Chapter 2

The Intertidal Zone of the North-East Atlantic Region

Pattern and Process


2.1 Introduction

In this chapter we consider the rocky intertidal zone of the region from Morocco and the Strait of Gibraltar to the Arctic coasts of Norway and Iceland. The offshore islands of the Azores are included, but not the southern Macaronesian islands of Madeira and the Canaries (but see Lawson and Norton, 1971; Hawkins et al., 2000). This chapter follows from Hawkins et al. (1992); but we broaden the scope beyond plant–animal interactions, while restricting focus to the intertidal zone. Much new work has been done since the 1990s in the region, particularly in extending observational and experimental studies to the Iberian Peninsula (e.g., Boaventura et al., 2002a, 2002b, 2002c, 2003; Lima et al., 2006, 2007; Schmidt et al., 2008; Vinagre et al., 2015).

We start with an overview of the history of study of the region and then outline the environmental setting and phylogeographic processes that have shaped the current biogeographic patterns. We briefly summarise distribution patterns in
response to local environmental gradients at the community level, before outlining work on the underlying processes causing these patterns. We then consider mesoscale processes (10–100s of km), such as upwelling in Iberia and coastal configuration and nearshore hydrography around Britain and Ireland that can determine pattern through bottom-up nutrient forcing and modification of larval distribution and hence recruitment regimes. The impacts of non-native species in the region are briefly considered. Finally, the role biodiversity plays in shaping ecological processes and hence ecosystem functioning is discussed. We conclude by making suggestions for further work, highlighting the special features of the north-east Atlantic and giving a prognosis of future changes.

2.2 History of Study

The intertidal zone of the north-east Atlantic has a long history of ecological and biogeographic study. This started with formal descriptions of distribution patterns, particularly the phenomenon of vertical zonation and how it is modified by exposure to wave action (Audouin and Edwards, 1833). There followed a further century of descriptive, largely qualitative, studies with various classificatory schemes (early work is reviewed by Southward, 1958), perhaps reaching their zenith in the work of the Stephensons (Stephenson and Stephenson, 1949, 1972) and the seminal book by Lewis on the British Isles (Lewis, 1964). Similar approaches were adopted elsewhere in Europe: in the Iberian Peninsula (Ardré, 1969, 1971; Saldanha, 1974), France (Fischer-Piette, 1929) and Scandinavia (Börgeisen, 1908; Børgesen and Jónsson, 1908).

With time, a more quantitative approach was adopted (e.g., Southward and Orton, 1954), including early application of multivariate statistical approaches to aid classification of geographic and local distribution patterns (e.g., Van den Hoek and Donze, 1967; Russell et al., 1971; Van den Hoek, 1984; Breeman, 1988; Lüning, 1990). Pioneering studies of geographic patterns of distribution of individual species were also made in the north-east Atlantic (e.g., Forbes, 1858; Orton, 1920; Nobre, 1940; Moore and Kitching, 1939). Fischer-Piette (1936) systematically studied both sides of the English Channel (La Manche) and extended observations throughout the Iberian Peninsula (Fischer-Piette, 1957, 1958, 1963) to what was then French and Spanish North Africa (Fischer-Piette and Prenant, 1957). Crisp and Southward took a similar approach in the British Isles and Ireland (Southward and Crisp, 1954; Crisp and Southward, 1958) including work with Fischer-Piette (Crisp and Fischer-Piette, 1959). Fischer-Piette and Hatton also undertook some of the earliest studies describing the dynamics of shore communities, realising early on the importance of recruitment fluctuations (Hatton and Fischer-Piette, 1932; Hatton, 1938). Southward (1967, 1980, 1991) started various time series, charting the influence of climate fluctuations on intertidal species, building on Southward and Crisp (1954, 1956). Lewis (1976) and co-workers also initiated work on long-term change in key species (Lewis, 1976; Bowman and Lewis, 1977; Kendall et al., 1985).

Beyond descriptive studies, the north-east Atlantic was the site of some of the earliest manipulative field experiments on rocky shores (e.g., Hatton, 1938; Fischer-Piette, 1948; Lodge, 1948), demonstrating the processes setting local distribution patterns in response to the gradients of stress associated vertically with tidal elevation and horizontally with wave exposure. These experiments investigated the role of biological interactions such as competition (Hatton, 1938, Connell, 1961a), facilitation (Hatton, 1938), grazing (Jones, 1946, 1948; Conway, 1946; Lodge, 1948; Burrows and Lodge, 1951; Southward, 1964), predation (Connell, 1961b) and biological disturbance by sweeping of algal canopies (Hatton, 1938). A variety of pioneering expeditionary experimental studies were made in both the intertidal and subtidal of Lough Hyne in West Cork, Ireland from the 1940s onwards (Kitching et al., 1959, 1966, 1976; Kitching and Ebling, 1961, 1967; Ebling et al., 1962; Goss-Custard et al., 1979; Kitching, 1987a, 1987b) exploring the role of physical and biological factors including competition, predation and behaviour in setting distribution patterns. The importance of settlement behaviour was also demonstrated in
barnacles (gregarious settlement; Crisp and Knight-Jones, 1953; Knight-Jones, 1953) and other invertebrates (Wilson, 1968). Laboratory experimentation investigated the causes of both local and geographic distributions (e.g., Southward, 1958), including how organisms responded to environmental stressors associated with periods of emersion, such as desiccation and temperature (Foster, 1971).

2.3 Environmental Context, Phylogeography and Biogeography

Rocky shores predominate on the coastlines of much of the north-east Atlantic region (Emery and Kuhn, 1982), which have a strongly erosive regime due to strong wave action arising from oceanic swell driven by south-westerly and westerly wind, and the large fetch on the Icelandic, Iberian, French, west Irish, south-west coasts of the United Kingdom and on the outer islands of Britain and Norway. Extensive areas of exposed sandy beach occur in south-west Spain and Portugal, central Portugal and the Bay of Biscay. The more enclosed shores of the Irish and North seas, eastern English Channel and the south-east coast of Iceland are largely made up of areas of mobile shingle and gravel which support little macrobiota (Ingólfsson, 2006). Sandy and muddy shores predominate in more sheltered areas. The southern North Sea and eastern English Channel plus much of the northern Irish Sea mainly comprise soft eroding coastline, but with considerable areas of artificial hard substrata due to port systems and sea defences (Firth et al., 2016a). Much of the region is macrotidal (4–10 m) with very low amplitude tides (<0.5 m) occurring in limited areas (southern Norway and west Sweden), especially around amphidromic points (e.g., south-west Scotland and north-west Ireland, central English Channel). Deep water abuts the Moroccan and Iberian coasts, leading to extensive wind-driven upwelling of cold, nutrient-rich water as far north as Galicia (Fraga, 1981) in late spring and summer (Pires et al., 2016). For much of the rest of the European coastline an extensive shallow continental shelf means that little deep upwelling occurs (Southward et al., 1995). The Azores, as recent volcanic islands adjacent to the Mid-Atlantic Ridge, do not have a continental shelf and are surrounded by deep, clear, oligotrophic oceanic waters with a small tidal range (2–4 m), but the littoral zone is extended by vigorous wave action (Santos et al., 1995; Hawkins et al., 2000).

The flora and fauna of the north-east Atlantic have been shaped by successive periods of glacial expansion and retraction during warmer interglacials for the last 3 million years (Maggs et al., 2008). In the 1850s, Forbes (1858 – reproduced in Hiscock et al., 2004) realised that the British Isles was an area of overlap between warm-water “southern types” on the south and west coasts, and cold-water species to the north and east. Many clades invaded the north-east Atlantic from the North Pacific in a trans-Arctic interchange approximately 3.8 million years ago when the Arctic Ocean was relatively ice-free (Wares and Cunningham, 2001). These include many genera of fucoïds and laminaïrans among the seaweeds. Similarly, littorinids, thaid whelks and balanoid barnacles all have North Pacific origins. Some species such as *Semibalanus balanoides* still occur on the shores of the North Pacific in both America and Asia, exhibiting pan-boreal distributions (Crickenberger and Wethey, 2017). As a consequence, the shores of both Atlantic seabords have many species in common; although diversity is higher in the north-east than the north-west Atlantic (Jenkins et al., 2008a) because recolonisation following ice ages occurred mainly from east to west, probably via Iceland and Greenland to North America (Wares and Cunningham, 2001). There is also a strong element of the flora and fauna whose origins are primarily from the warm waters in more southerly latitudes of the Atlantic. These include seaweeds of the genera *Sargassum* and *Cystoseira* plus *Bifurcaria bifurcata*. Many red algae also probably have south Atlantic origins (Lüning, 1990), as well as major animal clades including patellid limpets, trochids (*Phorcus*, previously called *Osilinus*, and *Steromphala*, previously called *Gibbula*) and chthamalid barnacles. Thus, the north-east Atlantic is an area where clades from different oceans
overlap and interact (Hawkins et al., 2009; Miesz-
kowski and Sugden, 2016).

Brown algae are more prevalent at higher lati-
tudes (Hawkins et al., 1992; Jenkins et al., 2008a),
probably as an outcome of these combined phy-
logeographic processes and the cooler thermal
environment in boreal oceanic waters. Another
process shaping allopatric speciation has been the
opening and closing of the Mediterranean,
coupled with the complex hydrography of the
Strait of Gibraltar, with the influence of the
Atlantic ceasing in modern times around the
Alboran Front (Pannacciulli et al., 1997). Success-
ive waves of colonisation of the Atlantic Islands
(Macaronesia) have also occurred, exemplified by
Phorcus spp. (Donald et al., 2012).

Continuing southwards from south-west Brit-
ain, B. bifurcata and Cystoseira spp. become more
common, occurring in rock pools and forming
conspicuous zones on open rock. From Brittany
southward the stalked barnacle Pollicipes pollicipes
dominates the lower parts of exposed shores,
providing a valuable fishery (Barnes, 1996; Van Syoc
et al., 2010). Sabellaria alveolata also forms exten-
sive reefs in the Bay of Mont Saint Michel and
further south throughout France, Spain and Por-
tugal (Anadon, 1981; Gruet, 1986; Dubois et al.,
2002, 2006; Ayata et al., 2009) and into the Medi-
terranean (Bertocci et al., 2017).

Further south in the diversity of grazing patellid limpets increases (Ballantine,
1961), with Siphonaria being present from its pole-
ward range limit in northern Portugal. There are
also several species of trochids, grapsid crabs and
herbivorous fish such as the salema (Sarpa salpa)
on southern European coasts. Thus, grazing pres-
sure is much greater in southern Europe than in
the north (Franco et al., 2015).

From the north of the British Isles polewards,
species diversity declines as many Lusitanian
invertebrates have failed to colonise that far
north following the end of the last ice age. For
example, the poleward range edge of the polychaete worm S. alveolata occurs in south-west
Scotland (Cunningham et al., 1984; Firth et al.,
2015), and Patella ulysiponensis reaches Shetland
and southern Norway. The poleward range edge of
Chthamalus stellatus is in Shetland, and for
Chthamalus montagui occurs in Orkney; but
neither species reaches Norway. The northern
range edge of Steromphala umbilicalis also occurs
in Orkney (Southward et al., 1995; Hawkins et al.,
2009).

At higher latitudes dominance by fucoid algae
can extend out onto exposed shores (Ballantine,
1961). Fucus distichus thrives in a highshore band
on the most exposed shores on the north of main-
land Britain and throughout Norway. Other Fucus
species, considered part of the F. distichus com-
plex, occur in more sheltered locations in Norway
e.g., F. evanescens). Fucoid algae retreat into more
sheltered conditions at lower latitudes in Europe.
In the south and west of Britain, patches of
fucoids occur on moderately exposed shores,
with dense cover only occurring on the most
sheltered shores. The non-bladdered dwarf form
of Fucus vesiculosus (var. vesiculosus) occurs on
more exposed shores, forming a habitat mosaic
with Mytilus spp. (Crowe et al., 2011). Further
south, successive species of Fucus become scarcer
and disappear from the shore, leaving only Fucus
spiralis and the recently described Fucus guiryi
occurring in patches between high- and mid-
shore (Zardi et al., 2011). Pelvetia canaliculata, F.
vesiculosus, Ascophyllum nodosum, F. serratus and
Himanthalia elongata are absent on the open coast
around the Basque country. They then reappear
further south, along with kelps, along the colder,
upwelling-influenced Galician and northern Por-
tuguese coasts where precipitation is high (South-
ward et al., 1995). Large range extensions and
retractions of fucoids have been reported along
the north coast of Spain and Portugal in response
to climate fluctuations and more recent climate
change (Arrontes, 1993; Lima et al., 2009; Duarte
et al., 2013; Nicastro et al., 2013).

The most southerly location to show a classic
(sensu Stephenson) sheltered shore zonation pat-
tern of P. canaliculata – F. spiralis – F. vesiculosus – A.
nodosum – F. serratus – laminarians (Laminaria
digita, Saccorhiza polyschides) is Viana de Castelo
in northern Portugal (Boaventura et al., 2002b).
In southern Portugal F. vesiculosus is only found in
estuarine refuges; it has disappeared from such
refuges in Morocco in recent years (Nicastro et al.,
2013). Carcinus maenas and Littorina littorea also
occur in estuarine refuges towards their southern
limits (Reid, 1996; Queiroga et al., 2006).
The rocky shores of the Azores bear some similarities to those of southern Portugal (Hawkins et al., 1990), but certain key taxa have failed to colonise the islands (Hawkins et al., 2000). Species that are absent include *C. montagui*, *Patella piperata*, *Siphonaria pectinata* and trochids of the genera *Phorcus* and *Steromphala* (although *Phorcus sauciatus* has recently colonised Santa Maria (Ávila et al., 2015) and São Miguel (Vale, personal communication). Many of these species occur in both Madeira and the Canaries (i.e., trochids, *P. piperata*) or the Canaries alone (*C. montagui*). Historically, the Lusitanian limpet *Patella rustica* was found in southern and central Portugal; it was absent from Galicia and Asturias but reappeared in the warm waters of the inner Bay of Biscay on the Basque coast (Nobre, 1940; Fischer-Piette, 1955; Southward et al., 1995). In recent years, this distributional gap has been bridged, linked to relaxation of upwelling (Lima et al., 2006). Despite this break in distribution being known to occur for at least 70 years, no evidence of genetic differentiation could be found between Biscayan populations and those in Portugal (Ribeiro et al., 2010). There are also Macaronesian endemics such as *Patella aspera*, the *Patella candei* complex (Côrte-Real et al., 1996; Weber and Hawkins, 2002, 2005; Faria et al., 2017, 2018; González-Lorenzo et al., 2015), *Megabalanus azoricus* and *Tectarius striatus*. The only canopy-forming species in the intertidal is *F. spiralis* (probably the newly described *F. guiryi*). *Cystoseira* canopies can form very low on the shore, in midshore rock pools and in the shallow subtidal zone of most exposed coasts.

There have been considerable fluctuations in climate in the north-east Atlantic region during the period of formal scientific study from the middle of the nineteenth century onwards, with alternations of colder (either side of the First World War [1900s–1920s], 1960s to mid-1980s) and warmer climatic periods (1930s–1950s), upon which more recent rapid warming due to anthropogenic climate change have been superimposed (Southward et al., 2004; Philippart et al., 2011; Birchenough et al., 2015). These have driven fluctuations in relative abundance and geographic distribution of species (Southward et al., 1995; Mieszkowska et al., 2006; Hawkins et al., 2009). There have been both retreats of the poleward or leading range edge of Lusitanian species during colder periods and advances during warmer periods, especially during the more recent period of rapid warming (Figure 2.1). Conversely, boreal species have thrived during colder periods, with some retraction of the trailing range limits in recent years. One of the most well-documented examples is the fluctuation in abundance of warm- (*Chthamalus* spp.) and cold-water (*S. balanoides*) barnacles in the south-west of England from the 1950s to date (Southward and Crisp, 1954, 1956; Southward, 1967, 1991; 2009).
Hawkins et al., 2008, 2009; Philippart et al., 2011; Mieszkowska et al., 2014a). During warmer years *Chthamalus* appears to be released from competition by early mortality of juvenile *S. balanoides* (Poloczanska et al., 2008), while *S. balanoides* does well in colder years (Wethey et al., 2011). *S. balanoides* is prone to recruitment failure towards its southern range edge (Jenkins et al., 2000; Svensson et al., 2005; Rognstad et al., 2014); this is because reproduction is inhibited in warmer winters (Rognstad et al., 2014), perhaps coupled with mismatches of larval release with the spring phytoplankton bloom (e.g., Hawkins and Hartnoll, 1982a) being more likely after warmer, windier North Atlantic oscillation-positive index winters (Broitman et al., 2008). Both *Chthamalus* species have more broods and an extended breeding season further south in the range (Burrows et al., 1992; O’Riordan et al., 2004) and hence are likely to have more broods during warmer years towards the poleward leading range edge. These changes in abundance and reproductive output have led to range extensions in the Irish Sea (*C. stellatus*) and North Sea (*C. montagui*) (Hawkins et al., 2009). They have not been observed in the English Channel (Herbert et al., 2007) where hydrographic barriers coupled with Allee effects, the lack of suitable substrata and the polishing action of sand on rocks prevent settlement, probably preclude further spread eastwards (Herbert and Hawkins, 2006; Keith et al., 2011). *S. balanoides* has shown a major contraction in range (Wethey et al., 2011) at the trailing southern range limit in France and north-west Spain; in north-west Spain it has contracted from widespread populations in the 1950s and 1960s to a single reproductive population in the Ría de Arousa in 2006 (Wethey and Woodin, 2008). The Lusitanian barnacle *Perforatus perforatus* (formerly *Balanus perforatus*) has shown range extensions at its north-eastern leading range limit in the English Channel (Herbert et al., 2003).

Around the British Isles and Ireland extensions in the leading range edges of a suite of Lusitanian species have been idiosyncratic and aphasis, reflecting the life history characteristics of individual species, including habitat requirements and dispersal capability (Hawkins et al., 2008, 2009; Keith et al., 2011). Trochids with a short planktonic larval phase have shown the capability for the greatest expansion at the northern and north-eastern leading range edges (Mieszkowska et al., 2005, 2007; Hawkins et al., 2009, 2016a). Consolidation of range extensions probably occurs by successful colonisation of shores that are a short distance beyond the existing range limit as soon as local climatic conditions become suitable for survival. *Phorcs lineatus* has recolonised the northern sector of its distributional range following the trim-back that occurred in the extreme winter of 1962/1963 and the subsequent cold winters of the 1960s, 1970s and early 1980s; extensions of the leading range edges have now occurred beyond its previous limits in North Wales and the English Channel (Mieszkowska et al., 2007). *Steromphala umbilicalis* has been even more successful, the leading range edge extending much further east into the eastern English Channel and along the north coast of Scotland (Mieszkowska et al., 2006). There have been fewer retractions in the trailing range limits of boreal species compared to expansions of southern species (Hawkins et al., 2009; Burrows et al., 2011). The boreal kelp *Alaria esculenta* is now much less common than it once was (e.g., in Ireland, Simkanin et al., 2005), with a retraction at its southern range limit. This species disappeared from much of the western English Channel in the 1950s and, interestingly, did not reappear when it got colder in the 1960s (Hiscock et al., 2004).

After decades of gradual warming, the cold winter of 2009–10 saw enhanced recruitment of the northern barnacle *S. balanoides*, subsequently leading to re-expansion of its range in France and Iberia, from where it had previously retracted (Wethey et al., 2011). The southern barnacles *C. montagui* and *C. stellatus* did not suffer adult mortality; however, recruitment failed at their northern limit. The southern limpet *P. rustica*, the soft-shore polychaete *Diopatra* and the mussel *Mytilus galloprovincialis* showed no change in distribution and no adult mortality at their northern limits (Wethey et al., 2011). *Testudinalis testudinala* has disappeared from the Isle of Man near its former southern range limit (Forbes, 1858; Hawkins et al., 2009) with a current trailing range edge...
currently in northern Scotland and Northern Ireland. Filling gaps in the distribution of *S. alveolata* has occurred in recent years following the cold winter of 1962/1963, aided by the presence of artificial habitat (Firth et al., 2015). Such artificial habitat may have also enabled range extensions in the English Channel and along the Belgian coastline (Johannesson and Warmoes, 1990; Moschella et al., 2005; Hawkins et al., 2008; Keith et al., 2011; Firth et al., 2013a).

There have been similar shifts in distribution patterns in Portugal and Spain, with advances of Lusitanian species and retreat of boreal species (Lima et al., 2006, 2007). Responses to climate may be more complex in upwelling areas such as the Iberian Peninsula. Upwelling may intensify in a warmer, windier world (Bakun, 1990), leading to persistence and even increases of boreal, subtidal and lowshore species (e.g., Lima et al., 2009). In contrast, higher shore species may suffer from warmer air temperatures. There is currently debate about whether upwelling has and will increase (Miranda et al., 2013; Ribeiro et al., 2016) or decrease (Lemos and Pires, 2004; Pardo et al., 2011) along the Iberian Peninsula (Santos et al., 2011; Varela et al., 2015). Recent observations suggest that several kelp species (*S. polyschides, Laminaria ochroleuca* and *Laminaria hyperborea*) have undergone range contractions and/or declines in abundance in recent decades in response to seawater warming along the Iberian Peninsula (see review by Smale et al., 2013). It is very likely that kelp forest biomass and productivity will diminish under warmer, stormier conditions; unfortunately, direct measurements of kelp forest structure, biodiversity, productivity, detritus production and export, and resistance and resilience to perturbation along a regional-scale temperature gradient along the north-east Atlantic coastline are lacking (Smale et al., 2013).

Latitudinal gradients of sea and air temperatures (Figure 2.1) are highly modified at the local scale by the topography of the shore, providing microclimatic refuges from high aerial temperatures in areas of shade or water retention (Figure 2.2) (Seabra et al., 2011; Lima et al., 2016) with consequences for the biota (Firth et al., 2016b). Emersion stress can also be modified by species interactions, particularly shading by canopy algae that might enable persistence of cold-temperate species (e.g., *Patella vulgata* under *F. vesiculosus*; Moore et al., 2007; Marzinelli et al., 2012). Loss or thinning of macro-algal canopies will have severe consequences for understorey species (Jenkins et al., 1999a, 1999b, 2004, 2005; Pocklington et al., 2017). Many lowshore species are found higher up the shore under canopies; loss of canopy leads to death of these species, especially juveniles (Marzinelli et al., 2012); particularly on sheltered shores where the long-lived canopy species *A. nodosum* often dominates, this can lead to long-term changes in community structure (Jenkins et al., 2004; Cervin et al., 2005; Ingólfsson and Hawkins, 2008).

### 2.4 Distribution Patterns in Response to Local Gradients of Tidal Elevation and Wave Action

The vertical distribution patterns of rocky intertidal species have been well described for the British Isles plus the Atlantic and Channel coasts of France. In sheltered conditions there is strong vertical zonation of algal species, all of which can form dense canopies of up to 100 per cent cover. *P. canaliculata* and *F. spiralis* dominate the highshore, followed by a band of *F. vesiculosus* giving way to a midshore dominated by the large, long-lived canopy-forming species *A. nodosum*, being succeeded in turn by *F. serratus* and then kelps (usually *L. digitata* but on extremely sheltered or boulder shores *Saccharina latissima*, formerly known as *Laminaria saccharina*) from the lowshore into the shallow subtidal zone. There is some local variation in these patterns (see Lewis, 1964 for details), but *A. nodosum* dominance in the midshore region is ubiquitous in sheltered areas of high salinity.

On moderately exposed shores, fucoid cover diminishes, with *A. nodosum* becoming increasingly stunted before disappearing and being replaced by a patchy mosaic of *F. vesiculosus*, barnacles and limpets. Highshore *P. canaliculata*
and *F. spiralis* become rarer with increasing exposure, as does *F. serratus* lower on the shore. In wave-exposed conditions *F. serratus* gives way to *H. elongata*, with only turf-forming algae occurring in extremely exposed conditions. In northern and western Britain (except the English Channel), a band of *A. esculenta* can occur in the most exposed conditions around the low-water spring-tide mark. On many exposed shores *Mytilus* spp. can form extensive beds; but they do not always occur because of mesoscale processes, especially larval supply and retention, that can influence distribution patterns (Wangkulankul, 2016; Wangkulankul et al., 2016). On the most exposed shores and those that are steeply sloping, fucoids become scarce. The exposed shore form of *F. distichus* occurs from Orkney northwards (with some relict populations on

![Fig. 2.2](https://www.cambridge.org/core/core/journals/marine-biology-review/issue/1487FCAE8A2A361E80D95D1DDB834E33/879A49082CF5A6286D86AD39002A540692923830/marine-biology-review-10.1017/9781108235792.003 fig2.jpg)

At the northern end of the range considered here, on the shores of Norway the tidal range is small, approximately 0.5 m, resulting in tight, monospecific vertical zones on many rocky shores. *L. digitata* and *L. hyperborea* are present in high abundances along the exposed coasts, with *S. latissima* being the most dominant kelp along the more sheltered shores of southern Norway, where *A. nodosum* is also abundant. In west Sweden, with a small tidal range (<0.3 m) and often larger irregular changes in the water level, the zonation pattern is similar to that described for macrotidal areas (see earlier), although *P. canaliculata* is missing. At a first glance these extremely narrow zonation patterns look very different to those on the mectrotidal shores. However, for *A. nodosum*, observations show that the morphology of individuals as well as the demography and life history traits of the populations in west Sweden are remarkably similar to those on the British Isles (Åberg and Pavia, 1997; Svensson et al., 2009). *A. esculenta* is found in high densities in the Lofoten Islands. The fucoids *P. canaliculata*, *F. spiralis*, *F. vesiculosus* and *F. serratus* are also present in high abundances along the Norwegian coastline. The boreal *S. balanoides* is the only barnacle found on rocky shores, with *P. vulgata*, *T. testudinalis* and the kelp-dwelling *Patella pellucida* being the species of limpet present. *L. littorea*, *Littorina saxatilis* and *Melarhaphe neritoides* decrease in abundance as latitude increases along the Norwegian coastline (Narayanaswamy et al., 2010).

These patterns can be modified by local topography, with differences between shaded north-facing and sunnier south-facing rocks (Firth et al., 2016b). North-facing surfaces are refuges from temperature-related stresses, with greater species richness.

### 2.4.1 Causes of Vertical Patterns of Distribution

Classic work on the roles of physical factors in setting upper limits and competition in setting lower limits of intertidal species, using barnacles as a model species, was done by Connell (1961a, 1961b) at Millport in Scotland. Schonbeck and Norton, also working in Scotland, showed that upper limits of intertidal fucoids could be set by physical factors, while lower limits were generally set by biological interactions (Schonbeck and Norton, 1980). This led to an emerging paradigm in the 1970s and early 1980s that upper limits of sessile intertidal species were generally set by physical factors and lower limits by biological interactions such as competition, grazing and predation. The importance of larval behaviour in sessile invertebrates (Knight-Jones, 1953; Crisp, 1955; Knights et al., 2006) and adult behaviour in mobile animals in directly setting distribution patterns has also been long recognised (Newell, 1979 for review).

Observations of proliferating cover of algae after mass mortality of limpets from toxic dispersants (Southward and Southward, 1978) or experimental removal (Jones, 1948; Lodge, 1948; Burrows and Lodge, 1951; Hawkins, 1981a, Hawkins et al., 1992) gave indications that the upper limits of lowshore seaweeds could also be set by biological factors such as grazing. There is evidence that zonation patterns of patchily occurring fucoids on more exposed shores was set by the rate of early growth and the probability of escape from limpet grazing (Hawkins, 1981a; Hawkins and Hartnoll, 1983a). Mixed zonation patterns could emerge following large-scale limpet removal experiments (Lodge, 1948; Burrows and Lodge, 1950).

Other experiments on fucoid-dominated shores showed that competition could also set the upper limits of zonation of species (Hawkins and Hartnoll, 1985). *A. nodosum* removal experiments on the Isle of Man, where there is a narrow band of *F. vesiculosus* above *A. nodosum* with a dense band of *F. serratus* below it, showed that, in the absence of *A. nodosum* canopy, both species could coexist on the midshore (Hawkins and Hartnoll, 1985; Jenkins et al., 1999c, 2004). Similar findings were observed in Iceland (Ingólfsson and Hawkins, 2008). Interestingly, Lewis (1964) suggested this was the case, but did not make any experimental tests of this hypothesis. Small-scale removals of *A. nodosum* in the Isle of Man, simulating natural disturbance events on sheltered shores demonstrated the mechanism by which patch of the lowshore *F. serratus* could
persist among dense beds of the dominant *A. nodosum* (Cervin et al., 2005).

Broadscale experiments in Portugal and the British Isles showed that the upper limits of algal turfs, *F. serratus*, and *H. elongata* could be set by limpets grazing (Boaventura et al., 2002a). The rapid growth of the algal turf was shown to exclude limpets and prevent them from extending down the shore: low on the shore the rate of algal growth exceeded the ability of limpets to control it (see Hawkins and Hartnell, 1983b for explanation of the causes of the Stephenson and Stephenson three-zone system). In the Azores, much of the midshore is dominated by extensive patches of algal turfs as a result of chronic exploitation of limpets that substantially reduce their numbers, particularly the larger *P. aspera* in the intertidal (Martins et al., 2008, 2010).

In the north-east Atlantic, it is clear that, while upper limits are mostly set directly by physical factors, this is not always the case. Highshore species (*P. canaliculata*, *F. spiralis*) plus broad-ranging species such as *P. vulgata* (Orton, 1920) and *S. balanoides* that extend higher up the shore (Connell, 1961a, 1961b) have their upper vertical limits set by physical factors (Hawkins and Hartnell, 1985). This is often the case for essentially subtidal species just extending into the intertidal, such as *L. digitata*; although removal of *F. serratus* can lead to a modest upshore extension (Hawkins and Hartnell, 1985) which can be subsequently trimmed back. Thus, the upper limits of *L. digitata* can be set by physical factors and/or by biological interactions, depending on the location and season (Araújo et al., 2016). Thus, there is mounting evidence that for many low- and mid-shore species upper vertical limits are set by biological interactions such as competition, where canopy cover is dense, or by grazing – especially for algal turfs on more exposed shores (Boaventura et al., 2002a).

It is instructive to review the relative role of physical factors and biological interactions by taking a slice down moderately exposed or exposed shores of the south and central British Isles (revisiting Hawkins and Hartnell, 1983b). In the highshore region above the barnacle zone (the littoral fringe [Lewis, 1964]), diatoms and ephemeral algae (*Ulothrix*, *Prasiola*, *B. diingia* and *P. Porphyra* species) proliferate in the winter months (Hawkins and Hartnell, 1983a), but die-off in the spring owing to warmer weather; only tough cyanobacteria (Thompson et al., 2005; Skov et al., 2010) and lichens remain over the summer. Ephemeral algae can, however, persist in cool summers and further north in the British Isles and in Norway and Iceland, or in areas of wet run-off. Littorinid snails (*M. neritoides*, the *L. saxatilis* complex) are numerous but restricted to pits and crevices by harsh conditions (Hawkins and Hartnell, 1983b), resulting in grazing haloes (Stafford and Davies, 2005) that can expand or contract seasonally. Physical factors are paramount here, with grazing restricted locally to around refuges from harsh physical factors (but see Stafford and Davies, 2004). Competitve interactions between ephemeral seaweeds have rarely been explored experimentally (but see Viejo et al., 2008), but the succession that occurs seasonally suggests that some species can dominate once released from harsh physical conditions over the winter. Further south in Europe, such proliferation of ephemeral algae is less commonly observed, other than on the most wave exposed shores.

The midshore region (the eulittoral zone [Lewis, 1964]) is dominated by barnacles and, in some places, mussels (Ballantine, 1961). In extreme exposure, the small, bladderless morph of *F. vesiculosus* can occur, especially among mussel mosaics. On these shores, grazing by patellid limpets is the predominant interaction. Occasionally, patches of *F. vesiculosus* do escape from limpet grazing. Predation by dog whelks may also be important, although there has been little work published on their community role in the north-east Atlantic (but see Hawkins et al., 1994). Their foraging is often constrained by the physical environment, with excursions occurring from refuges such as crevices (Burrows and Hughes, 1989; Johnson et al., 1998). Competition for space can occur between barnacle species (Connell, 1961b). Surprisingly little work has been done on mussel-dominated shores in Europe (but see O’Connor et al., 2006, O’Connor and Crowe, 2007; Crowe et al., 2011; Wangkulangkul et al., 2016).

Lower on the shore, *F. serratus* (moderate exposure), *H. elongata* (exposed) and *Cystoseira abies-marina* (very exposed) become more prevalent among red algal turfs (e.g., *Chondrus crispus*,...
Mastocarpus stellatus and Corallina spp.), which are the only lowshore algae present in the most exposed conditions. Here, the ability of algae to dominate space is the most important interaction, with grazing by P. vulgata or P. ulysippomonensis leading to small clearings among the turf. Around the low-water spring-tide level, the turf gives way to kelp (L. digitata, except in the most exposed locations where A. esculenta occurs in the British Isles). Removal of L. digitata on moderately exposed shores can lead to colonisation of opportunistic kelps: S. latissima primarily from more sheltered conditions and A. esculenta from more exposed shores (Hawkins and Harkin, 1985). Removal of the L. digitata canopy also leads to the proliferation of a dense understorey of opportunistic species (Ectocarpus spp., ephemeral green algae, Palmaria palmata) that swamps the few limpets (P. ulysippomonensis) and sponges (Hymeniacidon perlevis, Halichondria panacea) that are facilitated by the sweeping effects of the kelp lamina. Algal canopy effects are the predominant interaction either side of lowest astronomical tides (Hawkins and Hartnoll, 1983a).

2.4.2 Causes of Horizontal Patterns of Distribution

The interplay between the underlying physical gradient from sheltered bays to exposed headlands with biological interactions to set distribution patterns has long been a subject of study in the north-east Atlantic. It is important to emphasise that this environmental gradient – unlike the vertical gradient from low-water to high-water – cannot be considered a unidirectional stress gradient. Some species thrive in wave-exposed conditions; others are more successful in sheltered waters; while many have optima in moderate wave action (see Raffaelli and Hawkins, 1996 for further discussion).

Early explanations emphasised the importance of the direct effects of the physical environment in determining distributions, with fucoid algae being excluded from wave-exposed conditions by the direct effects of wave action (see Lewis, 1964 for review). While the exposure to wave action clearly has a role to play in determining fucoid survival (Jonsson et al., 2006), classic limpet removal experiments on the Isle of Man (Jones, 1946, 1948; Lodge, 1948; Burrows and Lodge, 1950; Southward, 1956, 1964) showed that grazing prevented establishment of fucoid seaweeds on barnacle-dominated shores. Observations following kills of limpets by excessive application of toxic dispersants (Southward and Southward, 1978) confirmed that limpet grazing prevented establishment of algae even on the most exposed British shores, such as Sennen Cove in west Cornwall (see also Hawkins et al., 1983, Hawkins and Southward, 1992). Jonson et al. (2006) by a combination of field experiments, measurements of wave action and modelling showed that establishment of fucoids was prevented by limpet grazing, but persistence was limited by wave action.

The importance of limpet grazing (Hawkins, 1981a, 1981b) in generating small-scale patchiness on moderately exposed British shores (Hartnoll and Hawkins, 1980, 1985; Hawkins and Hartnoll, 1983b) has been the focus of much small-scale experimentation (described in Hawkins et al., 1992). This has shown the complex positive and negative interactions between limpets, barnacles and fucoids on moderately exposed shores (see Hawkins and Hartnoll, 1983a; Hartnoll and Hawkins, 1985; Hawkins et al., 1992), especially the role of barnacles in facilitating fucoid escapes from grazing (Hawkins, 1981a, 1981b) by providing refuges for germlings and impeding foraging movements of Patella spp. (Hawkins and Hartnoll, 1982b). Clumps of fucoids not only provide habitat for Nucella lapillus and the anemone Actinia equina, they also act as nursery areas for juvenile limpets (Hawkins and Hartnoll, 1983a).

Detailed spatial statistical analysis described the grain of patchiness and how small-scale surface topography could override biological provision of habitat (Johnson et al., 1997). Individual-based spatially explicit models (Johnson et al., 1998) coupled with the use of cellular automata (Burrows and Hawkins, 1998), showed the importance of limpet homing and aggregation behaviour in the maintenance of patchiness on moderately exposed shores. Exploitation of limpets in southern Europe and the Azores may also drive low- and mid-shore communities to diverge towards those dominated by algal turfs.
(Martins et al., 2008, 2010). Ultimately, however, the patch dynamics on these shores are driven by recruitment fluctuations, especially of barnacles (Hawkins and Hartnoll, 1982a; Jenkins et al., 2000), but also of limpets and fucoids (Little et al., 2017). Thus, there is an external stochastic element leading to patch genesis and an internal deterministic element leading to patch demise (Hartnoll and Hawkins, 1985; Martins et al., 2018). This work has been criticised as lacking generality (Chapman, 1995) because it was primarily conducted on Isle of Man limestone ledges with limited replication. Subsequent work as part of the EUROROCK programme employed nested experimental designs to explore recruitment fluctuations (Jenkins et al., 2000; O’Riordan et al., 2004; Cruz et al., 2005) and grazing interactions (Jenkins et al., 2005; Coleman et al., 2006). This has shown the generality of process at a European scale, with midshore limpet grazing being important in controlling algae at all latitudes. EUROROCK work showed considerable interannual and locational variation in barnacle recruitment in both Chthamalus species (O’Riordan et al., 2004; Cruz et al., 2005) and S. balanoides (Jenkins et al., 2000). This broadscale work was turned into stage-structured models of population processes on a European scale (Hyder et al., 2001; Svensson et al., 2005, 2006).

Competition among grazing limpets was also analysed in situ through experimental work (Boaventura et al., 2002c, 2003; Firth et al., 2009; Firth and Crowe, 2010). Competitive interactions within and between size-classes of the limpet Patella depressa were investigated in central Portugal. Although both size-classes could negatively affect each other, the effect of large limpets on small was greater than the reverse. Large limpets were shown to be superior competitors that may modulate the abundance of small limpets on the shore. It is unlikely, however, that they will totally exclude small limpets due to intensity of competition within the large size-class. Niche differentiation and high recruitment at lowshore levels are other possible factors (Boaventura et al., 2003) that can contribute to reduce competition between the size-classes. Competitive interactions between P. depressa and P. vulgata were also examined close to the biogeographical limit of distribution of P. vulgata, in the north of Portugal. However, at the end of the experiment no significant differences were found in the effects of P. depressa on P. vulgata and vice versa (Boaventura et al., 2002c).

As with many limpets which are exploited worldwide, P. vulgata is a protandric sequential hermaphrodite that changes sex from male to female during its lifespan (Le Quesne and Hawkins, 2006; Guallart et al., 2013). Since exploitation of limpets is mainly size-selective, protandric limpet populations have been depleted of female cohorts which aggravates the harvesting pressure upon the stocks (OSPAR Commission 2010). Moreover, some limpet species have a fixed size at sex change, such as the limpet Cymbula oculus, while other species have plastic responses (Munday et al., 2006). For instance, experimental size-selective harvesting of the protandric limpet P. vulgata in the British Isles led to a decrease in shell size at sex change, suggesting an earlier switch of males to females to compensate for the harvested females (Borges et al., 2016): Size-dependent sex change was indicated by L50 (the size at which there is a 50:50 sex ratio), occurring at smaller sizes in treatments than controls, suggesting an earlier switch to females. These results were consistent with those shown by the protandric Patella ferruginea where individuals in populations with a low density of larger individuals switch to female at smaller sizes (Rivera-Ingraham et al., 2011). In parallel, Borges et al. (2015), when investigating the relationships between P. vulgata density and sex ratios of range edge and central range populations in the British Isles and Portugal, found that lower densities at range edge populations were correlated to higher proportions of females. It was suggested that relaxation of resource limitation resulting from reduced intraspecific competition at lower density (see Boaventura et al., 2003) would allow earlier promotion from males to females, resulting in more females at lower densities (i.e., sex change is density dependent). In fact, Boaventura et al. (2003) suggested that the higher percentages of males found in increased P. depressa density treatments could possibly be explained by a suppression of protandry due to competition, although this species is not widely considered as protandrous (Borges et al., 2015).
While the ecological processes determining the structure and dynamics of exposed rocky shores have received considerable attention, sheltered shores, dominated by fucoid canopy algae, have seen less work. Here the balance between the ability of macroalgae to recruit and grow and the ability of grazers to prevent them is shifted in favour of algae (Jenkins et al., 2008a). Removal experiments have demonstrated the important structuring role of large canopy-forming fucoids on understorey communities relative to a much-reduced role in patellid limpets (Jenkins et al., 1999a, 1999b, 1999c, 2004; Cervin et al., 2005). Long-term experiments in the midshore A. nodosum zone revealed interesting indirect effects of the dominant canopy; removal led to short-term loss of red turf-forming algae, a switch to a Fucus-dominated canopy and, in the long term, a six-fold increase in available bare space and patellid limpet populations (Jenkins et al., 1999a, 2004). Work on sheltered shores has also explored the interaction between canopy algae and settling barnacles. While at exposed sites the sweeping action of algal fronds reduces barnacle settlement thereby contributing to small-scale patchiness (Hawkins, 1983), on sheltered shores fucoids can limit barnacle populations to very low levels. Interactions are complex, with negative effects of sweeping on new arrivals, especially by the non-bladdered F. serratus, but also positive effects on post-settlement survival, presumably through amelioration of emersed conditions, especially higher on the shore among F. vesiculosus and F. spiralis (Hawkins, 1983; Jenkins et al., 1999d; Jenkins and Hawkins, 2003). Experimental manipulations have also shown that F. serratus (but not A. nodosum) can limit settlement through blocking access of cyprids to the substratum (Jenkins et al., 1999d; Jenkins and Hawkins, 2003).

2.5 Differential Patterns and Processes in Rock Pool Habitats Compared to Emergent Rock

Rocky shores typically comprise a mosaic of habitats with varying degrees of heterogeneity. Such complexity and spatial heterogeneity are important factors in the structure and functioning of rocky shore communities, contributing to community diversity and species coexistence in marine benthic systems (Johnson et al., 2003; Kostylev et al., 2005). Rock pools are ubiquitous features of rocky shores across the north-east Atlantic and worldwide. In comparison to emergent rock substrata, relatively little is known about the processes determining the structure and functioning of biotic communities in pools (but see O’Connor and Crowe, 2005; Martins et al., 2007; Noël et al., 2009, 2010; Griffin et al., 2010; Vye et al., 2014). Rock pools provide important nursery grounds (Orton, 1929; Lewis and Bowman, 1975; Thompson, 1980; Delany et al., 1998; Dias et al., 2016) and refugia from both abiotic stress and biological interactions (Schonbeck and Norton, 1978) for a wide range of organisms. Rock pools can extend the upper vertical limits of many organisms that are susceptible to desiccation, and, while some species tend to aggregate in pools, other species avoid them (e.g., Goss-Custard et al., 1979; Araújo et al., 2006).

Patterns in the community structure of rock pools differ greatly from those on emergent rock (Underwood, 1973; Hawkins and Hartnoll, 1983b; Noël et al., 2009; Firth et al., 2013b), leading to variation in the processes, shaping biological communities among habitat types, such as parasitism (Crewe, 1951; Kollien, 1996; Firth et al., 2017), grazing (Noël et al., 2009) and competition (Firth et al., 2009). For instance, patellid limpets have disjunct distributions in relation to rock pools and emergent rock at different stages in their life history. P. vulgata, P. ulyssiponensis and P. depressa are known to recruit into rock pools (Bowman and Lewis, 1977; Delany et al., 2002). P. ulyssiponensis is predominantly found in pools as well as on lowshore areas of rock covered by crustose coralline algae throughout its life (Lewis, 1964; Fretter and Graham, 1976; Delany et al., 2002). In contrast, P. vulgata and P. depressa are thought to migrate out of rock pools and are more abundant on emergent rock than in pools (Davies, 1969; Firth and Crowe, 2008). Furthermore, on emergent rock, P. vulgata tends to aggregate underneath Fucus spp. clumps and suffers mortality if they are removed, while P. depressa...
does not (Moore et al., 2007). In an experiment investigating habitat preference (emergent rock versus rock pools) and competition (intraspecific and interspecific) between *P. vulgata* and *P. ulyssiponensis*, Firth and Crowe (2010) found that *P. ulyssiponensis* exhibited increased growth in higher intraspecific densities on emergent rock and reduced growth in higher intraspecific densities in rock pools, indicating some degree of intraspecific facilitation on open rock and intraspecific competition in pools. There was no evidence of interspecific competition in either habitat.

Despite rock pools offering a potential refuge from the harsh abiotic conditions encountered on emergent rock (e.g., temperature and desiccation stress), they may also become stressful environments, with large fluctuations in temperature, salinity, pH and dissolved oxygen (Pyefinch, 1943; Naylor and Slinn, 1958; Goss-Custard et al., 1979; Morris and Taylor, 1983), especially higher on the shore. Rock pools in the upper shore are exposed to longer periods of emersion and exhibit greater variability in environmental conditions than pools located lower on the shore (Pyefinch, 1943). Small and shallow rock pools can exhibit significantly different temperature profiles than larger deeper ones (Martins et al., 2007), potentially making them thermally stressful environments. This is likely to be exacerbated in more extreme climates (e.g., Chan, 2000; Firth and Williams, 2009). Despite exhibiting dramatic fluctuations in physico-chemical conditions, natural rock pools often support greater diversity, abundance and/or biomass of organisms than emergent rock (Goss-Custard et al., 1979). While this is a very common assertion in the literature, there is surprisingly little quantitative evidence in the literature to support it (but see Firth et al., 2013b, 2014a).

Rock pools are complex habitats that can vary greatly in their area, depth, topography, degree of shading and inclination of surrounding rocks. Of the limited number of studies carried out in the north-east Atlantic on the physical properties underpinning rock pool communities, surface area is considered to have little influence on the biological structure of pools (Martins et al., 2007), while shading (Pyefinch, 1943) and slope (Firth et al., 2014a) have been shown to influence diversity and abundance of species. Far more is known about the influence of rock pool depth on species performance, diversity and community composition (Goss-Custard et al., 1979; Moschella et al., 2005; Bussell et al., 2007; Martins et al., 2007; Firth et al., 2014a). The relationship between diversity and function varies with depth depending on the response variable measured. Some studies have found that species richness was positively correlated with increasing pool depth (Moschella et al., 2005; Martins et al., 2007), while others have found the opposite pattern (Bussell et al., 2007; Firth et al., 2014a).

The growing body of literature emerging on the processes shaping the patterns of distribution of organisms among habitat types on rocky shores is playing an important role in informing the engineering design of coastal and marine artificial structures (e.g., sea walls, breakwaters, docks, offshore renewables, oil and gas platforms) through ecological engineering. Ecological engineering is the design of sustainable ecosystems for the mutual benefit of both humans and nature (Mitsch, 2012). Traditionally, artificial marine structures were built with a single function in mind (defence); however, changes in attitudes due to the proliferation of such structures (Morris et al., 2016; Evans et al., 2017; Strain et al., 2019) are leading to a shift in the way artificial environments (often referred to as ‘grey’ spaces) are perceived and designed (to become ‘blue’ spaces) (Sutton-Grier et al., 2015; Firth et al., 2016a; Mayer-Pinto et al., 2017; Strain et al., 2017). This can be achieved through the design of multifunctional structures providing habitat for marine life, while simultaneously serving their primary engineering function. Rock pools can be created easily and cheaply on artificial structures through a range of different techniques, ranging from creating water-retaining lips in sea walls (Chapman and Blockley, 2009), affixing precast units to vertical sea walls (Browne and Chapman, 2011, 2014; Morris et al., 2017), drill-coring directly into the substratum (Martins et al., 2010, 2016; Firth et al., 2014b; Evans et al., 2016) to pouring concrete among the boulders of rock armouring (Firth et al., 2016b). Other (more expensive) options...
include the deployment of large-scale precast habitat-enhancement units such as the BIOBLOCK (Firth et al., 2014b) and ECOcrete’s tide pools (Perkol-Finkel and Sella, 2015; www.econcretetech.com), which can replace boulders on rock armouring.

2.6 Latitudinal Patterns

The EUROROCK team used a simple approach based on limpets leaving grazing marks on wax discs (Thompson et al., 1997) to show that grazing pressure was less seasonal and more intense in southern Europe compared to further north (Jenkins et al., 2001). Such general patterns can, however, be modified by local topography, influencing foraging behaviour (Johnson et al., 2008). Using exclusion cages, limpets were shown to control algal vegetation on midshores in southern Portugal through to the Isle of Man (Jonsson et al., 2006). In general, this process was most deterministic in the Isle of Man (Figure 2.3) (Jenkins et al., 2005; Coleman et al., 2006) where propagule supply was high, with some escapes also occurring in grazed controls. Even in the British Isles, there were marked differences, with fucoid recruitment being more likely and more intense on the Isle of Man and much more patchy and stochastic in south-west England (Arrontes et al., 2004; Jenkins et al., 2005).

In southern and central Portugal, canopy-forming fucoids are restricted to F. spiralis and F. guiryi (Zardi et al., 2011). Other species of fucoid drop out in northern Portugal on the open coast, although F. vesiculosus can occur in estuarine refuges (Serrão et al., 1999; Pearson et al., 2000). The limited species pool, lack of propagule supply and physical stress probably all contribute to the absence of canopy-forming fucoids in southern Europe. Recent comparative survey and experimental work between the British Isles and Portugal have shown that reproductive output is less in Portugal (Figure 2.4) (Ferreira et al., 2015a) and there is greater physiological stress (Ferreira et al., 2014), which in turn interacts with propagule supply to affect the probability of fucoid survival and early growth to escape limpet grazing (Ferreira et al., 2015b). As referred to earlier, besides limpets, there are also several species of trochids, grapsid crabs and herbivorous fish such as the salema (Sarpa salpa) in southern European coasts, making grazing pressure much greater (Franco et al., 2015). Laboratory and in situ experiments with F. serratus suggested that three physical factors, solar irradiation, ocean and air temperatures, acting additively shape the distribution of this species in the Iberian Peninsula (Martínez et al., 2012).
Atlantic shores is predicted to change in the next few decades. The cold-temperate foundational seaweed *H. elongata* is predicted to become extinct at its current southern limit on the Iberian Peninsula in response to global warming, whereas the occurrence of southern Lusitanian *B. bifurcata* is expected to increase (Martínez et al., 2015).

Fig. 2.4  Densities of *Fucus* spp. with different grazing treatments after (a) 70, (b) 145 and (c) 365 days under different light intensities (Per.: perspex, procedure control; Uns.: unshaded, subjected to natural solar radiance levels; Sha.: shaded, under reduced solar radiance levels). Results demonstrate that reduced physical and biological pressures do not compensate for the lower supply of fucoid propagules at range edge populations in southern Europe (Portugal) compared to range centre populations in northern Europe (Wales). Data from Ferreira et al. (2015a).
2.7 Mesoscale Processes

Various processes operating at scales of 10s–100s of kilometres can influence species composition, community structure and functioning of ecosystems. These include upwelling and the topography of the coastline, both ultimately determined by the interaction of geomorphology and nearshore oceanographic processes. These in turn determine productivity of nearshore waters and the dispersal or retention of larvae.

In the north-east Atlantic there are extensive areas of upwelling off North Africa and on the coasts of Portugal and Spain (Southward et al., 1995; Jenkins et al., 2008a; Alvarez et al., 2011). In these regions, the bathymetry is steep with deep water close inshore, and wind-driven upwelling of nutrient-rich cold water occurs. On a geographic scale, this can lead to cold-water species persisting on the Asturian, Galician and Portuguese coasts that are absent in the warmer waters of the inner Bay of Biscay. Kelps, fucoid algae, littorinids and cold-water limpets such as P. vulgata are all able to survive in these areas (see Southward et al., 1995 for summary and review of early work). These shores are also more productive, supporting extensive raft culture of mussels in the Spanish Rias (Blanton et al., 1995; Jenkins et al., 2008a; Alvarez et al., 2011). As upwelling waxes and wanes, advances and retreats of fucoid algae have been reported along the coast of the Basque Country and Asturias (Arrontes, 1993).

Conversely, relaxation of upwelling has been suggested as the likely cause for the advance of the Lusitanian species of limpet P. rustica into Galicia in the last two decades (Lima et al., 2006; Sousa et al., 2012). This species was previously only found in southern and mid-Portugal, being absent from northern Portugal, Galicia and Asturias before reappearing in high densities in the Basque Country. In recent years, this gap has been bridged (Lima et al., 2006) as the species has advanced. Interestingly, there is no evidence for genetic differences between P. rustica from the Basque region and those found in southern Portugal (Ribeiro et al., 2010), suggesting this gap—known to occur for at least eighty years—was either relatively new or occasionally breached.

Upwelling also influences recruitment regimes. Although most work on this topic has been done along the north Pacific (e.g., Roughgarden et al., 1988; Connolly and Roughgarden, 1998; Connolly et al., 2001), some work has been done in the north-east Atlantic. In Portugal, recruitment of barnacle (Cruz et al., 2005) and crab (Queiroga et al., 2007) larvae has been shown to be strongly affected by intensification and relaxation of upwelling. This leads to intensive recruitment of barnacles but with differential effects between species: C. montagui which has a reasonably short larval life (Burrows et al., 1999) is favoured in upwelling regions; whereas C. stellatus with a longer larval duration does less well, presumably dispersed offshore by upwelling. A complexity of factors interacts to create recruitment peaks, including onshore transport during relaxation of upwelling and timing of tide influencing settlement behaviour (Cruz, 1999; Cruz et al., 2005; Jacinto and Cruz, 2008; Trindade et al., 2016).

Along more complex coastlines, such as around the British Isles, the topography of the coastline (bays, headlands, concave and convex coastlines) interact with nearshore processes such as tidal mixing and fronts, with stratified water influencing larval retention and dispersal (Davies and Johnson, 2006; Jessopp et al., 2007). Jenkins et al. (2008b) used nearshore plankton trawls and daily surveys of settlement at an exposed headland and sheltered bay to explore the scale of dispersal of chthamalid barnacle larvae in two species differentially distributed with respect to exposure. He showed that patterns in larval distribution set when larvae were released (namely domination of C. montagui in shelter and C. stellatus in exposure, respectively) were lost when larvae were ready to settle, demonstrating a lack of local larval retention close to the release site. Enclosed waters with strong nutrient inputs from freshwater run-off are also much more productive. The Firth of Clyde is an example of an area with strong larval retention and highly productive nutrient-rich water. Very high barnacle settlement has been reported here (Connell, 1961a; Hills and Thomason, 2003) compared to other areas (Hawkins and Hartnoll, 1982b; Burrows et al., 2010). This strong
recruitment in part explains the very clear-cut effect of competition setting the distribution patterns of barnacles, with *C. stellatus* (now known to be *C. montagui*) being outcompeted by densely settling *S. balanoides* (Connell, 1961b). The degree of coastal openness and regional variation in productivity (which at least in part is related to coastal topography) also influences barnacle larval nutritional reserves, or ‘larval quality’ (Giménez et al., 2017) with potential knock-on consequences for population- and community-level processes (Giménez and Jenkins, 2013; Torres et al., 2016).

Although studied much less, there is evidence that *S. alveolata* does well in large bays and inlets (Solway Firth, Liverpool Bay, Cardigan Bay, Bristol Channel, Baie de Mont St Michel, Rade de Brest) where both sediment supply is high and larvae are retained (Dubois, 2002, 2006; Firth et al., 2015).

Conversely, recruitment of species with planktonic larvae can often be low on isolated islands such as Rockall (Crisp, 1956; Johannesson, 1988), Lundy (Hawkins and Hiscock, 1983), the Scilly Isles (Crisp and Southward, 1958) and the Isle of Man (Hawkins and Hartnoll, 1982a; Jenkinds et al., 2000). On Anglesey (Bennell, 1981; Hyder et al., 1998; Jenkins et al., 2008b) there are very sharp differences in recruitment on different sides of the island, with recruitment being particularly high in the Menai Strait and the south-west of the island. On the Isle of Man, recruitment of barnacles is higher on the west coast than the east coast due to wind-driven processes (Hawkins and Hartnoll, 1982a). There is also an area of exceedingly dense recruitment of *L. littorea* on the west coast opposite a stratified patch of water compared to elsewhere on the island (Norton et al., 1990).

Headlands can be important boundary areas influencing connectivity, often being the proximate cause of biogeographic range limits (Crisp and Southward, 1958; Herbert et al., 2009). In recent years, the poleward spread of the leading range edge of Lusitanian species has been shown to be strongly modulated by the interaction of length of larval life and behaviour with nearshore hydrography (e.g., Keith et al., 2011 in the English Channel) with differential capability for spread being exhibited by different species (Mieszkowska et al., 2006; Hawkins et al., 2008, 2009). The Llyn Peninsula in North Wales has been a barrier for recolonisation by *P. lineatus* (Mieszkowska et al., 2007) and *P. depressa* following contraction during the cold spell of the 1960s to 1980s (Hawkins et al., 2008, 2009).

### 2.8 Non-native Invasive Species

The main non-native species found in high abundance in the rocky intertidal in the region are the seaweeds *Sargassum muticum* and *Undaria pinnatifida* (also found in the subtidal), the Australasian barnacle *Austrominius modestus* (formerly *Elminius*) and the Pacific oyster *Magallana gigas* (formerly known as *Crassostrea gigas*).

The Australasian barnacle, *A. modestus*, has been in Europe since the 1940s, first being recorded in the British Isles and subsequently spreading both northwards (Crisp, 1958) and southwards (Barnes and Barnes, 1963) in Europe. It is found primarily in estuaries, rias, harbours and sheltered bays (King et al., 1997; Lawson et al., 2004), settling on both natural and on temporary and artificial habitats, becoming less common on more exposed shores (Crisp, 1958). At a mesoscale it is particularly common on the coasts of the eastern English Channel, southern North Sea, the Irish Sea (Herbert et al., 2007) and the Bay of Saint Malo (O’Riordan and Ramsay, 1999). It is a multi-brooding species (O’Riordan and Murphy, 2000); thus, it is able to colonise free space made available by artificial structures (Bracewell et al., 2012), disturbance (Bracewell et al., 2013), predation by *N. lapillus* on the native species such as *S. balanoides* (Barnett, 1979) or intense intraspecific competition leading to hummocking and sloughing off *S. balanoides* (Barnes and Powell, 1950). Surprisingly few controlled experiments have been undertaken on interactions with other species. Observations in the North Sea suggest that recent expansion of *A. modestus* (potentially as a consequence of warming seas) has come at the expense of the native barnacles *S. balanoides* and *Balanus crenatus* (Witte et al., 2010), although experimental...
manipulations by Gallagher et al. (2016) in Ireland suggest *A. modestus* coexists without displacement of other intertidal species.

*S. muticum* invaded Europe in the 1970s (Critchley et al., 1983), spreading southwards and northwards from its point of introduction in France (Rueness, 1989). It can occur in the shallow subtidal zone as well as occupying rock pools (often as epibionts on the shells of limpets) on sheltered to moderately exposed shores. It is a highly seasonal species, overwintering in Europe as short shoots from which it proliferates to form dense canopies up to 100 per cent cover in rock pools during spring and summer, before dying back in the autumn (Engelen et al., 2015). Experimental manipulations in northern Spain have shown limited impacts on the native communities (Viejo, 1997), perhaps because of its autumn–winter dieback. In two out of three sites where *S. muticum* was experimentally removed, large leathery species (such as canopy-forming *B. bifurcata*) and total cover algae (excluding crusts and *S. muticum*) became more common (Olabarria et al., 2009). Functional impacts of this species have rarely been assessed (but see Vaz-Pinto et al., 2014; Vye et al., 2014). A recent experimental study in rock pools found that, even in the absence of large structural impacts associated with the invasion of *S. muticum*, the assemblages initially seeded with *S. muticum* presented higher rates of productivity and higher photosynthetic efficiency compared to non-invaded assemblages (Rodil et al., 2015a, 2015b; Vieira et al., 2017).

The invasive brown alga *U. pinnatifida* was first introduced in 1971 via accidental import with shellfish into French Mediterranean coastlines (Perez et al., 1981; Floc’h et al., 1991), followed by intentional introductions for mariculture into Brittany in 1981 (Perez et al., 1981). Across the north-east Atlantic, secondary spread is thought to have been facilitated by fouling on recreational and commercial vessels and transport to nearby locations (Lejart and Hily, 2005, 2011) where it can form a dense zone on the midshore of more sheltered shores and harbour walls, especially adjacent to oyster culture. There is no such native analogue in Europe, as the European oyster is particularly dense in more sheltered and embayed locations (Lejart and Hily, 2005, 2011) where it can form a dense zone on the midshore of more sheltered shores and harbour walls, especially adjacent to oyster culture. There is no such native analogue in Europe, as the European oyster is primarily a subtidal species, occasionally being found in the low-intertidal zone. *M. gigas* can form dense reefs on top of sedimentary habitats in estuaries and bays (Lejart and Hily, 2005, 2011; Smaal et al., 2008; Herbert et al., 2016; Holm et al., 2016) displacing *Mytilus* spp. beds (Diederich, 2005; Fey et al., 2010; Holm et al., 2016). Again, surprisingly little work has been done on experimentally removing these oysters to test effects, but warming seas and dense source
populations suggest expansion from frontier populations will continue at a rapid pace (Robins et al., 2017).

2.9 Biodiversity and Ecosystem Functioning

Considerable progress has been made in the study of biofilms (see Hill and Hawkins, 1991; Thompson et al., 1996 for methodological advances) since the late 1980s, including spatial and temporal patterns and ingestion by grazers (Hill and Hawkins, 1990), interaction with grazers (Hill and Hawkins, 1991; Jenkins and Hartnoll, 2001) and canopy-forming algae (Thompson et al., 2005), and providing cues for settling barnacles (Thompson et al., 1998). Their role in food provision for grazing gastropods (Thompson et al., 2000) and competition between grazers for microbial food has also been investigated (Boaventura et al., 2002b, 2003). Davies et al. (1992) showed that limpet mucus might also enhance available food as sedimenting phytoplankton would stick to mucus. This helped explain the greater diversity of diatoms in limpet guts than on rock chips viewed by scanning electron microscopy (Hill and Hawkins, 1991). Biofilms are energy rich (Davies et al., 1990; Davies and Blackwell, 2007), representing an important resource for grazers, and are likely to be formed at least in part through the movement of mucus trail-laying molluscs (Ng et al., 2013). The interactions between mucus-dominated biofilms and biotic processes such as settlement are poorly understood in the north-east Atlantic, although research elsewhere suggests significant activity (e.g., Johnson and Strathmann, 1989).

In an intensive experiment, Thompson et al. (2004) teased out the respective roles of bottom-up forcing by light and nutrients, and aphotic top–down control by limpet grazing in determining seasonal patterns of abundance of the photosynthetic component of biofilms. They emphasised the importance of ‘lateral modification’ by stressors in affecting total biomass and the relative importance of diatoms (dominating in late winter/early spring) and more tolerant cyanobacteria (dominating in the summer). This also showed the importance of grazing in controlling recruitment of fucoid germlings. A combination of grazing and desiccation stress may account for seasonal patterns of biofilm biomass throughout Europe (Thompson et al., 2000; Jenkins et al., 2001; Skov et al., 2010).

Rocky shore species and assemblages in the north-east Atlantic have been used as test systems to understand the relationship between biodiversity and ecosystem functioning in both field experiments (O’Connor and Crowe, 2005; Griffin et al., 2010) and laboratory mesocosms (Griffin et al., 2008, 2009; Russell et al., 2013). O’Connor and Crowe (2005) investigated the influence of diversity in an assemblage of three species of grazing gastropods (P. ulyssiponensis, L. littorea and S. umbilicalis) on productivity in shallow rock pools using algal biomass as a proxy. They showed strong idiosyncratic effects on algal biomass and productivity from removal of P. ulyssiponensis, known to be an important grazer in the region from previous experimental work (e.g., Boaventura et al., 2002a). Thus, identity of species was considered to be a primary factor influencing ecosystem functioning. Griffin et al. (2010) extended this work in rock pools denuded of all biota using the same three species of grazer to explore the influence of diversity during early succession. P. ulyssiponensis had the strongest effect in reducing algal growth, with little evidence of the influence of grazer diversity on algal biomass, diversity (both richness and evenness) and gross primary production. Griffin et al. (2009), however, showed in laboratory mesocosms an interaction between micro-habitat heterogeneity and grazer diversity on consumption of primary producers using three different species of grazer (P. vulgata, L. littorea and S. umbilicalis). On homogeneous substrata species identity was important, with individual grazers performing best on different preferred habitat types where they are more abundant. In heterogeneous habitats optimal conditions were present for all three species enabling spatial complementarity of feeding and the highest algal consumption rates by mixed assemblages.

At higher trophic levels, Griffin et al. (2008) explored the interaction between density and
diversity of predatory crabs on consumption of lower trophic levels (grazers and space-occupying suspension feeders) in laboratory mesocosms. The effects of diversity were only apparent at high densities, with prey consumption by mixed assemblages of predators being double that of single species, reflecting functional niche differentiation between species. Arenas et al. (2009) examined the relationships between biomass, species richness, spatial aggregation and evenness and the productivity of natural macroalgal assemblages. They found the expected positive relationship between biomass and species richness. Additionally, results showed relationships between both spatial aggregation and evenness and some of the productivity-related variables analysed: assemblages with a higher degree of spatial aggregation had reduced light capture and photosynthetic efficiency, while increasing evenness increased maximum net primary productivity. Similar results were found by Rodriguez et al. (2016) with synthetic macroalgal communities. Prestes et al. (2017) highlighted the importance of species differentiation among algal species in their responses to environmental heterogeneity, thereby ensuring stability of standing stock of primary producers.

2.10 Progress and Knowledge Gaps

Since the 1990s (Hawkins et al., 1992) much progress has been made, especially in terms of geographical coverage. A field experimental approach has now spread throughout Europe, including work in Portugal, Spain, France, Ireland, the UK and Scandinavian countries, giving an increased understanding of interactions between species. Due to missionary work on experimental design by Underwood and Chapman through successive training courses and workshops, most work is now well designed and amenable to statistical analysis. Planned research over large scales testing the same hypotheses, using nested experimental or survey designs is still comparatively rare and difficult to fund (but see outputs from EUROROCK). It is hoped that this will not become even more difficult for UK scientists post-Brexit (Hawkins, 2017). The recent fashion for large-scale macro-ecological analyses of publicly available data or meta-analysis of published work, while contributing to high-profile papers and giving much insight (e.g., Burrows et al., 2011; Sunday et al., 2011, 2012; Poloczanska et al., 2013) has not encouraged small-scale in situ experimentation which is now viewed by some as rather old-fashioned. The way forward is to combine approaches and tools giving a broadscale perspective on patterns (such as remote sensing and macro-ecology) with regionally nested smaller-scale experiments on processes. The importance of the temporal as well as spatial scale of such experiments has also recently been highlighted (Jenkins and Uyà, 2016). Review of the literature has shown no change in the median duration of observation following experimental manipulation over the past three to four decades despite clear benefits from such an approach. Experimental work also needs to be set in a phylogeographic context to understand the origins and direction of movement of species, following deglaciation and more recent anthropogenic-driven climate change. Long-term and broadscale ecological data are also crucial to disentangle local and regional stressors from global change (Hawkins et al., 2008, 2009, 2013, 2017; Mieszkowska et al., 2014b) and to understand how interactions may be altered in a rapidly changing part of the ocean (Burrows et al., 2011; Mieskowska and Sugden, 2016). Thus, there should still be a place for local experimentation, hopefully given elegance by insights from natural history (Hawkins et al., 2016b).

Techniques such as stable isotope analysis have been increasingly applied to rocky shores in the region (Dubois et al., 2007a, 2007b, 2007c; Lefebvre et al., 2009; Notman et al., 2016), giving insights into trophic interactions, especially the role of detritus. The consequences of changes in community structure for ecosystem functioning also need to be explored by measuring processes such as primary and secondary production, remineralisation, the fate of detritus and the role of import of pelagic productivity. Is any carbon produced in rocky coastal ecosystems sequestered in the long-term or does it just get stored in the short to medium term?
Recent work on micro-habitat modification of physical factors and consequences of microclimate for organisms at the individual level (Seabra et al., 2011; Lima et al., 2016) have major implications for understanding refugia from climate change-induced stress, as well as modification of outcomes of interactions and emerging community structure and functioning (Firth et al., 2016b). Some of these interactions will be modulated by the topographic template of the shore (Firth et al., 2016a); others will be modified by habitat-forming species (Moore et al., 2007; Marzinelli et al., 2012; Pocklington et al., 2017). In contrast, proliferating artificial structures, which often tend to have steeper gradients and less topographic complexity, will provide scant refuge from climate change (Chapman and Underwood, 2011; Firth et al., 2014a, 2014b, 2016a, 2016c), although porous structures do provide refuges (Sherrard et al., 2016).

The role of mobile predators, whether from on land (mainly birds) (Coleman et al., 1999, 2003; Kendall et al., 2004) or from the sea (fish, crabs, octopuses), must also not be ignored even though these are less tractable than sedentary invertebrates to experimentally manipulate. Recent work (Silva et al., 2008, 2010, 2014) has shown the important role crabs play in intertidal systems. With warming climate, herbivorous fish are likely to become much more important, especially in the south of the region (North Africa and Iberia) (Vergés et al., 2014; Franco et al., 2015; Gianni et al., 2017).

Despite the long history of both observational and experimental research in the region, host–parasite dynamics have been largely understudied. Some work has been done on species of commercial interest that are also found on rocky shores (e.g., the native oyster Ostrea edulis, Culloty et al., 1999, 2001, 2004 and the non-native oyster M. gigas, Holmes and Minchin, 1995), with comparatively little done on other species (but see James, 1968; Carrol et al., 1990; Elner and Raffaelli, 1980; Davies and Knowles, 2001; Powell and Rowley, 2008). Perhaps one of the best-studied systems is that of the trematode parasite Echinostephilla patellae (Lebour, 1911), which infects limpets and mussels as primary and secondary hosts and oystercatchers (Haematopus ostralegus) as definitive hosts (Kollien, 1996; Prinz et al., 2010a). Environmental factors affect the distribution and abundance of E. patellae, with a direct relationship between infection rates and increasing temperatures (Prinz et al., 2010b, 2011). Furthermore, prevalence in limpets appears to be higher in rock pools than emergent rock (Crewe, 1951; Thomas, 1965; Copeland et al., 1987, but see Kollien, 1996; Firth et al., 2017 for the opposite pattern) and is related to bird density and proximity to harbours (Copeland et al., 1987). More experimental work is required on host–parasite dynamics on rocky shores in the north-east Atlantic.

### 2.11 Overview and Synthesis

The north-east Atlantic region is an area where clades originating in the north Pacific (fucoids, balanoids, littorinids, thaids, laminarians) collide with clades from further south in the Atlantic (e.g., patellids, trochids, chthamalids). At high latitudes in the north, seaweeds dominate the midshore zone of all but the most exposed shores. Further south, midshore space-occupying invertebrates (mussels and barnacles) win, facilitated by grazing by patellid limpets that controls algal recruitment; propagule pressure is much less as fucoids become rarer, and juvenile growth is slower due to environmental stress, thereby reducing the probability of escapes from grazing (Figure 2.4) (Ferreira et al., 2014, 2015a, 2015b). Low on the shore seaweeds dominate space by forming algal turfs or kelp or fucoid canopies. These algae outpace the ability of grazing limpets to control them in the low-intertidal zone. L. digitata canopies can lead to rock covered by encrusting algae and sponges, facilitating limpets. If canopy is removed, then colonising ephemeral algae and turf-forming algae swamp the limpets. There is usually too much water movement immediately either side of low water for effective foraging by sea urchins. Psammechinus miliaris and Echinus esculentus only appear in the subtidal, and Paracentrotus lividus is confined to refuges in burrows relying mainly on the drift of food (Benedetti-Cecchi and Cinelli, 1995;
Boudouresque and Verlaque, 2007; Jacinto and Cruz, 2012).

High on the shore, physical factors dominate. At high latitudes in the north of the Atlantic, ephemeral algae are present all year round. Further south they are only present in the winter, dying-off in the summer. Grazing has limited effects, only occurring around refuges that littorinids maintain (Stafford and Davies, 2005; Skov et al., 2010, 2011).

Patterns are also strongly modified by mesoscale processes driven by upwelling that influences nutrient and larval supply (North Africa, Iberia) and coastal configuration, where embayed versus headlands also strongly influence larval supply (France northwards). In high-recruitment areas, interactions can be intense between space-occupying species, also driving predator abundance (e.g., dog whelks). Connell’s (1961a) classic paper on competition was possible on the Isle of Cumbrae because space was almost saturated; elsewhere lower larval supply would have created less intense interactions, as shown by Gordon and Knights (2017) in Plymouth.

The north-east Atlantic has faster rates of warming than any other ocean, although the region south of Greenland and Iceland is undergoing cooling due to a climate-driven slowdown in the Atlantic meridional overturning circulation, causing a weakening in the Gulf Stream (Rahmstorf et al., 2015).

Species are responding to rapid alterations in the marine climate by adapting or exhibiting range shifts, or by becoming locally extinct. There is a high degree of spatial and temporal heterogeneity in the resultant impacts on marine communities due to the idiosyncratic responses of individual species. Warming seas have resulted in biogeographic range shifts of intertidal and subtidal species in coastal waters of the north-east Atlantic. The leading range edges of Lusitanian species are expanding, while the trailing edges of boreal species are retracting to higher latitudes, but with some cold-water species showing surprising resilience (Southward et al., 1995; Mieszkowska et al., 2006, 2014b; Lima et al., 2007; Hawkins et al., 2008, 2009; Wethey and Woodin, 2008; Mieszkowska and Sugden, 2016). In addition to changes in the distribution of species, community structure is also altering as species dominance and interactions change (Poloczanska et al., 2008; Hawkins et al., 2008, 2009; Mieszkowska et al., 2014b).

In a warming world the midshore of France and the British Isles are likely to show much less cover by large canopy-forming fucoids as harsher warmer, drier and stormier conditions coupled with increased grazing pressure from more grazing species reduces the probability of fucoids recruiting to form adult populations. Lowshore kelp forests will likely change with less L. digitata and A. esculenta and more S. polyschides. The late autumn to early spring window of dense ephemeral algal growth high on the shore (Hawkins and Hartnoll, 1983a) will also constrict, except in the north and in extreme exposure. These changes will have consequences for biodiversity (Thompson et al., 1996; Smale et al., 2013; Teagle et al., 2017) and productivity (Hawkins et al., 1992) – particularly the decrease in export of algal detritus (Notman et al., 2016). More shores will become dominated by suspension-feeding barnacles and mussels. Thus, there will be switches on many mid-latitude shores as many become net importers rather than exporters of energy (Hawkins et al., 2008, 2009).

Dedication

This chapter is dedicated to pioneering giants of rocky shore research in the north-east: Edouard Fischer-Piette, Harry Hatton, Norman Jones, Dennis Crisp, Alan Southward and Jack Lewis. Most of the authors derive directly or indirectly from the J. H. Orton clade originating at the Marine Biological Association, Plymouth, and the Marine Biological Station, Port Erin.

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