. CONFIDENCE ASSESSMENT

What is already happening?

For some systems such as rocky intertidal and artificial habitats there are long-term, spatially extensive datasets and a wealth of experimental data on the impacts of climate stressors. Confidence in ascribing the role of climate in what we already know is happening is high. In contrast, for

soft sediment and chalk systems and biogenic reef forming habitats there are insufficient data on the past and current distributions and the impacts of changes in temperature, pH, salinity, precipitation, storminess etc. to be able to have high confidence in ascribing a value to the amount of observed changes that have been primarily caused by climate change.

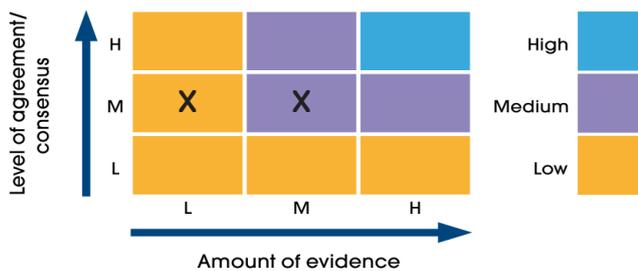
The “high” scoring relates to rocky shores and the “low” scoring relates to soft sediment and biogenic reef habitats.



What could happen?

The issues with current understanding and data availability translate into the future confidence score, with data and funding to collect necessary data to model and predict short and long-term future responses lacking.

The “medium” scoring relates to rocky shores and the “low” scoring relates to soft sediment and biogenic reef habitats.



CITATION

Please cite this document as:

Mieszkowska, N., Firth, L. and Bentley, M. (2013) Impacts of climate change on intertidal habitats, *MCCIP Science Review 2013*, 180-192, doi:10.14465/2013.arc19.180-192

REFERENCES

Airoldi, L., Abbiati, M., Beck, M.W., Hawkins, S.J., Jonsson, P.R., Martin, D., Moschella, P.S., Sundelöf, A., Thompson, R.C. and Åberg, P. (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coast. Eng.*, **52**, 1073-1087.

Atkinson, T.C., Briffa, K.R. and Coope, G.R. (1987) Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature*, **325**, 587-592.

Austen, M.C., Malcom, S.J., Frost, M., Hattam, C., Mangi, S., Stentiford, G., Benjamins, S., Burrows, M., Butenshon, M., Duck, C. *et al.* (2011) *Marine*. In: The National Ecosystem Assessment Technical Report. UK National Ecosystem Assessment, UNEP-WCMC, Cambridge.

Baer, J. and Stengel, D.B. (2010) Variability in growth, development and reproduction of the non-native seaweed *Sargassum muticum* (Phaeophyceae) on the Irish west coast. *Estuarine Coast. Shelf Sci.*, **90**(4), 185-194.

Barlow, J., Hill, P.S., Forney, K.A. and DeMaster, D.P. (1998) *US Pacific marine mammal stock assessments, 1998, California*.

Barnes, R.S.K. and Hughes, R.N. (1982) *An introduction to Marine Ecology*. Blackwell Scientific Publications. Oxford. 339pp.

Beesley, A., Lowe, D.M., Pascoe, C.K. and Widdicombe, S. (2008) Effects of CO₂-induced seawater acidification on the health of *Mytilus edulis*. *Clim. Res.*, **37**, 215-225.

Benjamins, S.J. *et al.* (2010) *Benthic Habitats*. In: Charting Progress 2 HBDSEG Feeder Report, 217pp.

Berge, J., Bjerkgeng, B., Pettersen, O. and Schaanning, M. S. (2006) Effects of increased sea water concentrations of CO₂ on growth of the bivalve *Mytilus edulis*. *Chemosphere*, **62**, 681-687.

Bjork, M., Short, F., Mcleod, E. and Beer, S. (2008) *Managing seagrasses for resilience to climate change*. IUCN. Gland, Switzerland. 56 pp.

Bode, A., Lombas, I. and Anadon, N. (1986) Preliminary studies on the reproduction and population dynamics of *Monodonta lineata* and *Gibbula umbilicalis* (Mollusca, Gastropoda) on the central coast of Asturias (N. Spain). *Hydrobiologia*, **142**, 31-39.

Borum J., Duarte C.M., Krause-Jensen D., Greve T.M. (2004) *European seagrasses: an introduction to monitoring and management*. The MandMS project. 95 pp. http://www.seagrasses.org/handbook/european_seagrasses_low.pdf

Boyes, S. and Allen, J.H. (2008) *Intertidal monitoring of Sabellaria alveolata reefs in Pen Llyn a'r Sarnau SAC 2004/5*. CCW Marine Monitoring Report No 29.

Boyes, S., Brazier, D.P., Burlinson, F., Mazik, K., Mitchell, E., and Proctor, N. (2009) *Intertidal monitoring of Zostera noltii in the Menai Strait and Conwy Bay SAC in 2004/05*. CCW Marine Monitoring report No 31.

Branch, G.M., Thompson, R.C., Crowe, T.P., Castilla, J.C., Langmead, O. and Hawkins, S.J. (2008) *Rocky intertidal shores: prognosis for the future*. Aquatic Ecosystems. Cambridge University Press, Cambridge.

Bulling, M.T., Hicks, N., Murray, L., Paterson, D.M., Raffaelli, D., White, P.C.L. and Solan, M. (2010) Marine biodiversity-ecosystem functions under uncertain environmental futures. *Phil. Trans. R. Soc. B*, **365**, 2107-2116.

Cain, S.A. (1944) *Foundations of Plant Geography*. Harper Brothers, New York, London.

Campbell, A. (2012) *Environmental control of reproduction, persistence and resultant impacts on native biodiversity of the Pacific oyster Crassostrea gigas*. Thesis, pp55 University of Plymouth.

Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R. and Largier, J.L. (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecol. Appl.*, **13**, 90-107.

Chapman, M.G. and Underwood, A.J. (2011) Evaluation of ecological engineering of “armoured” shorelines to improve their value as habitat. *J. Exp. Mar. Biol. Ecol.*, **400**, 302-313.

Crisp, D.J. (1964) The effects of the severe winter of 1962-63 on marine life in Britain. *J. Anim. Ecol.*, **33**, 165-210.

Cunningham, P.N., Hawkins, S.J., Jones, H.D. and Burrows, M.T. (1984). *The geographical distribution of Sabellaria alveolata (L.) in England, Wales and Scotland, with*

- investigations into the community structure of, and the effects of trampling on *Sabellaria alveolata* colonies. N.C.C. Contract No. HF3/11/22.
- Echavarría-Heras, H.A., Solana-Arellano, E. and Franco-Vizcaino, E. (2006) The role of increased sea surface temperature on eelgrass leaf dynamics: onset of El Niño as a proxy for global climate change in San Quintín Bay, Baja California. *Bull. S. Calif. Acad. Sci.*, **105**(3), 113-127.
- EUROSION (2004) *Living with coastal erosion in Europe: sediment and space for sustainability*. Part IV, Guidelines for implementing local information systems dedicated to coastal erosion management.
- Findlay, H.S., Kendall, M.A., Spicer, J.I. and Widdicombe, S. (2009) Future high CO₂ in the intertidal may compromise adult barnacle *Semibalanus balanoides* survival and embryonic development rate. *Mar. Ecol. Prog. Ser.*, **389**, 193-202.
- Firth, L.B. and Williams, G.A. (2009) The influence of multiple environmental stressors on the limpet *Cellana toreuma* during the summer monsoon season in Hong Kong. *J. Exp. Mar. Biol. Ecol.*, **375**, 70-75.
- Firth, L.B., Crowe, T.P., Moore, P., Thompson, R.C. and Hawkins, S.J. (2009) Predicting impacts of climate-induced range expansion: an experimental framework and a test involving key grazers on temperate rocky shores. *Glob. Change Biol.*, **15**, 1413-1422.
- Firth, L.B., Thompson, R.C., White, R.F., Schofield, M., Skov, M.W., Hoggart, S.P.G., Jackson, J., Knights, A.M. and Hawkins, S.J. (2013) Promoting biodiversity on artificial structures: can natural habitats be replicated? *Diversity and Distributions*, **19**, 1275-1283.
- Fitch, J.E. and Crowe, T.P. (2011) Combined effects of temperature, inorganic nutrients and organic matter on ecosystem processes in intertidal sediments. *J. Exp. Mar. Biol. Ecol.*, **400**, 257-263.
- Fitch, J.E. and Crowe, T.P. (2012) Combined effects of inorganic nutrients and organic enrichment on intertidal benthic macrofauna: an experimental approach. *J. Exp. Mar. Biol. Ecol.*, **461**, 59-70.
- Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M.A., Apostolaki, E.T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K.J. and Serrano, O. (2012) Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, **5**, 505-509.
- Fowler, S.L. (1999) *Guidelines for managing the collection of bait and other shoreline animals within UK European marine sites*. 132p. Peterborough: English Nature.
- Frost, M.T., Leaper, R., Mieszkowska, N., Moschella, P., Murua, J., Smyth, C. and Hawkins, S. J. (2004) *Recovery of a Biodiversity Action Plan Species in Northwest England: possible role of climate change, artificial habitat and water quality amelioration. Sabellaria alveolata*: Report to English Nature.
- Fujii, T. (2007) Spatial patterns of benthic macrofauna in relation to environmental variables in an intertidal habitat in the Humber estuary, UK: Developing a tool for estuarine shoreline management. *Estuarine Coast. Shelf Sci.*, **75**, 101-119.
- Garwood, P.R. and Kendall, M.A. (1985) The reproductive cycles of *Monodonta lineata* and *Gibbula umbilicalis* on the coast of Mid-Wales. *J. Mar. Biol. Assoc. UK*, **65**, 993-1008.
- Gruet, Y. (1982) *Recherches sur l'écologie des "récifs" edifiés par l'annélide polychète Sabellaria alveolata (Linné)*. Université de Nantes.
- Gubbay, S. and Earll, R. (2010) *Assessing the vulnerability of marine biodiversity in Wales to the impacts of climate change: workshop report*. CCW Contract Science Report Report No: 934, 21pp, CCW, Bangor.
- Hancock, D.A. (1954) *The destruction of oyster spat by Urosalpinx cinerea (Spay) on Essex oyster beds*. International Council for the Exploration of the Sea. Publications de circonstance - Conseil International Pour L'exploration De La Mer (20) 186-196.
- Hawkins, S. J., MacLean, M. A., Firth, L. and Mieszkowska, N. (2012) *MMEA Climate Change in Manx Waters*. In: Hanley, L.J., Gell, F.G., Kennington, K., Stone, E., Rowan, E., McEvoy, P., Brew, M., Milne, K., Charter, L., Gallagher, M., Hemsley, K., eds. 2012. Manx Marine Environmental Assessment. Isle of Man Marine Plan. Isle of Man Government.
- Helmuth, B. (1999) Thermal biology of rocky intertidal mussels: Quantifying body temperatures using climatological data. *Ecology*, **80**, 15-34.
- Helmuth, B.T. and Denny, M.W. (2003) Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces? *Limnol. Oceanogr.*, **48**, 1338-1345.
- Herbert, R. J. H., Roberts, C., Humphreys, J. and Fletcher, S. (2012) *The Pacific Oyster (Crassostrea gigas) in the UK: Economic, Legal and Environmental Issues Associated with its Cultivation, Wild Establishment and Exploitation*. Report for the Shellfish Association of Great Britain. Pp166.
- Hirst, J.A. and Attrill, M.J. (2008) Small is beautiful: An inverted view of habitat fragmentation in seagrass beds. *Estuarine Coast. Shelf Sci.*, **78**(4), 811-818.
- Holt, T.J., Rees, E.L., Hawkins, S.J. and Seed, R. (1998) *Biogenic Reefs: An overview of dynamic and sensitivity characteristics for conservation management of marine SACs*. Scottish Association of Marine Science/UK Marine SACs project, Oban, Scotland.
- Howson, C. (2009) *Intertidal SAC monitoring, Carmarthen Bay and Estuaries SAC (September 2009)*. CCW Marine Monitoring Report No: 79, Countryside Council for Wales, Bangor.
- ICES (2003) *Report of the ICES Advisory Committee on Ecosystems*. ICES Cooperative Research Report No. 262. Copenhagen. 220pp.
- Jenouvrier, S., Barbraud, C., and Weimerskirch, H. (2003) Effects of climate variability on the temporal population dynamics of southern fulmars. *J. Anim. Ecol.*, **72**, 576-587.
- Jochum, M., Schnieder, F.D., Crowe, T.P., Brose, U. and O'Gorman, E.J. (2012) Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Philos. Trans. R. Soc. B*, **367**, 2962-2970.
- Jones, D., Bain, V., Dawson, S. and Watt, T. (2011) *Assessing the vulnerability of marine habitats in Wales to the impacts of climate change*. CCW Contract Science Reports. Report No: 969,n192pp, CCW, Bangor.
- Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L. *et al.* (2011) Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *J. Exp. Mar. Biol. Ecol.*, **400**, 17-32.
- Karunaratna, H., Reeve, D.E. and Horrillo-Caraballo, J.M. (2012) Prediction of cross-shore beach profile evolution using a diffusion type model. *Continental Shelf Research*, **48**, 157-166.

- Keith, S.A., Herbert, R.J.H., Norton, P.A., Hawkins, S.J. and Newton, A.C. (2011) Individualistic species limitations of climate-induced range expansions generated by meso-scale dispersal barriers. *Diversity and Distributions*, **17**, 275-286.
- Krause-Jensen, D., Carstensen, J. and Dahl, K. (2007) Total and opportunistic algal cover in relation to environmental variables. *Mar. Pollution Bull.*, **55**, 114-125.
- Lefebvre, A., Thompson, C.E.L., Collins, K. and Amos, C.L., (2009) Use of a high-resolution profiling sonar and a towed video camera to map a *Zostera marina* bed, Solent, UK. *Estuarine Coast. Shelf Sci.*, **82**(2), 323-334.
- Lenihan, H.S., Peterson, C.H., Kim, S.L., Conlan, K.E., Fairey, R., McDonald, C., Grabowski, J.H. and Oliver, J.S. (2003) Variation in marine benthic community composition allows discrimination of multiple stressors. *Mar. Ecol. Prog. Ser.*, **261**, 63-73.
- Lewis, J.R. (1972) *The ecology of rocky shores*. English Universities Press, pp323.
- Lowe, J.A., Howard, T.P., Pardaens, A., Tinker, J., Holt, J., Wakelin, S., Milne, G., Leake, J., Wolf, J., Horsburgh, K. *et al.* (2009) *UK Climate Projections science report: Marine and coastal projections*. Met Office Hadley Centre, Exeter, UK, pp99.
- Lüning, K. (1990) *Seaweeds. Their environment, biogeography and ecophysiology*. New York: John Wiley and Sons, pp544.
- Maggs, C., Mineur, F., Bishop, J. and McCollin, T. (2010) *Non-natives*. MCCIP Annual Report Card 2010-11, MCCIP Science Review, 11pp. <http://www.mccip.org.uk/arc>
- Martin, D., Bertasi, F., Colangelo, M.A., de Vries, M., Frost, M., Hawkins, S.J., Macpherson, E., Moschella, P.S., Satta, M. P., Thompson, R.C. and Ceccherelli, V. U. (2005) Ecological impact of coastal defence structures on sediment and mobile fauna: Evaluating and forecasting consequences of unavoidable modifications of native habitats. *Coast. Eng.*, **52**, 1027-1051.
- Massa, S.I., Pearson, G.A., Aires, T., Kube, M., Olsen, J.L., Reinhardt, R., Serrao, E.S. and Arnaoud-Haond, S. (2011) Expressed sequence tags from heat-shocked seagrass *Zostera noltii* (Hornemann) from its southern distribution range. *Marine Genomics*, **4**, 181-188.
- McLaughlin, E., Kelly, J., Birkett, D., Maggs, C. and Dring, M. (2006) *Assessment of the Effects of Commercial Seaweed Harvesting on Intertidal and Subtidal Ecology in Northern Ireland*. Environment and Heritage Service Research and Development Series. No. 06/26.
- McLusky, D. (1989) *The Estuarine Ecosystem*. 2nd Edn. Blackie and Sons Ltd. London.
- Mercer, T. (2009) *Intertidal SAC monitoring, Pen Llyn a'r Sarnau SAC, July 2009*. CCW Marine Monitoring Report No: 78, Countryside Council for Wales, Bangor.
- Mieszkowska, N. (2009) *MarClim Annual Welsh Intertidal Climate Monitoring Survey 2008*. Report to Countryside Council For Wales. CCW Science Report No 874
- Mieszkowska, N. (2010a) *MarClim Annual Welsh Intertidal Climate Monitoring Survey 2009*. Report to Countryside Council For Wales. CCW Science Report No 921.
- Mieszkowska, N. (2010b) *Intertidal Habitats and Ecology*. In: MCCIP Annual Report Card 2010- 11, MCCIP Science Review, 19pp. www.mccip.org.uk/arc
- Mieszkowska, N. (2011) *MarClim Annual Welsh Intertidal Climate Monitoring Survey 2010*. Report to Countryside Council For Wales. CCW Science Report.
- Mieszkowska, N. (2012) *MarClim Annual Welsh Intertidal Climate Monitoring Survey 2011*. Report to Countryside Council for Wales. CCW Science Report.
- Mieszkowska, N. (2013a) *MarClim Annual Welsh Intertidal Climate Monitoring Survey 2013*. Report to Countryside Council for Wales. CCW Science Report.
- Mieszkowska N. (2013b) *South Wight SAC: Rocky Shore and Intertidal Sea Cave condition assessments*. Contract Report.
- Mieszkowska, N., Leaper, R., Moore, P., Kendall, M.A., Burrows, M.T., Lear, D., Poloczanska, E., Hiscock, K., Moschella, P.S., Thompson, R.C. *et al.* (2005) Assessing and predicting the influence of climatic change using rocky shore biota. *Occ. Pub. J. Mar. Biol. Assoc. UK*, **20**, 701-752.
- Mieszkowska, N., Kendall, M.A., Hawkins, S.J., Leaper, R., Williamson, P. Hardman-Mountford, N.J. and Southward, A.J. (2006) Changes in the range of some common rocky shore species in Britain - a response to climate change? *Hydrobiologia*, **555**, 241-251.
- Mieszkowska, N., Burrows, M.T., Pannaciuoli, F.C. and Hawkins, S.J. (2012) Multidecadal signals within co-occurring intertidal barnacles *Semibalanus balanoides* and *Chthamalus* spp. linked to the Atlantic Multidecadal Oscillation. *J. Mar. Sci.*, doi: <http://dx.doi.org/10.1016/j.jmarsys.2012.11.008>
- Mieszkowska, N. Sugden, H. and Hawkins, S.J. (2013a) *Report on the status of rocky intertidal reefs and sea caves in the South Wight European Marine Site*. Contract report for Natural England.
- Mieszkowska, N., Milligan, G., Burrows, M.T., Freckleton, R. and Spencer, M. (2013b) Dynamic species distribution models from categorical data. *J. Anim. Ecol.*, **82**(6), 1215-1226.
- Minchin, D., Duggan, C.B., Holmes, J.M.C. and Neiland, S. (1993) *Introductions of exotic species associated with Pacific oyster transfers from France to Ireland*. ICES. Mariculture, Copenhagen. DK. 1993. 1-11.
- Miossec, L., Le Deuff, R.M. and Gouletquer, P. (2009) *Alien species alert: Crassostrea gigas (Pacific oyster)*. ICES Cooperative Research Report No. 299. 47p.
- Moore, P., Thompson, R.C., and Hawkins, S.J. (2010) Phenological changes in intertidal con-specific gastropods in response to climate warming. *Glob. Change Biol.*, **17**, 709-719.
- Moschella, P.S., Abbiati, M., Åberg, P., Airoldi, L., Anderson, J. M., Bacchiocchi, F., Bulleri, F., Dinesen, G.E., Frost, M., Gcia, E., *et al.* (2005) Low- crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. *Coast. Eng.*, **52**, 1053-1071.
- O'Connor, N.E. and Crowe, T.P. (2007) Biodiversity among mussels: separating the influence of sizes of mussels from the ages of patches. *J. Mar. Biol. Assoc. UK*, **89**, 551-557.
- O'Gorman, E.J., Fitch, J.E. and Crowe, T.P. (2012) Multiple anthropogenic stressors and the structural properties of food webs. *Ecology*, **93**, 441-448.
- O' Riordan, R.M., Arenas, F., Arrontes, J., Castro, J.J., Cruz, T., Delany, J., Martinez, B., Fernandez, C., Hawkins, S.J., McGrath, D. *et al.* (2004) Spatial variation in the recruitment of the intertidal barnacles *Chthamalus montagui* Southward and *Chthamalus stellatus* (Poli) (Crustacea: Cirripedia) over an European scale. *J. Exp. Mar. Biol. Ecol.*, **304**, 243-264.
- OSPAR Commission (2008a) *OSPAR List of Threatened and/or Declining Species and Habitats*, 2008-6, 4pp.

- OSPAR Commission (2008b) *Case Reports for the OSPAR List of Threatened and/or Declining Species and Habitats*. Publication Number 358, 261pp.
- Paul, M. and Amos, C.L. (2011) Spatial and seasonal variation in wave attenuation over *Zostera noltii*. *J. Geophys. Res.*, **116**, C08019, doi:10.1029/2010JC006797.
- Pawlik, J.R., Butman, C.A. and Starczak, V.R. (1991) Hydrodynamic facilitation of gregarious settlement of a reefbuilding tube worm. *Science*, **251**, 421–424.
- Perkol-Finkel, S., Shashar, N., Barnea, O., Ben-Daviv-Zaslav, R., Oren, U., Reichart, T., Yacobovitch, T., Yahelb, G., Yahelb, R. and Benayahu, Y. (2005) Fouling reefal communities on artificial reefs: does age matter? *Biofouling*, **21**, 127–140.
- Porzio L., Buia M.C. and Hall-Spencer J.M. (2011) Effects of ocean acidification on macroalgal communities. *J. Exp. Mar. Biol. Ecol.*, **400**, 278–287.
- Power, A.M., McCrann, K., McGrath, D., O’Riordan, R.M., Simkanin, C., and Myers, A.A. (2011) Physiological tolerance predicts species composition at different scales in a barnacle guild. *Mar. Biol.*, **158**, 2149–2160.
- Reeve, D.E., Horrillo-Caraballo, J.M. and Magar, V. (2008) Statistical analysis and forecasts of long-term sandbank evolution at Great Yarmouth, UK. *Estuarine, Coast. Shelf Sci.*, **79**, 387–399.
- Reise, K. and van Beusekom, J.E.E. (2008) Interactive effects of global and regional change on a coastal ecosystem. *Helgoland Mar. Res.*, **62**, 85–91.
- Short, D.T. and Neckles, H.A. (1999) The effects of global climate change on seagrasses. *Aquatic Botany*, **63**, 169–196.
- Smith, P.E. (1985) Year-class strength and survival of O-group clupeoids. *Can. J. Fisheries Aq. Sci.*, **42**, 69–82.
- Smith, P.M., Dixon, R.O.D. and Cochrane, M.P. (2002) *Plant life of Edinburgh and the Lothians*. Edinburgh: Edinburgh University Press, 416pp.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. and Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.
- Thomsen, J., Gutowska, M.A., Saph.rster, J., Heinemann, A., Trübenbach, K., Fietzke, J., Hiebenthal, C., Eisenhauer, A., Krtzinger, A., Wahl, M. and Melzner, F. (2010) Calcifying invertebrates succeed in a naturally CO₂-rich coastal habitat but are threatened by high levels of future acidification. *Biogeosciences*, **7**, 3879–3891.
- Thompson, R.C., Crowe, T.P., and Hawkins, S.J. (2002) Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Env. Cons.*, **29**, 168–191.
- UKCIP (2009) *Climate Projections*. <http://ukclimateprojections.defra.gov.uk/content/view/1779/544/>
- Underwood, A.J. (1973) Studies on zonation of intertidal prosobranch molluscs in the Plymouth region. *J. Anim. Ecol.*, **42**, 353–372.
- Walne, P.R. (1971) *Introduction of Crassostrea gigas into the United Kingdom*. Lowestoft, Ministry of Agriculture, Fisheries, and Food. (Shellfish Information Leaflet, No 21.)
- Widdicombe, S., Dupont, S. and Thorndyke, M. (2010) *Laboratory experiments and benthic mesocosm studies*. In: Guide to Best Practices for Ocean Acidification Research and Data Reporting, U. Riebesell *et al.* (eds). Luxembourg: Publications Office of the European Union, 167–180.
- Wilding, C., Jackson, E., Langmead, O., Hiscock, K., Evans, J., Sewell, J., Oakley, J., Tyler-Walters, H. (2009) *Marine Health Check Update 2009*. Flagship Species Revisited. Godalming, WWF-UK, 68pp. www.wwf.org.uk/marineact
- Wilson, D.P. (1971) *Sabellaria alveolata* (L.) at Duckpool, North Cornwall, 1961–1970. *J. Mar. Biol. Assoc. UK*, **51**, 509–580.
- Ysebaert, T., Herman, P.M.J., Meire, P., Craeymeersch, J., Verbeek, H. and Heip, C.H.R. (2003) Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Scheldt estuary, NW Europe. *Estuarine Coast. Shelf Sci.*, **57**, 335–355.