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Rocky shores as tractable test systems for experimental ecology

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Abstract

Rocky shore ecology has been studied for a long time, starting with qualitative descriptions and becoming more quantitative and experimental over time. Some of the earliest manipulative experimental ecological studies were undertaken on rocky shores. Many, over time, have made considerable contributions to ecological theory, especially highlighting the importance of biological interactions at the community level. The suitability of rocky shores as convenient test systems for ecological experimentation is outlined. Here we consider contributions from rocky shores to the emerging concepts of supply-side ecology, the roles of competition, predation and grazing, disturbance and succession and positive interactions in structuring communities along environmental gradients. We then address alternative stable states, relationships between biodiversity and ecosystem functioning, and bottom-up and top-down control of ecosystems. We briefly consider the feedback and synergies between ecological concepts and experimental work on rocky shores, whilst still emphasizing the traditional values of marine natural history upheld in JMBA since its first publication. The importance of rigorous experimental designs championed by Underwood and co-workers is emphasized. Recent progress taking advantage of new technologies and emerging approaches is considered. We illustrate how experimental studies have shown the importance of biological interactions in modulating species and assemblage-level responses to climate change and informed conservation and management of coastal ecosystems.

Introduction

The intertidal zone has long been an entrance and window on the ocean: people have foraged for food since pre-history (Thompson *et al.*, 2002); pioneering studies were made by the first generations of modern naturalists (Audouin & Edwards, 1833; Darwin, 1854); and it was the playground for the early eco-tourists of the Victorian era (Gosse, 1856; Kingsley, 1859; Hawkins *et al.*, 2007). Early marine biologists used the seashore for collecting specimens for taxonomic, morphological, developmental, physiological and behavioural research (Hawkins *et al.*, 2016). Here we review the contribution that experimental studies on rocky shores have made to more general ecological concepts and theory.

Formal ecological studies on rocky shores stretch back at least 200 years with Audouin & Edwards (1833) describing zonation patterns on the rocky shores of northern France. There then followed a long period of qualitative description and classification of broad patterns of distribution of conspicuous organisms on rocky shores. How zonation patterns were shaped by tidal height and wave exposure locally and how these differed geographically, culminated in the work of Stephenson & Stephenson (1949, 1972), who proposed a universal scheme of zonation. Similar work, often by their many disciples, led to descriptions of zonation patterns worldwide, sometimes using versions of their three-zone scheme (e.g. Dakin, 1953, in Australia; Morton & Miller, 1968, in New Zealand; Lewis, 1964, in the British Isles and Ireland; Morton & Morton, 1983, in Hong Kong; Morton *et al.*, 1998, in the Azores) or developing new schemes fitting local or regional contexts (e.g. Ricketts & Calvin, 1968, on the Pacific Coast of America; Branch & Branch, 1981, 1986, in South Africa, updated in Branch and Branch, 2018; see Raffaelli and Hawkins, 1996, for review of classical descriptive zonation schemes worldwide). T.A. Stephenson was a superb artist, as were many of his later emulators, although as colour photography emerged this aided description (see plates in Lewis, 1964). Many caveats arose for such qualitative classifications, especially on the seaweed-dominated sheltered shores of the North Atlantic (see Lewis, 1964 and Lewis's chapter in Stephenson & Stephenson, 1972). Subsequently, Hawkins & Hartnoll (1983*a*), from the basis of largely experimental studies, provided a possible explanation of the causes of the three-zone system on non-sheltered north-east Atlantic shores.

Qualitative studies gave way to more quantitative descriptions of distribution patterns, with precise levelling of intertidal elevation and counts made in quadrats (Southward & Orton, 1954), or using semi-quantitative abundance scales (Moyse & Nelson-Smith, 1963). Colman (1933), publishing in the *Journal of the Marine Biological Association of the United Kingdom* (JMBA), related the limits of individual species to critical tidal levels on the shore (see also Doty, 1946; Evans, 1947). Colman's work was later revisited and statistically refuted by Underwood (1978). The phytosociological approach of the Zurich–Montpelier school was deployed to describe algal associations primarily in the Mediterranean Sea (above and below the water line; for examples see Boudouresque, 1971; Coppejans, 1980). Phytosociology was also used by Russell (1972, 1973) along with some early multivariate classification analysis to describe zonation patterns in the Irish Sea.

In parallel to descriptions, laboratory experiments were used to explore differential tolerances of species of algae (Baker, 1909, 1910) and invertebrates (Broekhuysen, 1940; Foster, 1971) from different tidal heights. Higher zoned organisms were shown to be more tolerant to desiccation and temperature extremes than those lower on the shore. Wolcott (1973) showed convincingly for mobile animals that whilst tolerance limits broadly matched zonation position, most limpet species stayed well within their tolerance limits, except for those bordering unexploited resources high on the shore; these took risks and got caught out when conditions changed. Experiments in the laboratory and on artificial panels on rafts, as well as on the shore, explored selective larval settlement behaviour. Barnacles and spirorbids were investigated by Knight-Jones (1951, 1953), then taken on by Crisp and colleagues (Crisp & Knight-Jones, 1953; Crisp & Barnes, 1954), initially at Menai Bridge in North Wales and then further afield in Britain (e.g. Millport, Barnes, 1956) and around the world (e.g. at Beaufort, North Carolina, Rittschof *et al.*, 1984), mostly on barnacles related to fouling.

The first experiments in the field probably started in north-west France before the First World War (Hariot, 1909). Fischer-Piette and Hatton examined many aspects of biological interactions from the 1920s onwards at the Dinard Laboratory of the Paris Natural History Museum, using what would be recognized now as controlled field experiments (Hatton & Fischer-Piette, 1932; Hatton, 1938). Post-war and encouraged by Orton, such approaches were taken up by Jones (1946, 1948), Lodge (1948), Burrows & Lodge (1951) and Southward (1956) at Port Erin, Isle of Man exploring the role of limpet grazing – although visibility of such work was not helped by publication in largely parochial journals (see Southward, 1964 for summary). Connell (1961*a*, 1961*b*) experimented on the shore at Millport in the early 1950s and subsequently took this approach back to California. Perhaps prompted by Renouf & Rees (1932), Kitching, Ebling and colleagues and students used Lough Hyne in south-west Ireland as a model experimental system starting in the 1950s (Kitching *et al.*, 1959; Kitching & Ebling, 1961; Ebling *et al.*, 1962). Some early work was also done in South Africa (Broekhuysen, 1940) and Australia (Guiler, 1954; May *et al.*, 1970). Paine started his experimental work in the early 1960s on the North-west Pacific Coast of the USA (Paine, 1966; Paine & Vadas, 1969) and elsewhere (New Zealand, Paine, 1971; Chile, Paine *et al.*, 1985; summarized in Paine, 1994). Such manipulative approaches expanded rapidly from the 1970s onwards, by the first students of Paine (Dayton, 1971, 1975; Menge, 1976, 1983; Vadas *et al.*, 1990, 1994) and Connell (Choat, 1977; Sousa, 1979*a*, 1979*b*) and in turn their numerous subsequent students, mentees and admirers (Lubchenco, 1978, 1980, 1983; Lubchenco & Menge, 1978; Gaines *et al.*, 1985) around the world. This led to significant early contributions in the southern hemisphere in Chile (Moreno & Jaramillo, 1983; Paine *et al.*, 1985; Castilla & Paine, 1987; including the classic papers on excluding humans collecting seaweeds and invertebrates by Castilla and co-workers, Castilla & Duran, 1985; Castilla & Bustamante, 1989), New Zealand (Luckens, 1970, 1975*a*, 1975*b*) and Southern Africa (Branch, 1975, 1976). Much of this work focused on the role of biological interactions among species in shaping distributions or community structure.

Following in the footsteps of Paine and Connell, much excellent work has been done since the 1970s on both coasts of North America, by Dayton, Menge, Lubchenco, Gaines, Vadas, Bertness and many others (for recent overviews see Dudgeon & Petraitis, 2019; Fenberg & Menge, 2019). This has in turn influenced work in Chile (Broitman *et al.*, 2001; Aguilera & Navarrete, 2007, 2012; Aguilera *et al.*, 2013, 2019*a*) and Argentina (Bertness *et al.*, 2006; Silliman *et al.*, 2011; Palomo *et al.*, 2019).

Underwood established a strong experimental ecology school in Sydney, Australia from the 1970s (e.g. Underwood, 1976, 1978, 1980, 1984, 1998; Underwood & Jernakoff, 1981, 1984; Underwood *et al.*, 1983) with worldwide influence. He emphasized the importance of hypotheses tested using well-designed experiments and rigorous statistical analyses – any experiments done should be done properly (Underwood, 1981, 1985, 1986, 1988, 1991*a*, 1992*a*). His approach was enthusiastically embraced by his numerous students (earlier ones including Creese & Underwood, 1982; Chapman, 1986; Fairweather, 1988; Chapman & Underwood, 1992), post-docs, visiting fellows, and a like-minded international network (e.g. Benedetti-Cecchi, A.R.O. Chapman, Coleman, Aberg, Pavia, Petraitis, Vadas).

Thus experimental studies on rocky shores had become mainstream from the 1980s – with several subsequent generations of students and post-docs worldwide (see reviews in John *et al.*, 1992; Bertness *et al.*, 2001, 2014; Hawkins *et al.*, 2019*a*, 2019*b*, 2019*c*). In New Zealand, Choat brought back insights from his time with Connell in California (Choat, 1977) and was an early champion of experimental approaches. Subsequently, Schiel has combined insight into the natural history of systems with rigorous experimental approaches (Schiel *et al.*, 2019*a*). In South Africa, Branch, McQuaid and students built on the classical work by the Stephensons to better understand, through experimentation, underlying processes (McQuaid & Blamey, 2019). Experimental approaches have also prospered in Hong Kong and beyond in greater China (Williams *et al.*, 2019).

The viewpoint of intertidal experimental ecology presented here started in the Isle of Man in the mid-1970s when the lead author (SJH) was prompted by Hartnoll to revisit the experimental work done by Jones, Lodge, Burrows and Southward in the late 1940s and 1950s. At the time key influences were the emerging experimental work by Paine, Connell, Menge and Lubchenco as well as the work by Southward at the Marine Biological Association (on long-term climate fluctuations and recruitment, Southward, 1963, 1967; recovery from oil-spills, Southward & Southward, 1978; plus Lewis, 1964, and colleagues at Robin Hoods Bay on the role of recruitment processes on rocky shores and environmental monitoring, Lewis, 1976; Lewis & Bowman, 1975; Bowman & Lewis, 1977). Another influence was Norton at Glasgow, a former student of Burrows, who had also commenced experimental work on fucoid distributions on the shore at Millport (e.g. Schonbeck & Norton, 1978, 1980*a*). SJH with subsequent students, many of whom have become colleagues (including two co-authors on this paper) continued the tradition at Port Erin, on the Isle of Man with further experiments (e.g. Jenkins *et al.*, 1999*a*, 1999*b*, 1999*c*, 2005; Thompson *et al.*, 2004 jointly working with Hartnoll and Norton), extending into spatial statistics (Johnson *et al.*, 1997) and modelling (Burrows &

Hawkins, 1998; Hyder *et al.*, 1998; Johnson *et al.*, 1998*a*, 1998*b*, 1998*c*). This has been aided by a wider network of colleagues in Europe (including an Italian co-author first met at a conference in Liverpool on plant–animal interactions in 1990), all interested in experimental ecology, and able to work together within European-funded projects and networks. This network of collaborators has been profoundly influenced by the Underwoodian approach to experimental ecology, promulgated by numerous training workshops by Underwood and Chapman and their advisory work on European projects such as EUROROCK.

Underwood *et al.* (2000) succinctly define and discuss different approaches to describing pattern in ecology, advocating the importance of logical and structured quantitative observations or surveys testing hypotheses about pattern, so-called mensurative experiments, as the essential basis upon which experimental studies of process can proceed. Such studies have advanced understanding of rocky shore ecology, and are often a stand-alone precursor (Menconi *et al.*, 1999; Benedetti-Cecchi *et al.*, 2000; Jenkins *et al.*, 2000; Johnson *et al.*, 2003; Martins *et al.*, 2007, 2008) or a component of wider manipulative studies (Sousa, 1979*a*; Thompson *et al.*, 2004) generating hypotheses or informing modelling approaches (Hyder *et al.*, 1998, 2001; Svensson *et al.*, 2005). We have not, however, extensively considered them here, other than in the context of supply-side ecology where experimental manipulations are less feasible.

Here we focus on the use of rocky seashores as a convenient tractable system for manipulative field experiments on processes that have contributed to ecological concepts and theory. Firstly, we outline the reasons why the shore is so amenable to descriptive and experimental research. Next, we summarize the contributions that manipulative experimental intertidal ecological studies have made to general ecological theory at population, community and ecosystem levels. We then discuss the intertwining of theory and experiment, the importance of advances in methodology in developing the field and the opportunities arising from such new technologies and approaches. We conclude by considering how experimental approaches have helped understand the role of biological interactions in responses of marine life to anthropogenic climate change as well as informing environmentally sensitive adaptation by society to climate-driven rising seas in the context of widespread coastal urbanization. We stress this is a selective and personal view of the topic – not an exhaustive review. We focus mainly on the seashore but occasionally stray into the shallow sub-tidal zone, especially in the virtually tide-less Mediterranean. Furthermore, we have highlighted work done in Britain and Ireland plus neighbouring north-east Atlantic and Mediterranean countries – the traditional hinterland of JMBA. This work has led to the shores of the north-east Atlantic being some of the most studied in the world (Hawkins *et al.*, 2019*b*), with much recent progress in the Mediterranean (Benedetti-Cecchi *et al.*, 2019).

The seashore as a tractable system

Paine (1966, 1969, 1971, 1974) and Connell (1961*a*, 1961*b*, 1972) as pioneers of experimental ecology have espoused the values of manipulative field experiments (Connell, 1974; Paine, 1994) and the appropriateness of the seashore as a test system (see also Menge & Branch, 2001). As Connell (1974) neatly summarized: in a laboratory experiment all conditions are held constant other than those being tested; in contrast, in a field experiment all the variables are allowed to vary, presumably the same way in adjacent similar treatment and control plots, other than those being manipulated (often one or two, rarely more at the time of his writing, but more complex designs are now more commonplace). The seashore has a sharp vertical environmental stress gradient from low water to beyond the influence of sea spray. This gradient is largely unidirectional, increasing up shore for the majority of organisms on rocky shores that have marine evolutionary affinities. For the few organisms of terrestrial origins, the stress gradient is reversed (Raffaelli & Hawkins, 1996). The environmental extremes encountered over the short, sharp intertidal gradient are experienced over much larger distances in other systems. For example, moving a few metres up a rocky shore from low water can be the equivalent of ascending a 3000 m mountain in terrestrial systems. There is a horizontal wave action or exposure gradient between sheltered bays and exposed headlands. This is not unidirectional and many species have optima at intermediate points between the two extremes (Raffaelli & Hawkins, 1996). These sharp gradients are locally modified by the topography of the shore with rockpools, cracks and crevices plus shaded and unshaded areas reflecting geomorphologically generated habitat complexity (Johnson *et al.*, 2003). This variety of environmental conditions in close proximity has made transplant experiments (with appropriate controls) a powerful tool in understanding the direct and indirect influences of the environment on the distribution, abundance, growth and survival of species (e.g. Schonbeck & Norton, 1978, 1980*a*). The modulation of the intensity of biological interactions by the physical environment can also be explored along these sharp local gradients (Bertness & Leonard, 1997), and amongst local mosaics of micro-habitats (Johnson *et al.*, 1998*b*, 2005).

The nature of rocky intertidal organisms also makes them amenable to manipulation. Most intertidal organisms are reasonably sized with the biggest algae being at most 2–3 m in length. Few animals are bigger than 30 cm and most are less than 10 cm. Most of the suspension feeders are sessile, and many of the grazers and predators are reasonably slow-moving and sedentary enabling removal and exclusion experiments. Work over the last 20 years, however, has emphasized the importance of mobile predators such as foraging by crabs (Silva *et al.*, 2008, 2010, 2014; Christofoletti *et al.*, 2011) and fish (Taylor & Schiel, 2010) when the tide is in, and birds when the tide is out (Hockey & Underhill, 1984; Coleman *et al.*, 1999; Coleman & Hockey, 2008) or by diving (e.g. eider ducks, Hamilton *et al.*, 1999). Few of the algae and animals live more than a decade or so – although there are exceptions such as *Ascophyllum nodosum* where genetic individuals may live well over 100 years, even if individual fronds are rarely older than 10 (Åberg, 1992). The relatively low cost and easy access to rocky shores also greatly facilitates the manipulation of these organisms for experiments.

Most conspicuous sessile animals and algae compete for a clearly definable and measurable resource – two-dimensional space to live on the rocks – providing access to light for plants and particulate food for suspension-feeders. The flora and fauna growing on rocky shores can also be partitioned into layers (canopy, understorey turf, encrustations) enabling non-destructive quantification of abundance and elucidation of interaction. There are none of the invisible and complex below-ground interactions that occur in soils and sediments – although bio-erosion by burrowing endolithic cyanobacteria and invertebrates such as sea urchins and molluscs, particularly burrowing piddocks (Pinn *et al.*, 2008) can modify softer rock habitats, creating complexity. These attributes make the flora and fauna easy to quantify and manipulate, and to measure response variables primarily non-destructively. Short lifespans and rapid growth mean that clearance or removal experiments of dominant canopy-forming or rock-covering species can occur within 3–5 years – the duration of most PhDs (but see note of caution from Jenkins & Uyà (2016) and a plea for longer duration of manipulative marine studies). Some species do take longer, with maybe 20 or more years for the recovery of *A. nodosum* following canopy removal

(Jenkins *et al.*, 2004; Ingólfsson & Hawkins, 2008). Recovery times are, however, generally much swifter than in terrestrial systems where, for example, removal of trees may take hundreds of years to recover. When recovery does not occur, it can point to interesting explanations such as alternative stable states (Benedetti-Cecchi *et al.*, 2015; Petraitis & Dudgeon, 2015; Menge *et al.*, 2017).

The hard nature of rocks enables various devices such as exclusion fences or cages, settlement plates or tiles, or transplanted rocks to be attached via screws or quick-set cement or epoxy glues. Once technological constraints were overcome (e.g. early use of generators and electric-drills, Dayton 1970, or compressed air drills, Hawkins & Hartnoll, 1979), the experimental approach proliferated, particularly since the introduction of petrol-driven and cordless drills and better fast-setting underwater epoxies. Thus, grazers and predators have been excluded or enclosed at varying densities, algal canopies and understorey turfs and encrusting invertebrates removed, thinned or transplanted, and the responses of individual species or whole assemblages measured.

In most regions of the world, the taxonomy of the common and important species is well understood. Cryptic speciation can, however, cause problems (e.g. in the North Atlantic and Mediterranean: *Chthamalus stellatus*, into *C. stellatus* and *Chthamalus montagui* by Southward, 1976; *Fucus spiralis* into *F. spiralis* and *Fucus guiryi* by Zardi *et al.*, 2011). Recent developments in molecular-based genetics and taxonomy have accelerated the detection of cryptic species (Chan *et al.*, 2007, 2012). However, whilst taxonomic accuracy is essential at the population level, it is not critical for many community and ecosystem level studies. For example many community-level studies such as those making comparisons amongst biogeographic regions, usefully lump algae and sessile animal species into functional categories (canopies, turfs, encrustations, barnacles) or more nuanced functional groups (e.g. for algae, Steneck & Dethier, 1994).

Contributions to general ecology theory

All of the above attributes have earned rocky shores the label as the fruit fly of ecology (Berlow, 1997). Below we consider how experimental research on rocky shores has contributed to general ecological theory at the population and especially the community level. Studies on rocky shores have made a major contribution to emphasizing how recruitment drives populations and the consequences for communities – what has become known as supply-side ecology (Lewin, 1986). Ground-breaking experiments on the roles of biological interactions in determining distributions and shaping communities through competition, grazing and predation, disturbance and succession, plus positive interactions are then outlined before turning to alternative stable states, the relationship between biodiversity and ecosystem functioning, and the relative importance of bottom-up forcing and top-down control in ecosystems.

Supply-side ecology

The mechanisms governing the distribution and abundance of populations of marine benthic invertebrates have been much debated. The majority of invertebrates living on rocky shores exhibit a complex life cycle with a pelagic larval phase. Hence local reproduction and input of new individuals to a particular site is often decoupled leading to extensive debate regarding the importance of processes that determine input of individuals (larval transport, supply and settlement) versus processes occurring after arrival (competition, predation, disturbance, facilitation following settlement) in determining patterns of adult distribution and abundance. Much early research on rocky shores focused on the dominant role of post-settlement processes in determining observed patterns (Connell, 1961*a*, 1961*b*; Paine, 1966; Dayton, 1971; Menge & Sutherland, 1976). For example, Connell's classic work on competition in Millport, Scotland showed clearly that the distribution of *Chthamalus* spp. on the shore was determined not by the pattern of settlement but by strong interspecific competition with *Semibalanus balanoides*. Connell (1961*b*) was very aware of the existence of failure years when *S. balanoides* recruitment did not occur, indicating a role for pre-settlement processes. The importance of larval supply and settlement in determining adult distribution can be represented by the recruitment limitation hypothesis (sensu Doherty, 1981) which states that when larval supply is insufficient for the total population size to reach a carrying capacity, increases in recruitment will lead to increases in adult population size (Connell, 1985; Menge, 1991).

The supply and settlement of both invertebrate larvae (Hawkins & Hartnoll, 1982*a*; Gaines & Roughgarden, 1985; Roughgarden *et al.*, 1988; Hunt & Scheibling, 1996; Jenkins *et al.*, 2000; O'Riordan & Murphy, 2000; McQuaid & Lawrie, 2005) and algal propagules (Reed & Foster, 1984; Åberg & Pavia, 1997) varies greatly in both space and time. Observational studies that identify the scales at which variation occurs have given important insight into the mechanisms determining the distribution of larvae and ultimately supply to the shore (Gaines & Roughgarden, 1985). Small-scale local variation tends to be ubiquitous (Fraschetti *et al.*, 2005), reflecting interactions occurring at or soon after settlement although larger-scale variability is common indicating the importance of patterns in the regional larval pool (Barnes, 1956) and regional physical transport processes (Hughes *et al.*, 1999). Decades of research have demonstrated clearly that understanding of processes such as upwelling (Roughgarden *et al.*, 1988), tidal and wind-driven currents (Hawkins & Hartnoll, 1982*a*, 1982*b*; Bertness *et al.*, 1996; McQuaid & Phillips, 2000), internal waves (Shanks, 1983), surf zone barriers (Rilov *et al.*, 2008) and wave action (Pfaff *et al.*, 2011), and the way these processes interact with local and regional coastal topography (Archambault & Bourget, 1996) is required to provide predictive understanding of supply to the rocky shore. Work of Roughgarden and colleagues on the central Californian coast showed convincingly that inter-annual variability in upwelling determines patterns of recruitment across large areas (Roughgarden *et al.*, 1988; Farrell *et al.*, 1991); while further north on the coast of Washington, barnacle recruitment rates are influenced by shoreward transport of offshore plankton, in surface slicks, generated by tidally forced internal waves (Shanks, 1983, 1986; Shanks & Wright, 1986).

While physical transport processes determine the rate and timing of arrival of larvae and propagules to the shore, consideration of behaviour is paramount in determining settlement patterns (Jenkins, 2005). Some population or community models assume that settlement is a function of larval supply and the amount of free space available (Gaines *et al.*, 1985; Roughgarden *et al.*, 1985; Hyder *et al.*, 2001). However, reality may be far more complex. For example, Minchinton (1997) demonstrated that recruitment of the tubeworm *Galeolaria caespitosa* into patches of free space was related not to patch area but to patch perimeter suggesting an important role for gregarious settlement close to conspecifics. The work of Crisp and co-workers in Menai Bridge, Wales throughout the 1950s and 1960s was critical in demonstrating the complex patterns of behaviour and finely tuned discriminatory abilities of invertebrate larvae in response to biological and physical cues to ensure that settlement occurs in a habitat that is conducive to survival, growth and, ultimately, reproduction. For example, the microbiofilm coating the rocky shore is

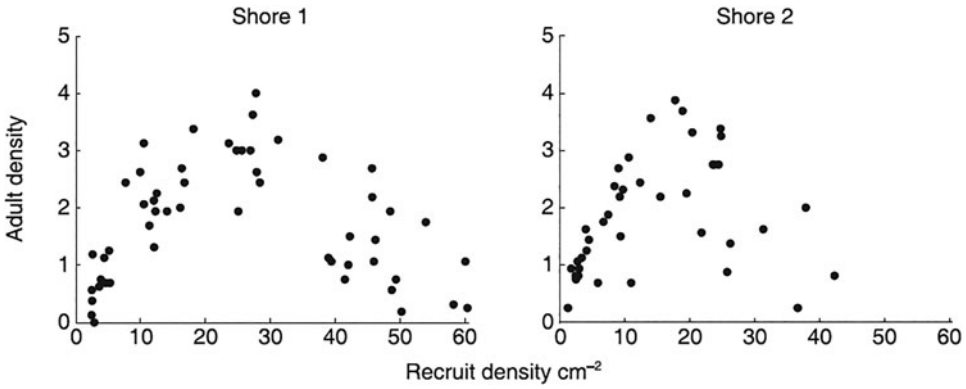

Fig. 1. The relationship between the density of manipulated recruits of *S. balanoides* in June 2002 on shores of North Wales and the density of surviving adults 2 years later. On both shores, adult density is positively related with recruitment at low densities, switching to no relationship at moderate densities and a negative relationship when recruitment is very high. From Jenkins *et al.* (2008*a*).

the point of first attachment for settling larvae and propagules. Such films have been shown to promote settlement in a range of invertebrate larvae (Todd & Keough, 1994; Qian *et al.*, 2007), with settlers responding to cues such as age of the film, specific taxa such as diatoms, and film characteristics related to tidal height (Strathmann *et al.*, 1981). Laboratory analyses of behaviour have demonstrated the discriminatory abilities of invertebrate larvae to a range of cues, but perhaps field tests of how larvae respond to multiple cues are more relevant. Thompson *et al.* (1998) showed that settling barnacle cyprids could discriminate among different microbial films in the laboratory environment, but this was irrelevant under field conditions where the presence of conspecific cues overruled cues from microbiota. Grosberg (1981) demonstrated that the larvae of species that are vulnerable to overgrowth by competitors avoid settling in the presence of a dominant space occupant, the colonial tunicate *Botryllus schlosseri*; whereas no avoidance was displayed by species that are not vulnerable. However, a contrasting response was recorded by Bullard *et al.* (2004), who failed to detect any avoidance of competitors during larval settlement.

The relevance of spatial and temporal variation in larval supply to adult populations is ultimately dictated by the fate of settlers. No matter how variable the supply of larvae to the shore, if the post-settlement process is density-dependent then the variability will be dampened out (Holm, 1990; Jenkins *et al.*, 2008*a*). New arrivals to the rocky shore are subject to radically different environmental conditions than those experienced in the pelagic larval environment, and early post-settlement mortality is high. For example, Gosselin & Qian (1997) reported levels of over 90% mortality during the juvenile period in 20 out of 30 studies reviewed on invertebrates. The same is true for algae; for example, Wright *et al.* (2004) showed that only 2 of 5395 embryos of *Fucus gardneri* survived to become visible recruits. Sources of mortality include desiccation and disturbance, both physical (Vadas *et al.*, 1990) and biological (Jenkins *et al.*, 1999*a*).

The integration of levels of larval supply, patterns of settlement and post-settlement mortality dictate the abundance and distribution of adults on rocky shores. Following much debate, based on work on rocky shores and by extensive work on coral reef fish (Doherty & Williams, 1988; Shima, 2001; Wilson & Osenberg, 2002), a general consensus was reached whereby populations may be limited by arrival of new individuals when supply and settlement is relatively low, but at high recruitment sites variability in supply and settlement has little impact on adult abundance owing to strong density-dependent post-settlement processes. This recruit-adult hypothesis (*sensu* Menge, 2000*a*) states that the relative importance of recruitment declines with increasing density of recruits (Connell, 1985; Roughgarden *et al.*, 1985; Sutherland, 1990; Menge, 2000*b*). Manipulative experimental work in North Wales on the intertidal barnacle *S. balanoides* which shows meso-scale variation in density and recruitment around Anglesey (Bennell, 1981; Hyder *et al.*, 1998), partially supports this view, but also shows that recruitment can be a useful predictor of adult density across all recruit densities, from very low to very high (Jenkins *et al.*, 2008*a*). Here the relationship between recruitment and adult density switched from positive, at low levels, to negative at high levels (Figure 1) owing to strong over-compensatory density-dependent mortality. Such considerations are clearly relevant to understand how populations are regulated. However, the supply of individuals across a range of taxa can also be used in a predictive manner to consider the structuring forces in whole communities. Consistent large-scale differences in recruitment intensity observed along the Pacific coast of North America (Connolly *et al.*, 2001) can lead to differences in the strength of interspecific interactions. Experimental determination of community organization in Oregon and Washington where recruitment is high has emphasized the role of competition and predation. In contrast, in California, where upwelling-induced larval loss from the coastline is high, the influence of settlement variation has been stressed (Connolly & Roughgarden, 1998).

The interplay of ecological theory, data collection, and modelling generated many excellent examples of early interdisciplinary research. Here, collaborations between ecologists and modellers led to significant advances in understanding of ecology, where cyclic interactions between experimental work and modelling occurred. Data were generated to understand processes that were then used to parameterize models; models highlighted data gaps and generated hypotheses for further experiments, which in turn improved models.

Mechanistic models of barnacles have successfully linked small-scale dynamics of adult benthic populations to large-scale hydrodynamic models of the larval stage (Roughgarden *et al.*, 1985, 1987, 1991; Possingham & Roughgarden, 1990; Shkedy & Roughgarden, 1997; Connolly & Roughgarden, 1998). Thus, a demographic theory for an open population with space-limited recruitment has been proposed and tested using data for the barnacle *Balanus glandula* in California (Gaines *et al.*, 1985; Gaines & Roughgarden, 1985; Roughgarden *et al.*, 1985). The model predicted cyclic fluctuations in free space at high settlement rates, but could not explain the 30-week period of these cycles (Roughgarden *et al.*, 1985), which led to further experiments and modelling to develop understanding of the system. Later models showed that at critical density of barnacles they are subject to density-dependent predation by starfish; but at low density the threshold for predation is not reached and free space is always present (Possingham *et al.*, 1994). Coupled models of oceanic processes of the larval stage and adult benthic stage were developed (Possingham & Roughgarden, 1990; Roughgarden *et al.*, 1991). Farrell *et al.* (1991) showed that the

supply of larvae was inversely proportional to the strength of upwelling and that larvae were passively transported offshore to the oceanic front. This gave rise to models where the larvae were produced and passively transported to the frontal boundary. The collapse of upwelling leads to areas of the front colliding with the shore and giving peaks of recruitment (Roughgarden *et al.*, 1991). The predictions from models coupling large-scale oceanic processes that affect the larvae with small-scale benthic dynamics have led to development of a community model for California and Oregon (Connolly & Roughgarden, 1998).

Modelling has also been used to examine the factors structuring barnacle populations across Europe (Hyder *et al.*, 1998, 2001; Svensson *et al.*, 2005). For example, Hyder *et al.* (2001) applied open models with space-limited recruitment to large-scale observations of *Chthamalus montagui* and other barnacles across Europe (Jenkins *et al.*, 2001; O'Riordan *et al.*, 2004). Modelling demonstrated differences between the processes structuring barnacle populations in the Atlantic and Mediterranean (Hyder *et al.*, 2001). The models showed the amount of free space varied within a year, but the pattern differed between sites in the Atlantic and Mediterranean (Hyder *et al.*, 2001). Modelled free space represented the balance between space-filling and space-creating processes, which may reflect differences in the timing of processes in the Atlantic (mortality due to storms and low growth in winter) and Mediterranean (mortality due to desiccation and low growth in summer) (Hyder *et al.*, 2001). Genetic differentiation has been found between Mediterranean and Atlantic *C. montagui* (Dando & Southward, 1980; Pannacciulli *et al.*, 1997), which could be driven by neutral processes resulting from hydrographic separation and/or variation in timing of selective pressures. This combination of modelling and experimental/empirical work has led to major advances in understanding of the processes driving open populations for which barnacles have proved an excellent test system.

Zonation along environmental gradients

Connell's (1961*a*) classical experiment on competition between fast-growing mid and low shore *Semibalanus balanoides* and slower-growing high shore *Chthamalus montagui* at Millport showed the importance of biological interactions along environmental gradients in setting lower limits of zonation of individual species (for similar work in New Zealand see Luckens, 1970, 1975*a*, 1975*b*). This idea was reinforced through observations of predation setting lower limits (Connell, 1961*b*, 1970; Paine, 1971, 1974; Paine *et al.*, 1985). In contrast laboratory simulations, early transplant/environment modification experiments (Luckens, 1970) and field observations of mortality at upper limits led Connell (1972) to propose that the upper limits of zonation of species were generally set by the direct effects of physical factors with lower limits being set by biological interactions. Connell's conceptual leap forward on understanding zonation patterns of species along environmental gradients was to suggest that the proximate causes of upper and lower limits had to be treated separately. Subsequent experimental removal and transplant studies, backed by realistic laboratory tolerance experiments on fucoid zonation on sheltered shores on both sides of the Atlantic, confirmed the role of physical factors setting upper limits (Schonbeck & Norton, 1978, 1979*a*, 1979*b*, 1979*c*, 1980*b*) and biological interactions, particularly competition in setting lower limits (Lubchenco, 1980; Schonbeck & Norton, 1980*a*).

Some exceptions have since emerged to Connell's synthesis. Low on the shore, upper limits were shown to be set by grazing on more wave-exposed shores (e.g. Southward & Southward, 1978; Underwood, 1980; Underwood & Jernakoff, 1981; Boaventura *et al.*, 2002*a*). On sheltered shores, competition was shown to set the upper limits of some low and mid-shore fucoids, as well as lower limits (Hawkins & Hartnoll, 1985, but see comments by Underwood, 1991*a*). *Ascophyllum* in particular was shown in removal experiments to exclude both higher shore *Fucus vesiculosus* and lower shore *Fucus serratus* from midshore plots (Jenkins *et al.*, 1999*b*, 1999*c*, 2004); this competitive ability is because it can grow large via vegetative proliferation and its longevity rather than fast early growth (Johnson *et al.*, 1998*c*). Ultimately the physical stress gradient from low shore to high shore determines survival, growth and hence competitive performance of algae and sessile invertebrate species. Proximately upper limits, especially for higher shore species, are set by physical factors and although generally lower limits are set by biological interactions, upper limits of mid and low shore species can also be set by biological interactions such as competition and grazing. There is no convincing evidence that lower limits of essentially marine organisms are set directly by too much emersion – in *Pelvetia canaliculata*, which rots when transplanted lower down the shore (Schonbeck & Norton, 1980*a*; Rugg & Norton, 1986), a pathogen has been shown to cause mortality at lower tidal levels.

Competition

Much valuable work has been done on competition amongst mobile animals, particularly grazing gastropods. Experimental designs that segregate intra- from interspecific competition are crucial when understanding interactions between species; such designs were pioneered by Underwood (e.g. 1978, 1984, 1986, 1988, 1992*a*) working with his students (e.g. Creese & Underwood, 1982; Fletcher & Creese, 1985). Intraspecific competition as expected is often more intense than interspecific competition (Creese & Underwood, 1982; Ortega, 1985; Boaventura *et al.*, 2002*b*), enabling competitively inferior species to persist, especially if they, like *Siphonaria*, have access to a resource untapped by the superior competitor such as algae growing on *Cellana* shells (Creese & Underwood, 1982; see comments in Underwood, 1992*a*, 1992*b*). Inter-age class interactions within a species can also be important, with larger animals impacting smaller size classes (e.g. Boaventura *et al.*, 2003), probably through competition for both food and space. The converse has also been found, with faster growing smaller animals outcompeting larger limpets (Marshall & Keough, 1994). Recently the potential role of competitive interactions among gastropods in limiting range expansion and hence determining range limits has been examined using scurrinid limpets in the south-east Pacific as a model system. Aguilera *et al.* (2019*b*) showed novel evidence of asymmetric competition between two congeners potentially limiting range expansion by *Scurria viridula*.

Whilst competition is clearly important there are emerging context-dependent caveats. Firstly resources, whether space or food, need to be in short supply. This can depend very much on local and mesoscale differences in larval or propagule supply discussed above. Competitive outcomes can also be modified by both fluctuating environmental conditions and recruitment – very common in intertidal systems – leading to co-existence of species due to absence of the equilibrium conditions theoretically needed for competitive exclusion. For instance, Connell (1961*a*) was able to demonstrate intense competition between barnacle species because space is highly saturated due to larval retention by fronts in the Firth of Clyde. Such retention leads to very high local recruitment compared for example with more dispersive coastal environments such as the Isle of Man (Hawkins & Hartnoll, 1982*a*). Work elsewhere can lead to different outcomes (e.g. Gordon & Knights, 2018), especially where space is undersaturated due to mesoscale recruitment differences (Jenkins

et al., 2001; Burrows *et al.*, 2010), or to low recruitment including failure years (Svensson *et al.*, 2005). Further south in the geographic range of *Semibalanus* in south-west England, early juvenile mortality of the dominant *Semibalanus* in warm years probably releases slower growing chthamalids from competition (Poloczanska *et al.*, 2008). Even where space is apparently undersaturated, gregarious settlement behaviour can lead to intraspecific competition (e.g. Gordon & Knights, 2018), whilst maximizing survival and mating opportunities (Kent *et al.*, 2003).

Predation and grazing

Pioneering work by Paine (1966), in which the large predator *Pisaster ochraceus* was experimentally removed from a mussel-dominated (*Mytilus californianus*) shore in Washington State, led to the keystone predator concept. Paine showed that diversity of conspicuous fauna declined in the absence of this large predator. In addition, continuation of this removal experiment for several years showed that predation could also set the lower limit of mussels (Paine, 1974). Paine went on to repeat this experiment in New Zealand (Paine, 1971) and Chile (Paine *et al.*, 1985), showing that in biogeographic settings where large starfish were prevalent (*Stichaster australis* in New Zealand and *Heliaster helianthus* in Chile) and mussels were the dominant space occupier, that a major 'keystone' predator could have a disproportionate effect on the diversity and distribution of species (Paine, 1969).

Ahead of these experiments, removals of patellid limpets in large squares or strips by Jones (1946, 1948) on the Isle of Man showed that the control of fucoid algal vegetation on moderately exposed rocky shores was by limpet grazing, not by wave action as previously assumed (see also Conway, 1946, for work in the Firth of Clyde). Although some of the work was published in *Nature*, the remainder of the more detailed follow-up work on the Isle of Man was largely published in local journals (Jones, 1948; Lodge, 1948; Burrows & Lodge, 1950; Southward, 1956). Southward (1964) summarized this work in a chapter for a conference organized by the British Ecological Society. The importance of limpet grazing was starkly confirmed by the toxic effects of first-generation dispersants used to clean up the Torrey Canyon oil spill in 1967 (Nelson-Smith, 1968; Smith, 1968). This was one of the first spills from the newer generation of super-tankers that ran onto reefs off the west Cornish coast. Vast amounts of 'detergents', a euphemism for a mix of surfactant, organic solvent and stabilizer, were applied to the crude oil that came ashore. A total of 10,000 tons of dispersant were applied to ~14,000 tons of oil that came ashore in Cornwall (Smith, 1968). This led to vast kills of limpets and other grazers leading to an immediate bloom of green algae, followed by fucoids, which even occurred on some of the most exposed shores in Cornwall such as outside Sennen Cove (Southward & Southward, 1978). Recovery of these treated shores took between 10–15 years (Southward & Southward, 1978; Hawkins & Southward, 1992; Hawkins *et al.*, 1983, 2017*a*, 2017*b*). Those observations confirmed that grazing, rather than physical factors, controlled algal vegetation and that limpets can be considered a keystone grazer on the rocky shores of the north-east Atlantic (Hawkins & Hartnoll, 1983*a*).

Starting with removing limpets from strips or patches (Hawkins, 1981*a*), a more nuanced approach using limpet exclusion fences (Hawkins, 1981*b*) was then adopted by the next generation of researchers on the Isle of Man (reviewed in Hawkins & Hartnoll, 1983*a*). This teased out the interactions between limpets, barnacles and fucoids (Hawkins & Hartnoll, 1982*b*, 1983*b*; Hawkins, 1983), and the role of recruitment fluctuations (Hawkins & Hartnoll, 1982*a*) in generating patchiness on exposed shores (Hawkins & Hartnoll, 1983*a*; Hartnoll & Hawkins, 1985). Some of this work was correctly criticized for lack of replication (Chapman, 1995). Subsequent studies used extensive replication over replicated patches, seasons and shores and on large geographic scales (Arrontes *et al.*, 2004; Jenkins *et al.*, 2005; Coleman *et al.*, 2006) confirmed the importance of limpet grazing in controlling algal vegetation, especially fucoids, in more northerly latitudes. Further north in Europe (i.e. the Isle of Man) the response to limpet removal was highly deterministic, but even in southern Britain a greater stochastic element was apparent (Jenkins *et al.*, 2005). Follow-up work comparing the factors determining fucoid recruitment in Portugal *vs* the British Isles showed that interactions between reproductive output, propagule supply and physical factors, particularly desiccation and grazing, influenced fucoid recruitment (Ferreira *et al.*, 2015). In the south of Portugal, fucoid cover and biomass is reduced, propagule supply is less and physical factors reduce early growth and recruitment; whereas in the north, in less stressful conditions with ample propagule supply, grazing has a prominent regulatory role (Ferreira *et al.*, 2014).

Spatial mapping of mosaics using geo-statistical tools (Johnson *et al.*, 1997), probabilistic individual-based modelling (Johnson *et al.*, 1998*a*) and approaches using cellular automata (Burrows & Hawkins, 1998) have built on the underlying experiments (summarized above and in Hawkins *et al.*, 1992) enabling simulation of the processes involved generating patchy mosaics on moderately exposed rocky shores. Jonsson *et al.* (2006), using a combination of experiments and modelling on artificial breakwaters, showed conclusively that limpets prevent establishment of fucoids, but wave action determines their persistence once established.

The keystone concept has received some criticism (Mills *et al.*, 1993; Power *et al.*, 1996). It is clearly context-dependent: appropriate large-bodied predatory and grazing species have to be present to be able to perform this role (i.e. large starfish in the Indo-Pacific; large limpets in the north-east Atlantic) and there have to be dominant space occupiers such as mussels or fucoid canopy-forming algae that are controlled by an important consumer (Power *et al.*, 1996).

Disturbance and succession

Rocky shores are naturally disturbed environments. The direct action of waves and indirect action through scouring as a consequence of movements of sand, gravel, and turning over cobbles and boulders (Shanks & Wright, 1986) remove biota thereby starting secondary succession (Connell & Slatyer, 1977). Primary succession can also be initiated by chunks of rock becoming cleaved away or the placement of new blocks on artificial shores (Hawkins *et al.*, 1983; Moschella *et al.*, 2005) creating virgin surfaces. In addition to physical processes, biological disturbance can arise from grazing, predation, sweeping or whiplash by canopy algae such as kelps or fucoids (Velimirov & Griffiths, 1979; Hawkins, 1983), and even intense intraspecific competition leading to hummocking of barnacles (Barnes & Powell, 1950). All these biological processes can lead to space being made available for secondary or even tertiary succession (on top of existing biota). This is particularly the case when grazing is relaxed, leading to algal colonization (Hawkins, 1981*b*). Grazing pressure can keep an invisible lawn of biofilm on apparently bare rock and on barnacles (Hill & Hawkins, 1991).

It is, therefore, not surprising that empirical studies of disturbance and succession have been made on rocky shores, and this work has led to conceptual advances (Connell & Slatyer, 1977; Sousa, 1979*a*, 1979*b*, 1984*a*, 1984*b*). Connell & Slatyer (1977) proposed three models of succession: classical facilitation where early stages are essential for progression to later arriving species;

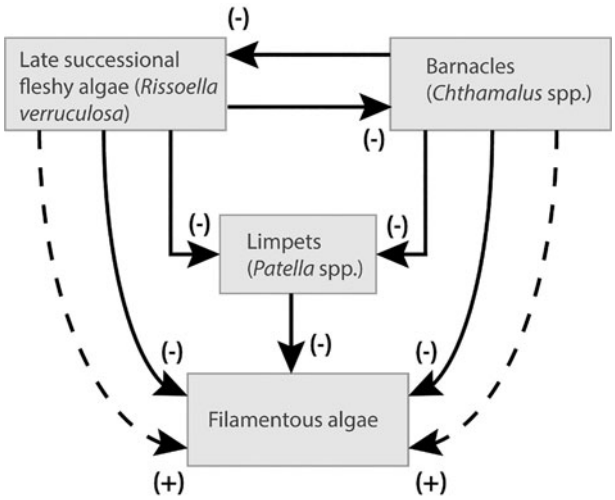

Fig. 2. Network of species interactions shaping rocky shores assemblages at late stages of succession on a Mediterranean rocky shore. Strong competition for space between late successional species (fleshy algae and barnacles) and limpets reduces grazing pressure in the mature assemblage, indirectly facilitating the persistence of early colonizers (filamentous algae) at late stages of succession. Continuous (dashed) lines indicate direct (indirect) interactions. (+) positive interaction; (–) negative interaction. Redrawn from Benedetti-Cecchi (2000*a*).

inhibition where early or mid-successional species delayed progression to later arriving species; and the tolerance model (which nowadays would be termed a neutral model) where there are no positive or negative interactions, but species eventually came to predominate because of life history characteristics such as longevity.

In the literature, there are many examples of facilitation and inhibition (Menge, 1995), although less for the tolerance model (but see Farrell, 1991). Facilitation can be particularly important during primary succession (Wahl, 1989), when microbial films condition the surface. There is, however, some evidence of inhibition even in microbial films (Wieczorek *et al.*, 1995). Inhibition commonly occurs when early colonizing macro-algae such as ephemeral greens and browns come to dominate rocks. Sousa (1979*a*) determined the importance of grazing in breaking dominance by intermediate stages thereby breaking inhibition to allow succession to proceed. The paucity of evidence for the tolerance model may simply be because studies have not been run for long enough (Jenkins & Uyà, 2016, for consideration of the temporal scale of manipulative experiments). In long-term experiments on *Ascophyllum*-dominated sheltered shores of the north-east Atlantic examples of the tolerance model may be found. Clearance areas were initially dominated by *Fucus serratus* and *F. vesiculosus*. However, slow recolonization over 10–20 years by *A. nodosum* occurred through its ability to grow up through an overlying canopy of shorter-lived competitors that led toward its return to dominance, maintained by proliferating vegetatively in long-lived clumps (Jenkins *et al.*, 1999*b*, 2004; Ingolfsson & Hawkins, 2008). These models are more classifications than a predictive framework, with Hawkins & Hartnoll (1983*b*) observing that some successional sequences can involve more than one model.

Benedetti-Cecchi (2000*a*) revisited the successional models of Connell & Slatyer (1977). He used a combination of traits from knowledge of natural history and outcomes of past experiments on the importance of positive and negative interactions to turn Connell & Slatyer's (1977) models of succession into predictive, but still qualitative models of succession (Figure 2). This study shows how positive indirect interactions may facilitate the establishment of species that characterize early successional stages later in succession, challenging the idea of succession as a directional sequence of species replacements.

Connell & Slatyer (1977) stated that 'succession never stops' and if the broadest definition of succession as a sequence of colonization following a disturbance event is adopted, then this is certainly the case, especially on rocky shores where both physical and biological disturbance is prevalent. The intermediate disturbance hypothesis (Connell, 1978) has been extensively explored on rocky shores. Sousa (1979*b*) worked on boulders of different sizes and their likelihood of turning over from wave action, showing middle-sized boulders experiencing intermediate disturbance had the highest algae diversity. Lubchenco (1978) examined biological disturbance by grazing littorinids in rockpools, finding the highest diversity of algae occurred in pools with intermediate levels of grazing. Intensity of wave action has also been shown to yield a parabolic pattern of species richness, which is lowest at very low disturbance sheltered shores and at exposed shores with very high levels of wave force (Blamey & Branch, 2009).

Succession following disturbance is ultimately driven by a combination of physical and biological processes. For example, the intensity of biological interactions may vary in relation to the physical attributes of the disturbed patches. Such interactions were identified by Sousa (1984*a*) in an elegant experiment in which the removal of gastropod grazers resulted in different patterns of succession depending on the size of the experimental clearings in mussel beds. Small clearings (25 × 25 cm) were entirely dominated by grazing-resistant encrusting coralline algae. In contrast, large clearings (50 × 50 cm) became colonized by fleshy macroalgae in the central part, with encrusting corallines developing only along the borders. Complementary measurements indicated that herbivores were more abundant and foraged mostly along the margins of large patches, whereas they could explore all the available space in small clearings. These patterns were likely a response of grazers to predators and to desiccation stress, both of which were mitigated by the intact mussel assemblage surrounding the disturbed patches. Thus, the central part of large patches offered a refuge from grazing to palatable algae, whereas only grazing-resistant species could survive in areas under the reach of herbivores. Patchy mosaics resulting from local escapes from grazing (tertiary succession) can also lead to higher diversity intertidal landscapes (Hawkins & Hartnoll, 1983*a*).

Positive interactions

Positive interactions between species have been known for a long time, especially in the intertidal zone (Bertness & Leonard, 1997; Bertness *et al.*, 1999). These can involve habitat provision or amelioration of conditions for other species during succession following disturbance or steady-state conditions. Some of the first experimental work identifying positive interactions was undertaken by Hatton (1938) in France (for reviews, see Connell, 1972; Hawkins *et al.*, 2016). Hatton noted that higher on the shore positive interactions were important, whilst lower down negative interactions such as competition were more prevalent.

More recently, the term 'facilitation' borrowed from successional studies has been brought into ecological mainstream studies with work on both rocky shores (Silliman *et al.*, 2011) and saltmarshes (Bertness & Shumway, 1993; Bertness & Callaway, 1994; Shumway & Bertness, 1994). This was formalized by Bertness & Callaway (1994) in the stress-gradient hypothesis (Figure 3).

In physically stressed environments, both intra- and interspecific interactions can increase survival and influence demographic processes (Menge & Sutherland, 1987). In areas with intense biological interactions, co-defences can be important in providing protection. Examples from rocky shores include work in the physically stressed

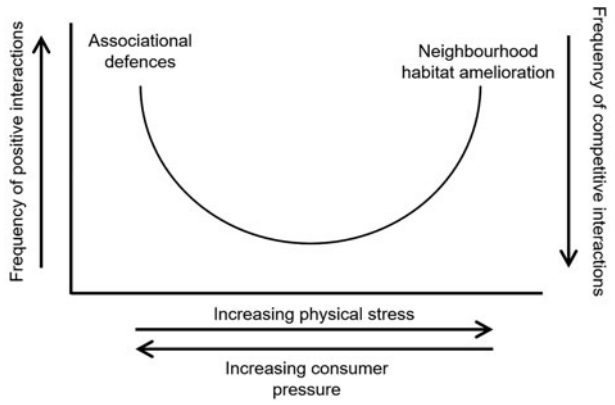

Fig. 3. Model of occurrence of positive interactions in natural communities. Positive interactions are predicted to be rare under mild physical conditions and consumer pressure. Associational defences under high consumer pressure, and neighbourhood habitat amelioration under high physical stress lead to a higher frequency of positive interactions. Redrawn from Bertness & Callaway (1994).

low-humidity environments of Patagonia (Silliman *et al.*, 2011) that emphasized the importance of positive interactions.

Mid-shore canopy-forming algae such as *A. nodosum* enable species to thrive higher up the shore, especially turf-forming algae (Jenkins *et al.*, 1999*b*, 2004, 2005; Ingólfsson & Hawkins, 2008; Pocklington *et al.*, 2018). These tend to die when the canopy is removed. The canopy also facilitates persistence of algal turfs that trap sand and inhibit limpet grazing (Airoldi & Hawkins, 2007). Once the canopy is removed, the turf declines and limpet numbers increase (Jenkins *et al.*, 2004).

Some species can have both positive and negative effects on other species, depending on environmental context and life history stage (Bulleri *et al.*, 2018*a*). Canopy algae high on sheltered shores can enhance barnacle recruitment, presumably by reducing mortality of recently settled juveniles (Hawkins, 1983). In contrast on more exposed shores, clumps of fucoids can reduce numbers of settling cyprids leading to reduced recruitment (Hawkins, 1983). Lower on sheltered shores, *F. serratus* prevents settlement by sweeping (Hawkins, 1983; Jenkins *et al.*, 1999*a*).

Whilst limpets can prevent establishment of fucoids in the north-east Atlantic, once a patch becomes established, juvenile *Patella vulgata* move under these patches along with adults (Hawkins & Hartnoll, 1983*b*; Hartnoll & Hawkins, 1985). Not only do the limpets benefit from shelter (amelioration of tide-out temperatures and relative humidity), but recent observations and work using isotopes (Davies *et al.*, 2007; Notman *et al.*, 2016) have confirmed that the limpets also eat the fucoids, confirming earlier work (Jones, 1948). Thus, a complex mix of positive and negative interactions plus chance recruitment events help generate and maintain patchiness on moderately exposed shores in the north-east Atlantic (Hawkins *et al.*, 1992). Similar processes have been shown in Australia (Underwood *et al.*, 1983) and on the Pacific Coast of North America (Dungan, 1986).

In recent years, the concept of facilitation cascades has emerged (Stachowicz, 2001; Silliman & Bertness, 2002), where a species provides habitat for another species that in turn provides habitat for a further species and so on (Stachowicz, 2001). Such cascades are typical of large macroalgae on rocky shores, but have also been described for sessile invertebrates (Peterson & Heck, 2001; Harley, 2006; Zhang & Silliman, 2019).

Alternative stable states

Although the earliest work on alternative stable states focused on lakes and ponds as model systems (Scheffer *et al.*, 1993; Carpenter

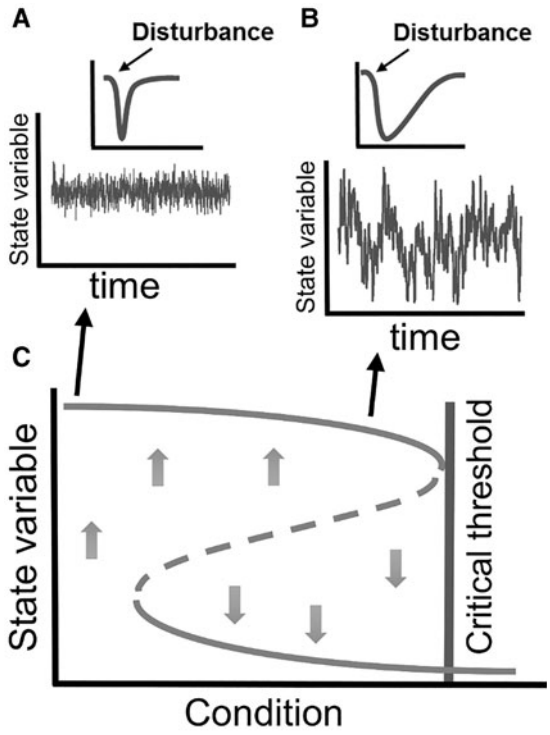

Fig. 4. How alternative stable states or extreme hysteresis can lead to slow or no recovery. Whilst a pulse disturbance can initiate succession or push a system to another state, press disturbance, repeated frequent pulse disturbance, or chronic pollution such as eutrophication or sedimentation can keep a system in another state unless they cease (Benedetti-Cecchi *et al.*, 2019).

et al., 2011; Hawkins *et al.*, 2015), some work has been done in subtidal and intertidal rocky systems. In the shallow subtidal, comparisons between two physically comparable adjacent islands on the west coast of South Africa by Barkai & McQuaid (1988) led them to argue that their communities existed in alternative stable states, one maintained by the predatory effects of rock lobsters that eliminate many prey species and promote kelp growth because of the absence of grazers, and the other by an unusual predator–prey reversal in which whelks consume and prevent colonization by lobsters. Sea urchin barrens prompted by overfishing (Steneck *et al.*, 2003) or driven by climate change (Ling *et al.*, 2009) have also been considered an alternative stable state. In *Cystoseira*-dominated shallow-water systems in the Mediterranean, storm-driven disturbances, the frequency of which are likely to have increased due to climate change, have been demonstrated to result in alternative stable states (Benedetti-Cecchi *et al.*, 2015). Experiments and models have shown how this system followed non-linear dynamics and exhibited hysteresis (Figure 4), displaying a tipping point at about 70–75% of canopy loss, beyond which the canopy-dominated communities gave way to those dominated by algal turfs (Benedetti-Cecchi *et al.*, 2015; Rindi *et al.*, 2017). This experimental work was used to probe statistical early warning signals of an approaching tipping point, such as rising variance and autocorrelation of response variables. Early warning signals of approaching regime shifts have been studied mostly under controlled laboratory conditions or using whole-ecosystem (yet pseudo-replicated) experiments (Carpenter *et al.*, 2011). Rocky shores have proved a tractable system to extend these tests under real world conditions, using properly replicated experiments.

There is growing evidence to suggest that urbanization of coasts, especially increased silt-load can also lead to domination by turfs, both in subtidal and intertidal habitats (Benedetti-Cecchi *et al.*, 2001; Airoldi, 2003; Gorgula & Connell, 2004). Using long-term observational data and path analysis, Bulleri

et al. (2018*b*) showed how wave action and anthropogenic disturbance may mediate the biological interactions that regulate regime shifts on rocky reefs in the north-west Mediterranean, including canopy-turf interactions and grazing by sea urchins. Indeed, algal canopies, turfs and barrens produced by sea urchins can form complex mosaics on subtidal rocky reefs, suggesting that these assemblages may be organized around three alternative states. Although the interactions that control the shift from one habitat type to another are reasonably well understood, the conditions maintaining the balance among the three putative alternative states have not been fully explored. In particular, improving knowledge of the reinforcing feedback mechanisms that maintain each habitat state is an important area for further research to understand the dynamics of algal-dominated rocky reefs globally.

Communities dominated by *A. nodosum* canopies in the mid-intertidal of the north Atlantic can be very slow to recover, taking over 20 years in Europe following experimental removal (Burrows, 1947; Jenkins *et al.*, 1999*b*, 2004; Cervin *et al.*, 2005; Ingólfsson & Hawkins, 2008; Pocklington *et al.*, 2018), or highly destructive harvesting (Boaden & Dring, 1980). Experimental work in North America has asserted that ice-scouring leading to loss of *A. nodosum* can lead to an alternative stable state – mussels (Petraitis & Dudgeon, 1999; Dudgeon & Petraitis, 2005). This interpretation has been challenged by other workers on New England shores (Bertness *et al.*, 2002). More recently, Menge *et al.* (2017) revisited sites experimentally cleared in 1974 and showed that *Ascophyllum* had not as yet recovered 39 years later, the cleared area being dominated by *Fucus* spp. They concluded that conditions for an alternative state were in operation. On European shores the limited recovery following *A. nodosum* removal after 20 years has been interpreted as very slow succession, with domination during mid-succession by other fucoids such as *F. serratus* and *F. vesiculosus* for some years. There are intrinsic differences in the biota on shores in New England and the British Isles. Most of the canopy species are the same (*A. nodosum*, *F. vesiculosus*, but with *F. serratus* largely absent except in Nova Scotia) and *S. balanoides* is the dominant barnacle in colder regions. However, due to differential post-glacial colonization processes, grazing by patellid limpets is absent and *Littorina littorea* is probably an invasive species in New England (Jenkins *et al.*, 2008*b*). On the shores studied by Petraitis & Dudgeon (1999), mussels dominated the alternative state, but they were generally absent from *A. nodosum*-dominated shores in north-west Europe. Context may play a role in whether alternative stable states occur or not. Such apparently stable states might still be an outcome of extremely slow succession, especially given the generally low recruitment of *A. nodosum* in some systems (Åberg & Pavia, 1997). Very strong inhibition may, therefore, occur by species present in intermediate successional stages. Given the estimated lifespan of individual *A. nodosum* of over 100 years, it is not surprising that succession is slow given that their dominance is maintained by vegetative proliferation of clump-forming genetic individuals (Åberg, 1996).

Biodiversity and ecosystem functioning

The realization that biodiversity could drive the functioning of ecosystems has been a major topic of interest in mainstream ecology for the last three decades (Loreau *et al.*, 2002), having been explored in terrestrial (Hector *et al.*, 1999; Loreau *et al.*, 2001), freshwater (Giller *et al.*, 2004; Woodward, 2009) and marine ecosystems (Solan *et al.*, 2012). Most work in marine ecosystems has used synthetic assemblages of species from soft sediment communities in mesocosms (Emmerson *et al.*, 2001; Solan *et al.*, 2008), strongly linking diversity to ecosystem processes such as nutrient remineralization (Emmerson *et al.*, 2001). Some pioneering work in the field on rocky shores explored the influence of biodiversity on primary production, showing strong idiosyncratic effects of individual dominant species such as *Patella* (O'Connor & Crowe, 2005). Rockpools have been used as semi-enclosed mesocosms in the field enabling ecosystem processes such as primary productivity to be measured as a response variable (Noël *et al.*, 2009), whilst manipulating diversity in the pool at the species or functional group level (Griffin *et al.*, 2010).

Rocky shore organisms have also been taken into the laboratory and experimentally assembled in mesocosms mimicking rock pools. Griffin *et al.* (2008) investigated the interaction of diversity and density in assemblages of predatory crabs. They showed the importance of considering density in such experimental work; predators were shown to occupy distinct fundamental niches but loss of predator diversity impacted ecosystem processes only at high predator densities. Using a similar mesocosm approach, the influence of spatial heterogeneity on the role of biodiversity was shown in assemblages of grazing gastropods (Griffin *et al.*, 2010). More complex mesocosms have been used to investigate the effect of predator diversity on subtidal food webs, showing that changes in the diversity of predatory fish can cascade to lower trophic levels by reducing grazer abundance, which in turn translates to different levels of increases in algal biomass (Bruno & O'Connor, 2005). Experiments by O'Connor *et al.* (2013) compared the influence of predator loss and independent manipulations of lower trophic level grazers on algal composition and biomass on exposed and sheltered shores. Cascading negative effects of predator loss were identified on grazers and indirect effects on primary producers, mediated by grazer identity.

The diversity of functional groups within a habitat has been suggested to be important in determining the invasibility of assemblages (Arenas *et al.*, 2006). Using mosaics of tiles in rock pools with different diversity and assemblage compositions, Arenas *et al.* (2006) showed that invasibility may be facilitated by the disappearance of whole functional groups, which is increasingly likely with human activity.

Whilst biodiversity has been demonstrated to have a role in shaping ecosystem processes, this has mainly been shown in closed systems – often artificially, such as in mesocosms. More attention has focused on biodiversity at the numbers and types of species level. In open highly fluid systems typical of most marine ecosystems, especially rocky shores, habitat patch diversity may be more important (Giller *et al.*, 2004; Hawkins, 2004). This will influence the balance of primary producers, consumers such as filter feeders, predators and mosaics of hard substrata dominated by production processes and soft sediments as the primary site for remineralization and carbon sequestration. There will also be export and import of material between these habitat patches. Alsterberg *et al.* (2017) demonstrated this in sedimentary systems. Recent work on rocky shores has also emphasized the strong context-dependency of biodiversity-ecosystem functioning relationships (Mrowicki *et al.*, 2015), reminding us of the importance of environmental gradients (summarized in Raffaelli & Hawkins, 1996) in setting patterns and ultimately determining potential composition of biodiversity, outcomes of interactions and hence processes at the community and ecosystem level (Hawkins *et al.*, 2019*b*, 2019*c*).

Bottom-up forcing and top-down control

The limnological and oceanographic research communities have long pondered the importance of bottom-up forcing by physico-chemical processes relative to top-down control by higher trophic levels. These concepts can be best explored in closed systems such as small lakes and ponds where bottom-up nutrients and top predators can both be manipulated at the scale of the whole

ecosystem in very similar adjacent lakes, ponds or large mesocosms (Scheffer *et al.*, 1993; Moss *et al.*, 1994; Williams *et al.*, 2002).

These concepts of bottom-up forcing have been explored in intertidal ecosystems, especially those strongly influenced by nutrient-rich upwelling on the Pacific coasts of North America (Menge, 2000*a*; Menge & Menge, 2013; Fenberg & Menge, 2019), New Zealand (Menge *et al.*, 1999), Chile (Wieters *et al.*, 2003; Wieters, 2005; Reddin *et al.*, 2015), and South Africa from the Atlantic to the Indian Ocean (Bustamante *et al.*, 1995*a*; Bustamante & Branch, 1996; McQuaid & Lindsay, 2000). Bottom-up forcing by greater nutrient supply can lead to greater productivity by both microbial biofilms and macro-algae on the shore, leading to faster growth and larger sizes of grazers and greater densities of filter feeders (Bustamante *et al.*, 1995*a*, 1995*b*). Similarly, rich inshore phytoplankton can enhance growth of sessile filter feeders (Bertness *et al.*, 1991; Xavier *et al.*, 2007), especially if it proliferates during upwelling events and is then transported onshore by downwelling, coined the intermittent upwelling hypothesis (Menge & Menge, 2013). This in turn can support larger numbers of predatory animals. Larval supply can also be viewed as a form of bottom-up forcing as it intensifies both intraspecific (Jenkins *et al.*, 2008a) and interspecific interactions (e.g. competition in high recruitment areas such as the Firth of Clyde, Connell, 1961*a*, 1961*b*) as well as providing more food for predators.

Using both comparative studies and field experiments, research on South African west-coast islands that are occupied by dense colonies of seabirds has shown that guano boosts nutrient levels in the surrounding seawater (Bosman et al., 1986). This elevates intertidal algal growth and infaunal abundance, thus respectively increasing food supplies for herbivores and waders such as turnstones. As a consequence of enhanced algal biomass, growth rates and sizes of limpets rise substantially. However, oystercatchers reach greater abundance on the islands because they are protected there from predators, and they exert a strong influence on limpet abundance, micro-habitat occupation and grazing; and smaller waders deplete the infauna of algal mats on a seasonal basis determined by their migration patterns (Hockey & Underhill, 1984; Branch, 1985). Bottom-up nutrient effects are thus countered to some extent by top-down predation.

Conversely the role of top-down control by predators (Paine, 1966) and grazers (Jones, 1946, 1948) has been long known in intertidal systems with some of the first demonstrations of how lower trophic levels can be controlled. If bottom-up forcing is great then lower trophic levels can escape or swamp top-down control, especially if predation is constrained by water flow or wave action (Leonard *et al.*, 1998); but then in species like barnacles which hummock, intense intraspecific competition can lead to mass mortality (Barnes & Powell, 1950).

In many cases the relative importance of top-down control and bottom-up forcing is a balance, varying from place to place with mesoscale hydrography and coastal morphology (Menge, 2000*a*). It can also change temporally with season in temperate zones, or with intensity of upwelling in boundary current dominated systems. In the plankton in temperate regions physico-chemical factors control primary production in the winter (low light, much turbulence even though nutrients are not limiting). With increased light in spring and a less turbulent water column due to stratification, phytoplankton can bloom, this being ended by a combination of lack of nutrients coupled with grazing by copepods that lag the phytoplankton bloom. Similar processes have been shown in cold-temperate intertidal rocky shores on the Isle of Man that are driven by microbial films (Thompson *et al.*, 2004). In the winter light is limiting but in late winter/early spring as light increases there is an increase in biomass as shown by chlorophyll. Grazing activity is driven by temperature and is still low in February/March at the time of coldest sea temperatures enabling a window of opportunity for benthic diatoms to flourish. Later in the year this bloom is halted by increased grazing as well as light and desiccation stress, leading to cyanobacterial domination in the summer. Parallel experiments by Thompson *et al.* (2004) showed the primacy of grazing and seasonal summer stresses over nutrient forcing, suggesting both bottom-up forcing, top-down control and what they termed lateral stresses were important in this simple system (see Figure 5). Thus, there is interplay between abiotic factors (some bottom-up, some modulating stresses) and biological control in this highly seasonal system.

Experimental work in rock pools (Masterson *et al.*, 2008) has shown the interactive effects of top-down control by grazers and bottom-up nutrient enrichment on early successional algal assemblages following disturbance, with composition, cover and community productivity being used as response variables. Negative effects of grazing tended to override positive effects of nutrient-forcing, except at peak algal growth when top-down control was swamped. Interestingly, nutrient levels had an important influence on the identity of dominant macroalgae, leading to a mismatch between effect estimates based on cover and those based on productivity. While loss of grazers under ambient nutrient conditions led to high cover estimates (mainly of red algae such as *Ceramium*) but little enhancement of productivity, under elevated nutrients ephemeral green algae were favoured leading to a three-fold increase in productivity.

Overview and synthesis

Concepts and experiments

The above examples show how important experiments have been in understanding how patterns on rocky shores are shaped by processes (see various chapters in Hawkins *et al.*, 2019*a*), but also, perhaps more importantly, how rocky shore experiments have contributed to the ecological mainstream across a range of concepts. The papers by Menge & Sutherland (1976, 1987) perhaps epitomize the link between theory and empirical experimentation, taken further forward by Menge (2000*a*). Menge & Sutherland (1976) synthesized how environmental gradients of tidal elevation and exposure to wave action influenced the outcomes of interactions, especially the respective roles of competition, predation and what they at the time called temporal heterogeneity (in essence what now would be called disturbance). This synthesis was re-visited in Menge & Sutherland (1987), who clarified the role of disturbance (perhaps prompted by the work of Sousa, 1984*b*) and considered the importance of recruitment regimes as the importance of supply-side processes re-surfaced in the 1980s (Underwood & Fairweather, 1989). Menge (2000*a*) then considered how top-down control and bottom-up forcing could be incorporated to enhance understanding. He emphasized how environmental context on various spatial and temporal scales can influence how shore communities are structured – particularly by mesoscale nearshore oceanographic features such as upwelling influencing both productivity (Bustamante *et al.*, 1995*b*; Wieters *et al.*, 2003; Xavier *et al.*, 2007) and larval delivery (Pineda, 1991).

As Menge (2000*a*) pointed out: theory helps ecologists rise above a morass of local and idiosyncratic natural history studies enabling a predictive framework and some generalization. At the very least theory provides the concepts and vocabulary to formulate hypotheses and interpret experimental results. However, papers emphasizing the contextual nature of many ecological processes (Crowe *et al.*, 2011; O'Connor & Donohue, 2013) are, perhaps, a

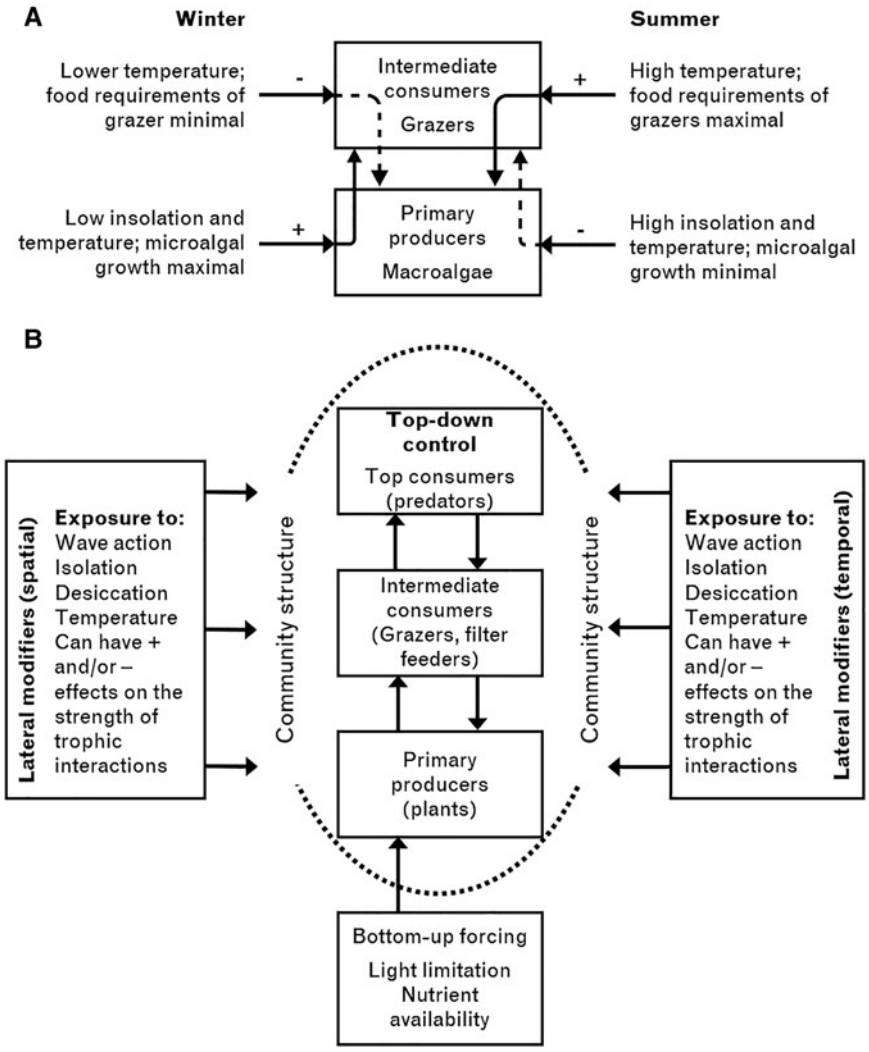

Fig. 5. Bottom-up forcing and top-down control of microbial films on rocky shores in the north-east Atlantic: (a) Regulation of the balance between producers (photosynthetic microbiota) and consumers (grazers) in the rocky intertidal during summer and winter. The positive (+) and negative (–) lateral effects of contrasting physical factors on bottom-up and top-down control of trophic interactions are illustrated. Strong effects are shown as solid lines, weak effects as dashed lines. (b) Conceptual model incorporating the role of physical stresses operating laterally at all trophic levels (sideways-facing arrows) together with bottom-up forcing (physical and chemical limiting factors; upward arrows) and top-down control (predation and grazing; downward arrows) in regulating community structure on temperate rocky shores (From Thompson *et al.*, 2004).

warning about not overgeneralizing. Good natural history is essential in experimental ecology (Hawkins *et al.*, 2016): it is often the first phase in exploring patterns by observation and getting to know traits of species. It helps stratify surveys and experimental designs and minimize variance influencing factors being tested experimentally and can help get rid of co-variance. Good natural history leads to more elegant experimentation; just as good physiology depends on expertise in morphology and anatomy.

Approach and methodology

The most important development in the last 30 years has been better experimental designs matched with appropriate statistical analyses in a formal hypothesis-testing framework. The seminal work of Hurlbert (1984) on pseudo-replication made ecological studies more demanding and forced the ecological community to think more carefully about the nature and the design of ecological studies. Considerable progress has been made in this direction and for this Underwood can take much of the credit (Underwood, 1978, 1981; Underwood & Chapman, 1985, 1992). Underwood and Chapman have educated young experimental ecologists worldwide, calling for more rigour and logic in the way experiments are designed, conducted, analysed and interpreted. Underwood's work on the scientific method has made Popperian falsification widely accessible, defining an operative framework whereby observations, theories (models), hypotheses (predictions) and experiments are logically connected (Underwood, 1981, 1997; Underwood & Denley, 1984). The framework offers a decision-making tool to arbitrate among alternative explanations and to eradicate false models, contributing to pursuing values of objectivity when interpreting the outcome of ecological experiments and observational studies. By emphasizing the cyclical nature of observations, models, hypotheses and experiments, the approach advocated by Underwood has disclosed the complexity of rocky shores in an unprecedented way, documenting variation in the structure of assemblages over multiple scales in space and time and challenging the assumed generality of many ecological processes. This work has spilled beyond the boundaries of rocky shore ecology and has influenced the work of peers in other fields as well. It has also stimulated better sampling designs to assess ecological impacts through beyond-BACI (Before-After/Control-Impact) sampling designs (Underwood, 1991*b*, 1992*b*, 1994). The Underwoodian approach has demonstrated the value of looking beyond the most obvious explanations, showing the power of disproving alternative models to break paradigms, eradicate myths and disclose the unexpected.

Focus on rigorous experimental design has allowed interactions between multiple factors to be disentangled plus encouraged hierarchical designs that test for generality over spatial scales (e.g. Coleman *et al.*, 2006). Ease of testing multivariate data, for example, packages such as PRIMER with the PERMANOVA extension (Anderson *et al.*, 2008), and free R software (R Core Team, 2019) have led to much more complex and effective statistical analyses. Nevertheless, increasing availability of libraries and functions to perform complex analyses may also lead to mistakes and abuse of statistics. Only the judicious choice and correct use

of well understood methodologies will guarantee progress and ensure that the ecological community can take full advantage of the increasing availability of open statistical software.

New technological approaches in the last two decades such as digital photography, remote sensing, better and cheaper GPS, and online identification resources, have greatly increased the scope of what can be done between tides. Digital photography has revolutionized non-destructive sampling enabling much greater sample sizes, and faster processing of acquired images back in the more clement environment of the laboratory. Cheap and robust underwater cameras can provide insights into tide-in conditions, especially presence and activities of mobile predators (Silva *et al.*, 2008; Harasti *et al.*, 2014). *In situ* sensors and data loggers can characterize the environment, especially temperatures, experienced at fine temporal and spatial scales over long periods and help better define environmental gradients and micro-scale mosaics of conditions (Lima & Wethey, 2009; Seabra *et al.*, 2011). Thus, the context of experimental manipulations can be much better described. Hard-to-access areas have become more accessible through the use of remote sensing technologies such as satellites and aerial photography using drones (Guichard *et al.*, 2000; Brodie *et al.*, 2018; Gomes *et al.*, 2018; Rosenthal *et al.*, 2018). The ability to collect large numbers of images over a wide area has enabled assessments of species distribution and temporal and spatial fluctuations, such as examining distribution patterns of mussels in Portugal (Gomes *et al.*, 2018) and investigating changes in kelp forests over time on a global scale (Rosenthal *et al.*, 2018). Incorporating remote sensing techniques into experimental design has applications for investigating large-scale impacts of disturbance on rocky shores, such as commercial macroalgal harvesting (Bennion *et al.*, 2019), oil spills (see Gilfillan *et al.*, 1995; Mishra *et al.*, 2012 for examples on coastal marshes) and earthquakes (Schiel *et al.*, 2019*b*).

Ease of access to rocky shores has made them amenable to citizen science, where volunteers carry out scientific tasks (Delaney *et al.*, 2008; Dickinson *et al.*, 2012; Vye *et al.*, 2020) such as sample collection, processing and analysis. This is not a new concept, with examples of bird surveys that have been done by citizen scientists for over 100 years (Silvertown, 2009). This approach is becoming more common in marine and coastal environments (Hughes *et al.*, 2014; Cigliano & Ballard, 2017) and is increasingly being used to support policy and management (Hyder *et al.*, 2015; Townhill & Hyder, 2017). For rocky shores, most examples relate to descriptive observations or monitoring of biodiversity (Delaney *et al.*, 2008; Vye *et al.*, 2020), but more recently experimental approaches (e.g. www.capturingourcoast.co.uk) and internet-based citizen science (e.g. www.zooniverse.org; Newman *et al.*, 2012) have become more common. With care this can also include simple experimental procedures such as re-colonization or clearance experiments at multiple locations with appropriate controls. Obviously, there are training, ethical, conservation and quality-control issues to be overcome, but the scope is limitless for both describing patterns and understanding processes on broad spatial scales.

New spectroscopic approaches have also recently revolutionized intertidal ecology. Biomass of photosynthetic biofilms can be measured non-destructively and over much greater spatial extents (Murphy *et al.*, 2005, 2006), than with traditional destructive chlorophyll extraction techniques (Underwood, 1984; Hill & Hawkins, 1990; Nagarkar & Williams, 1997; Thompson *et al.*, 1999). They have enabled photosynthesis of macro-algae to be measured including stress responses (Ferreira *et al.*, 2014).

Technological innovation for the acquisition, storage and dissemination of digital information makes large environmental and biological datasets increasingly available. This boost from large datasets opens new opportunities for ecological analysis at unprecedented spatial and temporal scales. Recent developments have encouraged a synthesis between observations and experiments using hybrid datasets resulting from the combination of observations and experiments (Benedetti-Cecchi *et al.*, 2018). This approach leverages the scope of large-scale observational data with the ability to attribute causality typical of experimental studies. Large datasets are mostly observational, but distributed experiments across large spatial scales are becoming increasingly common (see Sanford & Bertness, 2009, for review). Building on recent developments in time-series analysis and spatial modelling, hybrid datasets can take advantage of the data generated by distributed experiments embedded in large-scale observation networks – combining observational and experimental data provides a promising approach to uncover causal relations in large-scale phenomena, beyond the limits of causal inference inherent in observations and beyond the scales encompassed by individual manipulative experiments.

The development of ever-more sophisticated and well-controlled mesocosms mimicking rock pools have allowed more controlled factorial experiments to understand how complex interactions between biodiversity loss and elements of global change (including rising temperatures, stormier seas, the introduction of non-native species and eutrophication) modify community composition and ecosystem functioning. Whilst strictly not field experimentation, such approaches have stemmed from work on rocky shores in general and rock pools in particular whether natural or drilled on the shore (Arrontes & Underwood, 1991; Atalah & Crowe, 2010). Such mesocosms have been particularly powerful in disentangling the effects of multiple stressors or environmental context crossed with biodiversity loss (e.g. O'Connor *et al.*, 2015 – biodiversity loss and nutrient enrichment; Mrowicki & O'Connor, 2015 – wave action on warming and biodiversity loss; White *et al.*, 2018 – biodiversity of predators with warming and nutrient enrichment; Vye *et al.*, 2015 – impacts of invasive species with water temperature and nutrient enrichment).

One of the criticisms of experimentation is that it is often done on very local scales. Broader-scale insights can come from rapid response to large cataclysmic events whether from major acute pollution incidents such as oil-spills (Southward & Southward, 1978; Hawkins *et al.*, 2017*a*, 2017*b*), nuclear weapon testing lifting whole atolls (Lebednik, 1973) or major tectonic events, particularly earthquakes. Earthquakes in Chile (Castilla & Oliva, 1990), Mexico (Bodin & Klinger, 1986) and New Zealand (Schiel *et al.*, 2019*b*) have provided insights into diverse topics such as factors setting zonation patterns due to uplift or submergence of coastal rock platforms, as well as connectivity during recolonization. Whether from acute pollution incidents such as oil-spills, outbreaks of pandemic disease such as COVID 19 reducing tourism and recreational use of the foreshore, or natural disasters such as earthquakes or tsunamis, insights come best when they impact well-studied sites with previous time-series data, ideally where experimentation has revealed some of the processes causing patterns. The network of sites studied by the Southwards for a decade before the Torrey Canyon oil spill (Southward & Southward, 1978) provided an unintended beyond-BACI design of multiple impacted and un-impacted areas beyond the influence of the spill – ultimately allowing some disentangling of the impacts of the spill and the role of climate fluctuations in recovery processes (Hawkins *et al.*, 2017*a*, 2017*b*). Likewise in New Zealand the work at Kaikoura over many years by Schiel and colleagues will enable some major scientific insights to be recovered from the wreckage caused by the earthquake (Schiel *et al.*, 2019*b*), including the closure of the laboratory at Kaikoura.

Conservation and management of rocky shores in a rapidly changing world

Understanding from experiments has also contributed to better conservation and management of rocky shore ecosystems

(Thompson *et al.*, 2002; Branch *et al.*, 2008) including the use of rocky shore organisms as indicators of global change and understanding interactions with more regional and local scale impacts (explored in detail in Branch *et al.*, 2008; Hawkins *et al.*, 2019*c*). Here we focus mainly on global change, but emphasize that many of its more pernicious impacts are usually in concert with regional or local-scale impacts such as overfishing of nearshore predators (Ling *et al.*, 2009) or over-collection of intertidal grazers (Borges *et al.*, 2015), sediment and nutrient run-off from land both from agricultural (Schiel & Howard-Williams, 2016) and urban sources (Airoldi, 2003), plus habitat loss and fragmentation (Airoldi & Beck, 2007), often as a result of urbanization or ocean sprawl (Bugnot *et al.*, 2020; Hawkins *et al.*, 2020).

Ecosystem responses to climate change fluctuations (Southward & Crisp, 1954; Southward, 1967) and subsequent rapid climate change have been detected using rocky shore indicators (Southward *et al.*, 1995; Hawkins *et al.*, 2003; Mieszkowska *et al.*, 2006, 2014). Knowledge of species interactions derived from experiments have shown the importance of modulation of climate warming by biological interactions. Based on the classical work of Connell (1961*a*), coupled with a space-limited model (Roughgarden *et al.*, 1985), modelling has shown how responses of cold-water and warm-water species of barnacles to climate were mediated by competition (Poloczanska *et al.*, 2008). In warmer years, the warm-water *Chthamalus* spp. prospered as they were released from competition with faster growing northern species. Predictive models using climate change scenarios only worked well when competition in addition to physical drivers was built into the models. Experiments have been used to explore how competitive interactions can be shaped by additional species expanding polewards in response to climate change (Firth *et al.*, 2009). How facilitation can modulate stresses resultant from climate change for mobile animals such as limpets has been shown by Moore *et al.* (2007), finding lower survival of the northern species, *P. vulgata*, when clumps of *Fucus* were removed, unlike the more southern *P. depressa* that does not aggregate under algal clumps. Changes in the species composition of these two species have implications for the dynamic patchiness on rocky shores (Hartnoll & Hawkins, 1985; Hawkins *et al.*, 2008). Thinning of fucoid canopies resulting from climate change (Hawkins *et al.*, 2009; Yesson *et al.*, 2015) has been experimentally simulated and can lead to reductions in sub-canopy species (Pocklington *et al.*, 2018). Positive interactions have been advocated as a tool to combat loss of biodiversity in the face of climate change (Bulleri *et al.*, 2018*a*). Experimentally derived knowledge has also enabled the impacts of oil spills and their subsequent clean up to be better understood (Southward & Southward, 1978; Hawkins & Southward, 1992; Hawkins *et al.*, 2017*a*, 2017*b*).

Extreme events such as hurricanes, marine heatwaves and floods are predicted to become more frequent with climate change (Easterling *et al.*, 2000; Oliver *et al.*, 2018). Climate models also predict that extreme events are becoming more clustered in time, which implies a change in the distribution of time intervals between consecutive disturbance events compared with historical climate scenarios (Easterling *et al.*, 2000). Experimental work has been performed to assess the ecological effects of changing the intensity and temporal distribution of perturbations on rocky shore assemblages. Some studies have done so by manipulating the frequency of events. This approach allows a direct test of the ecological effects due to the expected increased frequency of extreme events. However, manipulating the frequency of perturbations has the drawback of confounding intensity with temporal variability (clustered vs regularly distributed) of perturbations (Benedetti-Cecchi, 2003). Appropriate experimental designs have been proposed to disentangle the effects of changes in mean intensity from those due to variation in the temporal patterning of events, also allowing tests of interactions between intensity and degree of temporal clustering of perturbations (Benedetti-Cecchi, 2000*b*, 2003).

These designs have been used to assess the impacts of waves (Bertocci *et al.*, 2005, 2010; Maggi *et al.*, 2012), desiccation stress (Benedetti-Cecchi *et al.*, 2006), sediment regimes (Vaselli *et al.*, 2008) and heatwaves (Dal Bello *et al.*, 2017) on rocky intertidal assemblages. Overall, the results have shown that the effects of increasing intensity of perturbations can be offset in part by increasing degree of temporal clustering. In other words, regardless of the nature of the perturbation, results have shown that the temporally clustered events are in general less detrimental to rocky shore assemblages than events that are more regularly distributed in time. Interestingly, an observational study on the impact of hurricanes on coral reefs in the Caribbean has shown a similar pattern: impacts were less severe in years when hurricanes occurred clustered in time compared with years when they were regularly distributed (Mumby *et al.*, 2011).

The mechanisms behind this apparent general positive effect of temporal clustering of perturbations have not been elucidated yet, but one possibility is that a clustered perturbation scenario allows for longer periods of recovery compared with where the same number of perturbations is distributed regularly over the same time window. A longer period of recovery may be particularly advantageous if individual perturbations are intense enough so that one event is sufficient to wipe out most of the organisms from an area. In this scenario the cumulative effect of a cluster of perturbations will not be much more different from that of an individual one. Regardless of the specific mechanism, a positive response to increased clustering of extreme climate events injects some optimism in the ability of rocky shore assemblages to cope with the expected increase in intensity (and temporal clustering) of climate-related perturbations.

The zonation of intertidal organisms has been shown by observations and experiments to be squeezed from environmental extremes such as desiccation stress at the top of the shore coupled with greater consumer pressure from lower down due to biogeographic shifts (e.g. colder water fucoids in the Azores stressed by more frequent warmer weather and the spread of herbivorous fish northwards; Martins *et al.*, 2019). Late winter and early spring seasonal blooms of light-driven micro-algae and macro-algae are likely to get curtailed by earlier onset of temperature-driven grazing pressure (Thompson *et al.*, 2004) as has been shown on latitudinal gradients in Europe (Jenkins *et al.*, 2000).

Experimental approaches have informed both ecological enhancement of highly modified urban coastlines as well as adaptational responses to climate change by design of environmentally sensitive sea defences in the face of rising and stormier seas (Morris *et al.*, 2019). Ironically, early studies of artificial structures used them primarily as simple surrogates of natural systems with low topographic complexity and hence ease of study – in many cases cubist rocky shores. Examples include describing distribution patterns in relation to tidal height and wave exposure (Southward & Orton, 1954), plus succession on large breakwater blocks of known age (Hawkins *et al.*, 1983) both using Plymouth Breakwater. The importance of grazing interactions in limiting the lower limit of kelp in the shallow subtidal zone was shown on the ruined breakwater in Port Erin, Isle Of Man (Jones & Kain, 1967). Interactions between barnacles and limpets (Hawkins & Hartnoll, 1982*b*; Santini *et al.*, 2019) and settlement patterns of barnacles in relation to wind patterns (Hawkins & Hartnoll, 1982*a*) were all investigated on the same Raglan Pier in Port Erin. The simplicity of replicated artificial shore parallel breakwaters at Elmer in Sussex, UK, enabled the respective roles of grazing by limpets in preventing establishment of fucoid algae and wave action reducing persistence of older plants to be disentangled by a combination of field experiments and modelling (Jonsson *et al.*, 2006).

The full battery of experimental approaches has been deployed to better understand the efficacy of various interventions to enhance biodiversity and deliver ecosystem services on artificial hard substrate habitats in ports and on sea defences – an approach now termed eco-engineering. Much of this work has been led from Sydney, Australia, with the development of artificial rockpools (Browne & Chapman, 2011) and boulder-fields (Chapman, 2017), including better understanding of the diversity deficit typical of artificial communities compared with natural ones (Bulleri & Chapman, 2010). Similarly in Europe the outcomes of experimental ecology were used in early efforts to inform guidelines on the design of sea defences (Moschella *et al.*, 2005; Burcharth *et al.*, 2007) and understanding their impacts (Martin *et al.*, 2005), enabling putting this work into a broader ecological and conservation context (Airoldi *et al.*, 2005). This early work has proliferated to understand the impacts of what became known as ocean sprawl (Duarte *et al.*, 2012; Firth *et al.*, 2016; Bugnot *et al.*, 2020; Hawkins *et al.*, 2020) and how these impacts can be at least partially offset by eco-engineering interventions (Dafforn *et al.*, 2015; Morris *et al.*, 2019). Worldwide experimental trials have tested the efficacy of different types of crevices (Coombes *et al.*, 2015), complexity of tiles (Loke *et al.*, 2014, 2015), boulder size and mix in gabions (Firth *et al.*, 2014) and retro-fitted artificial rockpools (Browne & Chapman, 2014; Evans *et al.*, 2016). Guidelines on practice are emerging (Morris *et al.*, 2019; O'Shaughnessy *et al.*, 2020) and this approach is now entering the planning (Evans *et al.*, 2016; Evans *et al.*, 2019) and engineering mainstream (Burcharth *et al.*, 2007). Additionally along the way some interesting insights have emerged on rock pool ecology (Firth *et al.*, 2013), topographic complexity and diversity (Loke *et al.*, 2016; Loke & Todd, 2016), mobile predators using the intertidal zone (Morris *et al.*, 2017), connectivity of matter and propagules (Bishop *et al.*, 2017; Heery *et al.*, 2017) plus difficult-to-study boulder shores (Chapman, 2017). Furthermore, understanding of the nature of biogeographic boundaries has resulted with breakwaters acting as 'experimental' stepping-stones, enabling range expansions (Hawkins *et al.*, 2009; Keith *et al.*, 2011; Firth *et al.*, 2015) – an experiment that no ethical committee would ever allow (Sugden *et al.*, 2009), nor would a funding body finance.

Concluding comments

Experiments on rocky shores have contributed to both ecological theory and better understanding of patterns and processes in coastal ecosystems. It is now informing responses to global change and creeping urbanization. The coastal zone is being increasingly squeezed and impacted by both development and climate-driven change. Experiments help explain patterns and can feed into forecast and prediction of future states. They can also inform better understanding and hence management of the interactions of multiple regional and local-scale impacts with global change.

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