Tipping points, regime shifts and species interactions within shallow marine ecosystems

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Abstract

Understanding the response of ecosystems to perturbation is of great importance in a rapidly changing world. Research has shown that in response to pressures such as climate change or over exploitation, entire ecosystems can shift to alternative states, a phenomenon termed regime shifts, and in extreme cases can collapse. Ecological regime shifts, or shifts between different ecological states, can be triggered by pulse disturbances (short term effects) or press pressures (longer term effects). However, understanding which pressures are most important to a system can prevent the ecological deterioration of the system into a poorer state, or even aid with ecosystem restoration. We investigate which pressure may be more important on rocky shore boulder systems in the south of England. Surveys at mid tide level demonstrated three systems were present on multiple shores, those dominated by green algae, those dominated by barnacles and those dominated by brown algae. Grazer number and biodiversity was higher on the latter of these boulder states. We then manipulated a green algae dominated system, by either removing 20% of the algae on the rock or by the addition of 20 grazing topshells (Steromphala umbilicalis). Removed algae (pulse pressure) regrew quickly, but when grazers were added (press pressure) the green algae was rapidly reduced, regardless of whether algae had also been initially removed or not. Long-term press pressure clearly has a much bigger role in shifting boulder ecosystems from green algal to other ecological states. While it is not possible to indicate a full regime shift has occurred as a result of press pressure, the results indicate that long-term pressures, such as addition of grazing species, may be important in shifting intertidal communities from early successional states to more complex, and potentially more resilient, systems.

Introduction

Pressures on natural resources and biodiversity are vastly increasing (Foley et al., 2005; Aderhold et al., 2012; Steffen et al., 2015) and in turn these pressures increase perturbation of ecosystems. The planetary boundary concept was created to define the environmental limits within which humans can safely survive (Steffen et al., 2015). Understanding the response to change in an ecosystem is of great importance in a rapidly shifting world (Van der Putten et al., 2004).

Ecosystems are a highly intricate network of interactions (Bland et al., 2016); altering any aspect of the ecological process and/or biodiversity can cause cascading effects on other linked organisms and functions (Henneman and Memmott, 2001; Scheffer et al., 2001).

In response to pressures such as climate change or over-exploitation, entire ecosystems can shift to alternative states and in extreme cases collapse (Fields et al., 1993; Beisner et al., 2003; Helmuth et al., 2006, Cheung et al., 2009; Somero, 2010; Newton et al., 2021). For example, as a response to warming temperatures, many biodiverse coral reefs have diminished into algae dominated 'graveyards' (Bellwood et al., 2004; Steneck et al., 2019). Defaunation is the local, functional, or global extinction of animal species (McCauley et al., 2012). It reduces cross-system connectivity, ecosystem resilience, stability, and the fundamental biological cycles that allow for life on earth (McCauley et al., 2012; Britten et al., 2014; Roman et al., 2014). When key aspects of ecosystem functions are lost, the system is susceptible to further disturbances that previously may have been absorbed (Folke et al., 2004; McCauley et al., 2012). A prime example documented globally is the mass release of plant fertilizers leaching into freshwater systems. These excess fertilizers then flow into coastal areas, fuel the growth of algae and microbes, which is further encouraged if vital grazing species have been lost from overharvesting-facilitating an algae and microbe productivity explosion (Pandolfi et al., 2005; Palumbi and Palumbi et al., 2014). In this case, a bloom can cause anoxic conditions where oxygen is depleted from the water, it may also block sunlight and clog the gills of fish; in combination many blooms produce harmful toxins.

An ecosystem enters a collapsed state after the permanent or long-term loss of environmental or natural features (IUNC 2021). Tipping points are a point at which an ecosystem can no longer cope with environmental change, and the ecosystem suddenly shifts from one state to another (Scheffer, 2012; Wernberg et al., 2016). Yet defining the tipping points, also known as the collapse threshold, can be a challenge (Bland et al., 2018). Small changes in an environmental indicator e.g. temperature, can produce inconsistent large responses in biotic indicators (MacNally et al., 2014). These indicators can be metrics that quantify complex changes in ecosystem structure relating to the possible threats or responses to threats within an ecosystem (Niemeijer and de Groot, 2008).

Regime shifts and alternative states

Every natural system is exposed to gradual change e.g. changes in climate or nutrient loading. However, these relatively smooth changes can be interrupted by sudden drastic switches to alternative states (Scheffer et al., 2001; Beisner et al., 2003; Scheffer and Carpenter, 2003). These are known as regime shifts and are often large, abrupt, persistent changes in the structure and functioning of ecosystems, the climate, or other complex systems (Deyoung et al., 2008; Scheffer, 2012). These shifts have profound ecological, social and economic implications (Bertram et al., 2001; Collie et al., 2004; Cury and Shannon, 2004; Wernberg et al., 2016). Recent research suggests that the loss of resilience to these shifts usually paves the way for such changes in state (Folke et al., 2004), suggesting that maintaining resilience could be a sustainable management strategy (Scheffer et al., 2001). Regime shifts were first recognized in terrestrial ecosystems, it became apparent that if predators were removed from a grazing system, their prey species would overgraze causing plant diversity to decrease, changing the system to an alternative, less biodiverse state (Noy-Meir, 1975). However, early efforts to encompass these ideas were criticized and lacking in long term reliable data and modelling techniques. By the 2000s the regime shift conceptual framework was formed, considered theoretically robust and ecologically coherent (Scheffer et al., 2001; Folke et al, 2004).

Drivers of Marine Regime Shifts

The phrase 'regime shift' is now extensively used to describe changes in the marine environment globally. Regime shifts have been identified in all major ocean basins with substantial evidence of most marine regime shifts occurring in coastal regions e.g., kelp forest, coral reefs, mangroves, seagrass and rocky shores (Rahmstorf, 2002; Steele, 2004; Collie et al., 2004; DeYoung et al., 2008; Lee et al., 2006; DeYoung et al., 2008).

Global assessments have suggested that wildlife living in coastal ecosystems have been altered and degraded by human activities, more so than any other marine environment (Halpern et al., 2008; World Bank, 2013). Coastal zones are easily accessible from land, making them extremely vulnerable. Research has shown that marine wildlife closest to human settlements and trade networks generally decline faster and are at higher risk of extinction (McCauley et al., 2013; Cinner et al., 2013). Marine environments are at a higher risk of defaunation than the terrestrial environment as marine species are a natural resource, harvested directly from a natural system (Dulvy et al., 2003; Harnik et al., 2012; McCauley et al., 2015; Stafford et al., 2015).

There are three main causes of oceanic regime shifts, often acting in combination (Vasconcellos et al., 1997; Hare and Mantua 2000; Parsons and Lear 2001; Benson and Trites 2002; Beaugrand et al., 2002; Daskalov 2002; DeYoung, 2008).

1. Abiotic processes, which is the non-living part of an ecosystem shaping the environment. Examples are climate change or large-scale alteration in ocean or atmospheric chemistry. Often, these are more straightforward to identify than biotic processes (Mantua, 2004). There are abiotic alterations associated with climate change such as increased temperature or salinity, changes in stratification, ocean circulation shift and anoxia (McCauley et al., 2012b).

2. Biotic processes, which can be living changes in community structure or population dynamics. Biotic factors can include altered food webs from processes like overfishing (Cury et al., 2000) or the alteration of keystone species such as the organisms of upwelling systems (Cury and Shannon, 2004). Examples include tipping points related to declines in anchovy and sardines (Schwartzlose, et al., 1999; Chavez et al., 2003).

3. Changes in structural habitat like benthic topography. It can be difficult to separate whether these drivers are natural (e.g. natural disaster or introduction of invasive species (Bellwood et al., 2004)) or anthropogenic (e.g. clearing mangroves or dynamite fishing in coral reefs (Mumby, et al., 2004)).

Regime shifts tend to occur over short periods of time, while the timescale of the new altered state is long and often irreversible (DeYoung et al., 2004; Hughes, 1994). As seen in the case of the Caribbean coral reef, a decade prior, persistent overfishing and nutrient overload burdened the system (Mumby et al., 2004; Bellwood et al., 2004; Hoegh-Guldberg et al., 2007). Tipping points were exceeded, and a regime shift occurred in the space of 1 year, resulting in a new habitat of a thick algae dominated system with extremely low diversity. These impacted areas haves remained in this state for the last 20 years (Hughes, 1994; Scheffer et al., 2001). Regime shifts can occur over a range of spatial scales, from a few miles (e.g. a coral reef (Mumby, et al., 2004)), to a few hundred miles (e.g. the northwest Atlantic Scotian Shelf shift (Frank et al., 2005)), to thousands of miles (e.g. North Pacific basin (Hare and Mantua, 2000)), or even globally (e.g. Global warming (Chavez et al., 2003)). Large scale shifts can be very difficult to manage sustainably, as they require multi-country cooperation and management (DeYoung et al., 2008). Therefore, it is of great importance to assess the vulnerability of local regions in order to prevent or at minimum predict large scale shifts to then enforce measures to alleviate pressures.

In recent years, planetary warming has been accelerating (IPCC, 2018). Oceans have a huge capacity to store heat and have had a historically robust capability to buffer temperature change over daily, annual, and even decadal time scales (Burrow et al., 2011). However, marine species are unprepared for the intense temperature increases associated with global warming (Tewksbury et al., 2008). Oceans absorb heat and remove CO2 from within the atmosphere, created by anthropogenic activities such as burning fossil fuels. This causes a decrease in pH levels, causing ocean acidification. This directly impacts the growth, development, survival, and consequently the abundance of a wide range of species, amplifying the effects of global warming (Doney et al., 2009, 2020).

Temperature increases are predicted to alter the overall structure and dynamics of entire marine communities (O'Connor et al, 2007; Pinsky et al., 2013; Cheung et al., 2013). This change in temperature has and continues to shift the ranges of many marine species to higher latitudes (IPPC, 2018), one example is northward range expansion of great white sharks (*Carcharodon carcharias*) into the Northwest Atlantic. Sightings are now considered common with an increasing presence (Bastien et al., 2020). Ocean warming will be detrimental for polar marine fauna who are trapped within thermal dead ends in their range e.g. Arctic species (Cheung et al., 2009). Tropical marine species are also highly sensitive to temperature changes (Stillman, 2003; Hoegh-Guldberg et al., 2007). In recent years, coral bleaching events induced by high temperatures are becoming more frequent and widespread. Scientific research suggests we may lose all coastal coral reefs if temperatures continue to rise (Logan et al., 2014; Palumbi et al., 2014). Not only will temperatures increase, changes in precipitation patterns, rate of sea level rise, changes in atmospheric and oceanic circulation and the intensity and frequency of large storms are on the rise (Trenberth, 2011). The magnitude of these physical changes will subsequently continue to progressively effect all oceanic biota (Stillman, 2003; Trenberth, 2011; Pinsky et al., 2013; Cheung et al., 2013). As such, global warming may be an important trigger for regime shifts in the future, causing further loss of biodiversity.

Impacts on marine ecosystem services (ES)

Our human relationship with the marine environment is defined by the ES benefits they provide to society (Costanza et al., 1997; Haines-Young, 2012). ES are the direct and indirect contributions of nature to human wellbeing, such as fishing (UNEP, 2020). Globally, 60% of ES have already been degraded by human impacts (Palmer et al. 2004; Millennium Assessment 2005; Palumbi et al., 2009), a value which is continually increasing as populations and demand increase. Generally, ES are divided into 4 groups: provisioning, regulation, culture, and support (Costanza et al., 1997; MEAB, 2005). ES provide food, shelter, climate regulation, waste recycling, and many other mechanisms fundamental to human wellbeing (Palmer et al. 2004; Covich et al., 2004; MA, 2005; Palumbi et al., 2009). Despite the ecological, economic, and recreational importance of ES, the biodiversity that underpins them is being lost at an unprecedented rate (IUNC, 2020).

By altering oceanic function there are direct consequences on ES (MA 2005; Palmer et al. 2004; Palumbi et al., 2009). For example, ocean acidification is resulting in a decline of calcifiers (e.g. coral, molluscs and plankton) as it inhibits their growth trajectories along with weakening their sensory

organs (Branch et al., 2013; Hofmann et al., 2010). Calcifiers are often integral to the functioning and wellbeing of many systems and provide numerous ES. For instance, molluscs and crustaceans are calcifiers that are highly valuable in commercial consumption (Coolet and Noey, 2009). Scleractinian corals are calcifiers and support a variety of biota that make up the diets of many fished species worldwide (Bryant et al, 1998). Furthermore, the reef structure that they create acts as a physical buffer zone to the coast, providing protection from storm surges and tsunamis (Cooley et al., 2009). Another threatened coastal habitat are mangrove forests, which also act as a storm shield and offers precious shelter for juvenile fish, as well as recycling terrestrial runoff (Palumbi et al., 2009). Oysters were once considered so abundant that they posed a hazard to sea travel (Ingersoll, 1881). They are now functionally extinct in many places around the world (Jackson et al., 2001). Structure forming species like mangroves, coral, kelp, oysters, etc are specifically important because their physical form provides many microhabitats and niches (Stachowicz, 2001; Palumbi et al., 2009).

Marine organisms, primarily fish, make up an enormous proportion of world protein consumption and in many impoverished coastal regions they are the main food source (FAO, 2012). Marine ecosystem collapse, due to overfishing, is a major concern preceding all other negative anthropogenic activities, including climate change and pollution (Jackson et al., 2001; Brashares et al., 2014). As stated by the United Nations' Food and Agriculture Organisation (FAO), over 40 times more wild animal biomass is extracted from the marine environment than on land (FAO, 2012). Research has shown that numerous species harvested for human consumption have become morphologically smaller, less productive, and reproduce at smaller sizes (Jørgensen et al., 2007; McCauley et al., 2012). Further evidence reveals that harvesting species reduces their genetic diversity, adaptive potential and ultimately their resilience (Walsh, 2006; Pinsky and Palumbi, 2014). The most well-known case of overfishing is the 'Cod Disaster' in 1992 where the Atlantic cod (*Gadus morhua*), a species that for over 500 years supported the largest and most economically valuable fishery in the Northwest Atlantic, collapsed and was reduced to less than 0.1% of its pre-harvested level (COSEWIC, 2003).

Hutchings and Reynolds (2004) write an interesting review of data from over 230 marine populations revealing a mean reduction of 83% in breeding population size from historical levels. Large marine vertebrates such as whales (Cetacea), sharks (Selachimorpha), rays (Batoidea), manatees (*Trichechus*), dugongs (*Dugong dugon*), sea cows (*Sirenia*), monk seals (*Monachini*), crocodiles (Crocodylidae), cod fish (*Gadus*), jewfish (*Argyrosomus japonicus*) and swordfish (*Xiphias gladius*), which were once widespread, are now either functionally or entirely extinct in most coastal ecosystems (Bertram, 1973; Estes et al., 1989; Dayton et al., 1998; Casey and Myers, 1998; Kenyon, 1997; Hutchings, 2000; Jackson et al., 2001). It is evident that human activities are affecting all aspects of biodiversity in the marine environment.

Coasts

Coasts comprise less than 5% of the planet's terrestrial landmass (Tiner, 1984) yet the UN estimate that ¾ of the mega cities are coastal and over 80% of human population resides less than 100km from a coast (Jacobsen 2019). Coasts are not only socially important but economically critical therefore it is crucial to understand coastal processes and how they could be affected by anthropogenic activities.

Ocean warming has been linked to extreme weather events, such as storm surges, periods of intense heat waves, flooding, and sea level rise (Stillman, 2003; Trenberth, 2011; Pinsky et al., 2013; Cheung et al., 2013). This is putting serve pressure on coastal zones to survive such intense and repetitive extremes (Tsyban et al., 1990; Klein and Nicholls, 1999) as continued exposure degrades environmental features, decreasing the stability of the habitat and presenting the risk of ecosystem collapse (Rahmstorf, 2002; Steele, 2004; Collie et al., 2004; DeYoung et al., 2004; Lee et al., 2006; DeYoung et al., 2008). Research has shown these pressures often result in a loss of biodiversity and ecosystem goods, functions and services (Tsyban et al., 1990; Klein and Nicholls, 1999; MA 2005; Palmer et al. 2004; Palumbi et al., 2009).

More recently the Intergovernmental Panel on Climate Change (IPCC - the UN body for assessing the science related to climate change) has developed technical guidelines for assessing the impact of climate change in terms of coastal vulnerability (IPCC, 2018). Based on these guidelines the United Nations Environmental Program (UNEP) published a guidebook to aid in identifying the potential consequences on coastal regions due to climate change and offers options to respond (Feenstra et al., 1998). However, they cannot yet be modelled and predicted with confidence (Warrick et al., 1996; Jacobsen et al., 2019). This presents a problem for United Kingdom (UK), as there is a knowledge gap on how our coastal zones are responding to these changes and if regime shifts are already underway. Based on current understanding of climate change, coastal zones of the UK are expected to experience higher tides and an increase in intensity of storm surges (Hulme et al., 2002; Few et al., 2007), as well as an influx of non-native species (Mumford et al., 2010). and reduced biodiversity through overharvesting of species (EAC, 2021).

Shallow intertidal rocky shores

The shore is the transition between the terrestrial and marine environment, due to the movement of water through daily tides and waves (Raffaelli and Hawkins, 2012). This transition gradually produces organisms that are neither fully marine nor terrestrial (Lewis, 1995). Generally, a transitional gradient between diverse environments consists of a mean number of organisms from both sources (Barnes and Hughes, 1999). However, shore habitats largely contain species of marine origin (Kaiser et al., 2011; Barnes and Hughes, 1999). Research suggests that organisms that reside on rocky shores can withstand varying degrees of stress considered a fundamental biological phenomenon (Stephenson and Stephenson 1949; Raffaelli and Hawkins, 2012, Steele, 2013).

Rocky shore ecosystems are globally the most common coastal ecosystem (Emery and Kuhn 1982; Granja 2004; Livore et al, 2021) they are found in the tropics, subtropics, temperate and boreal zones (Emery and Kuhn 1982). Research on a large scale has shown that the trophic structure and function across global rocky shores are considerably similar (Blanchette et al., 2009; Livore et al, 2021). Regionally, studies comparing different biogeographical locations suggest there is a significant variation in abundance of coastal taxa (Bustamante and Branch 1996; Broitman et al., 2001; Menge et al., 2004; Schoch et al., 2006; Livore et al, 2021). On sheltered rocky shores, zones are less obvious (Benson, 2002). Biodiversity is high and mainly dominated by seaweeds due to the lack of strong wave action (Barnes and Hughes, 1999; Raffaelli and Hawkins, 2012; Archer-Thomson and Cremona, 2019). Exposed rocky shores have much lower biodiversity than those of sheltered rocky shores, as organisms need to adapt to stronger wave action which subjects them to harsher environmental conditions (Barnes and Hughes, 1999; Raffaelli and Hawkins, 2012; Archer-Thomson and Cremona, 2019) Here, zones tend to be more clearly defined (Benson, 2002). Barnacles are an example of a species who are well modified for exposure and generally become a dominant species (Colman, 1933). On exposed shores large seaweeds are often absent from the middle shore due to the damaging effect of the waves (Archer-Thomson and Cremona, 2019).

Shore communities are dependent upon two major factors, the tides and wave action. Tides expose organisms to the air, large temperature variation and altering inundation. This results in species which withstand different gradients replacing each other along the shore (Barnes and Hughes, 1999; Raffaelli and Hawkins, 2012). In general, conditions become more stable further down the shore, due to the amount of time underwater. However, as sunlight increases higher up the shore and

competition is generally reduced, species adapted to survive the harsh conditions can potentially do very well (Archer-Thomson and Cremona, 2019). If instabilities are extremely regular, species diversity will be low and even null in some parts of the intertidal zone (Johannesson, 2003).

The replacement of species inhabiting equivalent tidal height has occurred on top of changing zonal boundaries between shores (Little and Kitching, 1996; Knox 2000; Steele, 2013). In the UK this is evident in the presence of fucoid seaweed on more sheltered shores which are then replaced by mussels (Mytilidae) and barnacles (Cirripedia) at the same tidal height on exposed shores (Baker, 1909). This is because wave action on the more exposed shores rips algal fronds from substratum, leaving space for the colonization of barnacles and mussels (Bell and Denny, 1994; Barnes and Hughes, 1999).

Zonation

Zonation differs between shores, in terms of width and degree of overlap (Stephenson, and Stephenson, 1949; Chappuis et al., 2014). Zonal width ultimately depends on the degree of suitable microclimate conditions (Knox 2000). Yet, the order in which organisms are zoned remains the same (Bennett and Pope, 1960; Raffaelli and Hawkins, 2012) and rarely will organisms move to lower tidal levels (Lewis 1955). Rocky shores tend to be highly zoned because of the restricted potential of any species to preform optimally under environmental conditions combined with competition for resources (Dayton, 1971). Therefore, biological factors interacting with physical environmental conditions control species replacement along the transitional gradient (Bennett and Pope, 1960; Baker 1909; Lewis 1955; Stephenson, and Stephenson, 1949; Steele, 2013; Chappuis et al., 2014).

Community structure on rocky shores is evidently influenced by physiological factors, which limit the possible range in combination with competition and disturbances (Connell, 1972; Wieters et al., 2009). This results in the familiar patterns of zonation along the gradients of tidal level (Colman, 1933; Stephenson and Stephenson, 1949; Southward, 1958; Bolton, 1981; Norton, 1985; Chappuis et al., 2014). However, these patterns are delicate and require a balance of limiting factors (Connell 1972).

The basic main intertidal zones on rocky shore in the UK are as follows (Lewis, 1955; Benson, 2002; Raffaelli and Hawkins, 2012):

•The splash zone is the most hostile area to species of marine origin, and only receives splashes of seawater and spray, occasionally submerged during storms. It is generally dominated by lichens and a small number of land vertebrates.

•The upper shore is the area at the limit of the tide. It is only fully submerged for a few hours each day. It is dominated by small periwinkles (*Littorina saxatilis*), barnacles (Cirripedia), limpets (*Patella vulgata*) and various encrusting lichens. Some species of algae such as channelled wrack (*Pelvetia canaliculata*) can be found but species must be adapted to extreme temperature variation and desiccation.

•The middle shore is the main tidal belt that is covered and uncovered at every tidal cycle. This zone is dominated by brown seaweeds, barnacles, mussels, limpets (*Patella vulgata*), crabs (Brachyura), anemones (Actiniaria), and some types of green and red algae. Inhabitants must be equally able to survive being submerged or being exposed to the air.

•The lower shore is only uncovered for a short period during spring tides and has the greatest diversity of the 4 zones due to its stable conditions. It is dominated by large seaweeds such as kelp (Laminaria spp.) and Serrated wrack (Fucus serratus).

•The subtidal zone is not theoretically within the intertidal zone; however, the shallow subtidal zone is occasionally exposed during extreme low water spring tides during periods of high pressure. It is home to more common marine species, including kelps, anemones, fish, and many other marine organisms (Archer-Thomson and Cremona, 2019).

Changes in climate, in combination with the other limiting factors, greatly influence the characteristics of rocky shore organisms (Sims et al, 2004; Hawkins et al., 2008). Research suggests that physical factors mostly define upper zonal limits and boundaries but that biological factors mostly fix lower limits (Colman, 1933; Southward, 1958; Bennett and Pope, 1960; Foster 1971; Bolton, 1981; Norton, 1985; Benson, 2002; Somero, 2010; Chappuis et al 2014). Zonation indicates species which are resource reliant and dependant on competition with each other (Janke, 1990; Barnes and Hughes, 1999; Aguilera and Navarrete, 2012; Raffaelli and Hawkins, 2012). The behaviour of organisms also plays a factor, in terms of where they choose to settle within their own zone of optimal performance (Aguilera and Navarrete, 2012; Raffaelli and Hawkins, 2012).

A common characteristic of shores is the presence of the fucoid family; a brown algal seaweed (Baker 1909). They illustrate the occurrence of zonation typical of intertidal sessile organisms (Barnes and Hughes, 1999). Sedentary organisms refer to animals that move about infrequently or are permanently attached to substratum (Paine and Fenchel, 1994). After settlement and once metamorphosis has occurred, many sedentary animals are immobile e.g. barnacles, sponges (Porifera), hydroids (Hydrozoa), oysters (Ostreidae) etc (Underwood, 1979). Other sedentary animals such as anemones and mussels are capable of very slow movement (Ellis, 2007; Underwood, 1979). Sedentary animals are often filter feeders purifying water quality and are an integral part of the marine food chain (Barnes and Hughes, 1999).

The core physical factors that influence the range and zonal limits of suitable microhabitat for the sedentary of intertidal shores are:

•Shore slope. The steeper the slope, the less width of the substratum lying between a given interval of tidal height. (Schoch and Dethier 1996; Raffaelli 1996; Knox, 2000; Helmuth and Hofmann 2001; Raffaelli and Hawkins, 2012).

• Amplitude of tide. This refers to the change in tidal height (Colman, 1933).

•Wave exposure. The average wave action contributes to the degree of wetting a substratum receives. The greater the wave action, the further zonal boundaries are pushed up shore. Wave exposure also enhances benthic primary productivity because it facilitates nutrient uptake by increasing effective submersion times (Little and Kitching 1996; Raffaelli and Hawkins, 2012; Flores et al., 2015).

•Shore features. This can include the rock type (Nienhuis, 1969), the presence of cracks and crevices (Raffaelli and Hughes, 1978) or rock pools (Wright, 1981) and water quality e.g. levels of pollution, salinity or nutrients (Bassindale, 1943).

•The aspect of the habitat. This affects the degree of drying out known as desiccation, particularly at low tide (Foster, 1971). For example, in the northern hemisphere, north facing slopes are likely to be very shady and damp (Baker and Crothers, 1987).

The proximate factors that regulate sedentary organisms also determine the zonal width of mobile animals. Along with addition of mobility, they must compete for the availability of refuge at low tide (Barnes and Hughes, 2009). An example of this can been observed with the small periwinkle

(Melarhaphe neritoides) which is often confined to rock crevices above high tide level (Raffaelli and Hughes, 1978; Yamanda, 1987; Johannesson, 2003; Chappuis et al., 2014).

The biological factors known to effect zonal limits of all intertidal organisms are interactions of predation (Dayton, 1971; Connell, 1972; Menge, 1976; Menge, 1978; Janke, 1990; Paine and Fenchel, 1994; Raffaelli and Hawkins, 2012), herbivory, also known as grazing (Dayton 1971; Lubchenco, J., 1978; Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983; Williams, 1994; Coleman et al., 2006; Raffaelli and Hawkins, 2012; Flores et al., 2015) and competition for food and space (Dayton, 1971; Menge, 1976; Menge and Sutherland, 1987; Paine and Fenchel, 1994; Janke, 1990; Aguilera and Navarrete, 2012). Competition is an inevitable process, when species overlap occurs, they are forced to lower densities by grazing, predation, or physical factors (Menge, 1976). If competition is prolonged, poorer competitors become locally extinct and the better competitors expand their range (Dayton, 1971; Aguilera and Navarrete, 2012). Competitive ability depends on efficiency and various aspects of performance (Lubchenco and Menge, 1978). Some of these aspects include growth rate or growth form, degree of specialization, reproductive rate, aggressiveness and feeding productivity (Nienhuis, 1969; Yamada, 1987; Nielsen and Jensen, 1990). Higher performance elsewhere (Raffaelli and Hawkins, 2012).

Population ecology

Population ecology refers to the dynamics of species abundance, distribution, and how they change over time (Begon et al., 2009). It explains how populations of organisms interact with the environment, affecting birth rates, death rates, immigration, and emigration (Dempster, 2012).

Renewable resources, like food, control population ecology and are vital to survival (Barnes and Hughes, 1999). Research of environmental factors, specifically temperature, has been confirmed to play a limiting role, impacting feeding productivity (Sanford, 1999; 2002), reproductive rates and larval mortality (Hoegh-Guldberg and Pearse 1995). Other environmental influences such as daily weather conditions like humidity, rain and sunshine can also cause major variations in organism productivity (Helmouth et al., 2006). Diurnal tidal cycles relate directly to activity; many rocky shore organisms like limpets, winkles and crabs are more actively grazing during emersion periods (Little and Kitching, 1996; Barnes and Hughes, 1999).

For sedentary organisms, the physical space available on the substratum is a crucial resource and is the largest population controlling factor (Raffaelli and Hawkins, 2012). This is either primary space like a rock face or as secondary space on a biological surface e.g. kelp. Finding room for growth when space is the limiting factor depends on the death of an inferior individual. Other physical constraints include deformed growth, smoothing, undercutting, or crushing (Dayton 1971). As individuals grow, mean individual mass becomes a control factor of population density. The possibility of density dependant mortality is then decreased by body shape modification or a hindered growth rate (Barnes and Hughes, 1999). Due to the absence of mobility, these sedentary organisms have extremely adaptable growth forms which can be modified to adapt to their localities (Raffaelli and Hawkins, 2012).

Population dynamics differ in mobile animals. Space is not a limiting factor as they can freely move to better conditions. The limiting resources that effect these organisms are directly related to food and availability of protective microhabitats such as holes and crevices. It is very problematic to quantify the availability of resources due to mobility (Colman, 1933; Brosnan, 1992; Archer-Thomson and Cremona, 2019).

In most temperate regions of the world, a seasonal to semi-permanent component of rocky shores is the presence of ephemeral species (Hawkins and Hartnoll, 1983a, Hawkins et al., 1992, Jenkins et al., 2008, Poore et al., 2012, Wieters et al., 2009). They are characterized by short life spans with high productivity (Nielsen and Sand-Jensen, 1990, Steneck and Dethier, 1994). These species, such as green algae (*Ulva, Blidingia*), colonize available substratum at a rapid rate (Lubchenco and Gaines, 1981; Kennish et al., 1996, Williams, 1993, Williams, 1994). Many ephemeral algae lack the evolutionary defences against grazers and therefore are eagerly consumed by a vast range of intertidal and subtidal species, including fish and invertebrates (Aguilera and Navarrete, 2012, Hawkins and Hartnoll, 1983b, Hawkins et al., 1992, Kennish et al., 1996, Lubchenco, 1978).

Evidence shows the defencelessness to herbivory is generally related to lower biomass of ephemeral macroalgae observed on many temperate shores (Coleman et al., 2006, Hawkins, 1981, Nielsen and Navarrete, 2004, Poore et al., 2012, Steneck and Dethier, 1994) and many tropical intertidal shores (Kennish et al., 1996, Menge et al., 1985, Vinueza et al., 2006). Therefore, the mechanisms that permit the abundance and distribution of ephemeral algae are crucial in understanding the pathways that regulate ecosystem functioning and the population ecology of communities found in most rocky shores.

Studying rocky shores

The global change in climate resulting from anthropogenic actives is predicted to severely impact marine ecosystems (Benson, 2002; Helmuth et al., 2006a; Hawkins et al., 2008). The rocky intertidal zone is an outstanding model system to research and then use to forecast the potential impacts that climate change will have on marine systems (Fields et al. 1993, Southward et al. 1995, Sagarin et al. 1999, Helmuth et al. 2006). Under natural tidal cycles, rocky shore organisms experience diurnal variation of sea and air temperatures depending on their gradient of zonation (Connell, 1972). The body temperature of intertidal flora and fauna at low tide are critical determinants of survival and productivity (Benson, 2002; Somero 2002, 2005). These are examples of organisms already living near, or on the edge of, their physiological and thermal tolerance limits due to low tide emersion events (Sanders et al. 1991; Roberts et al. 1997; Hofmann 1999; Somero 2002; Benson, 2002; Tomanek 2002, Tomanek and Sanford 2003; Dahlhoff 2004; Li and Brawley 2004; Davenport and Davenport 2005). Therefore, they are extremely sensitive to changing thermal environments (Helmuth et al., 2006a; Somero, 2010; Han et al., 2018).

Research of rocky shores has long documented change in species range limits and abundances (Benson, 2002; Hawkings, 2008). The early classic research by Wilson (1935) and Yonge (1949) reflects on shore life and demonstrates such changes. They report instances like the appearance and disappearance of the boreal arctic limpet (*Tectura testudinalis*), which was located at its southern limit on the north coast of the UK. A report summarising the Climate Change summit (Frost, 2011) suggests that rising temperatures are causing marine species to travel polewards faster than on terrestrial species, likely due to many having planktonic dispersal phases. An example is the purple topshell (*Steromphala umbilicalis*) which has been documented moving northwards and eastwards the UK coast at 50km per decade (Chen, 2011).

Community structure relating to food webs is comparatively simple and limiting factors are typically clear (Benson, 2002; Raffaelli and Hawkins, 2012). Paine (1966) presented how star fish (*Pisaster ocharceus*) are a keystone species and maintain a high species diversity within their niche. The study showed they thin out their prey populations of mussels, which in turn allows more space for the settlement of other species such as limpets, barnacles, or algae.

Dayton (1971) continued the theories of Paine, building on previous studies examining the biological and physical environmental factors that control mussel-barnacle populations of the upper intertidal zones on Washington's coastline. He used an experimental design with sedentary species to measure levels of competition. He focused particularly on inter-specific competition, and the biological disturbances through grazing and predation. He created an inventive experimental design of fences and cages. By doing so he could look at the limiting factors working individually and in combination. This allowed for the species to be arranged in a hierarchy in terms of competitiveness. His results showed that community structure is controlled by both biological and physical factors which alleviate competition by the added pressure of limiting resources e.g., space on a rock.

Menge (1976) conducted a study in New England, focusing on the main elements of community structure in the mid to high zone of sheltered and exposed rocky shores. The findings on the East coast, were highly similar to that of Dayton's on the West coast. Community structure is determined by physical and biological interactions. These interactions enhance biodiversity in the intertidal zones, eliminating large numbers of the dominant competitors.

Luchencos (1978) created an experimental investigation of algae community structure in mid to high intertidal zones of a moderately exposed shore. His findings confirmed that the species diversity on the shore depended on two things. Firstly, the intensity of grazing, heavy grazing prevented the growth to maturity of all germlings. Moderate grazing allowed diversity to increase as dominant species were kept at bay. Low intensity grazing demonstrated dominant competitors out competing inferior species. The second factor is whether the grazer prefers the flora species which is the superior competitor or inferior. If the inferior algae are preferred, this always causes competitive exclusion by accelerating the competitive dominance. For example, Irish moss (*Chondrus crispus*) is a superior seaweed with spatial domination, therefore grazing or predation on competitively dominant species like Irish moss (*Chondrus* crispis) can promote species diversity by the freeing of substratum space. To maintain species diversity, biological and/or physical disturbances are crucial.

Research suggests that intertidal organisms are relatively easy to study and respond well to experimental manipulation (Barnes and Hughes, 1999; Raffaelli and Hawkins, 2012). Algae and sedentary species can be thinned out, while herbivores and carnivores can be excluded or enclosed e.g. caged or fenced off (Dayton, 1971; Benson, 2002). Intertidal organisms are diverse, abundant and recover rapidly from small scale perturbations. They usually have slow-moving or sessile adult life-stages that are relatively easy to manipulate, and interactions typically occur at a small spatial scale, which is convenient for experiments (Underwood, 2000, Allison, 2004). Studies on intertidal rocky shores have contributed greatly to the development of experimental marine ecology because, among other reasons, the logistical constraints for setting up experimental treatments and adequate conditions are not so severe as in some other benthic marine habitats (Connell, 1972, Paine, 1977).

A classic type of experiment in rocky intertidal habitats is the manipulation of densities of species or guilds of consumers, by removal from or addition to natural assemblages, to study their effects in contrast to unmanipulated areas. Experimental marine ecologists have used this approach extensively to investigate a wide range of processes, with particular emphasis on competition (Connell, 1985; Schoener, 1983; Branch, 1984; Underwood, 1986), predation (Sih et al., 1985, Wootton, 1994, Menge, 1995) and herbivory (Underwood, 1979, Lubchenco and Gaines, 1981, Hawkins and Hartnoll, 1983, Vadas, 1985).

Manual removals or additions are the simplest experimental procedures. They cause the least disturbance to the assemblage, thus minimizing the potential for uncontrolled changes in other factors (Connell, 1974). This approach is, however, only effective for populations of animals displaying territorial behaviour or with limited mobility. In addition, extensive areas are required for

each treatment, and they must be placed at a considerable distance from controls to avoid edge effects. Otherwise, unmanipulated individuals will forage across the boundary of the manipulated area (Hawkins and Hartnoll, 1983).

Manipulating species densities within a rocky shore allow opportunity to explore how the environment responds to change and examine if new alternative states are induced. It is evident that there is a gap in the research of UK rocky shores. Specifically, how they will respond to changes that will occur due to climate change (Warrick et al., 1996; Feenstra et al., 1998; Hulme et al., 2002; Few et al., 2007). As previously mentioned, it is likely that marine ecosystems will continue to shift with increasing anthropogenic and climatic stresses. Hawkins et al., (2008) suggest that the characteristics of rocky-intertidal organisms are greatly influenced by changes in climate. Therefore, it is of great importance to develop a greater understanding of the stability of community structure within shallow marine ecosystems in the UK. Moreover, there has been no published research on the role intertidal UK fish species play in the food chain and if they impact habitat diversity (Barrett et al., 2016). Our coastal habitats are some of our most naturally dynamic ecosystems, homing a variety of specialised species and supporting valuable ecosystem services (Costanza et al., 2014) currently valued at £48 billion (UK NEA, 2020). Therefore, it is imperative that we conserve and protect our native environments.

Summary of literature review:

Regime shifts can be caused by several factors, working in combination or alone, including changes to biodiversity and climate change. They result in reduced ecosystem services and generally poorer levels of biodiversity. However, few studies have examined the dynamics of community change between different states or regimes.

Rocky shores are a useful test-site for examining the dynamics of community or regime change. They function as marine systems but are heavily affected by human activities including climate change. They are also well studied, with many interactions well evaluated. However, research is heavily focussed on algal/invertebrate interactions, and the role of highly mobile species which interact with the system at high tide are poorly understood.

Aim: To assess species' present and overall community states of rocky shore habitats in Southern England and assess if states can be changed by physical disturbance or biological pressures.

Objectives:

- To determine the community states present at 3 rocky shore locations in Spring and Autumn.
- To investigate whether changes in community state can be made through experimental manipulations of boulder mesocosms.
- To examine how communities change as they transition between different states.
- To identify the potential role of mobile fauna, such as crabs and fish, in structuring marine intertidal communities.

Methods

Study Sites

Research was conducted at 3 rocky shore locations (Sandbanks, Swanage and Osmington) along the Jurassic coastline, Dorset. Data collection was carried out from April to September 2021 to take into consideration seasonal variation. These areas show double highwater separated by a short duration ebb tide (ABP, 2021). Both Swanage and Osmington are natural rocky shores habitats showing clear zonation patterns of a rocky shore ecosystem. The Sandbanks site is the only man-made site, consisting of large boulders forming a groyne, which is used primarily as a sea erosion defence mechanism. Rocky shore sites are relatively uncommon around Bournemouth, and these specific sites were chosen due to the presence of large boulders (> 30 x 30 x 30 cm) which had previously shown to be suitable for manipulations of grazer and predator density (Stafford et al. 2015).



Figure 1: Study location one: (50.686671, -1.9383189) Sandbanks. Study location two: (50.629251, 1.943523) Swanage. Study location three: (50.633179, -2.372752) Osmington. *Map generated using ArcGIS.*

Establishing natural community states Sampling

To establish community structure, and whether seasonal changes occurred to community structure, boulder communities were surveyed at the start and end of summer (April and September). At each location (Sandbanks, Swanage and Osmington), 30 boulders were chosen haphazardly within the mid-shore intertidal zone at ~ 1.5m above chart datum (sample size recommended by Crawley, 2015, and also providing 90 points in each season for multivariate analysis, ensuring robust case to variable ratio). These boulders were surveyed by noting the flora and sessile fauna such as barnacle percentage cover and total number of mobile fauna residing on the surface area. This was to understand the current state of each location and monitor natural change over the survey period. Boulders were approximately 30x30x30 cm in dimension, although standardisation was not fully possible. Dimensions were measured in the field and surface area was used to standardise all community analysis results by dividing species counts (but not percentage cover) by the estimated surface area.

Experimentally manipulating community states

This experiment was carried out in the Swanage rocky shore habitat. This site is an east facing bay with a gentle slope, it consists of an intertidal limestone covered shore and is well drained during low tides. Boulders at the location of the experimental manipulations were dominated by algae with very few grazers present, although more complex communities were present > 300m away and used in the community analysis above.

This manipulation aimed to show if regime shifts can be induced, and if alterative states would be achieved using Dayton's (1971) community manipulation techniques. Twenty boulders were randomly selected, a minimum sample size to allow for 'robust' analysis of experiments, as per Underwood (1996), and allowing minimum transportation of grazers from other locations. Boulders were chosen at similar heights in the intertidal area, ~1.5metres above Chart datum, distances between them varied considerably, from between 1 to 5 metres apart, with all boulders in a circular area of ~15 metres radius. The boulders were numbered 1-20 using outdoor waterproof paint safe for aquatic life and photographed for later comparison.



Figure 2 a and b: Shows boulder number 7 at Swanage, a treatment of 20 purple topshells were added, (a) is Premanipulation photographed in June, (b) is post-manipulation photographed in September.

There were 4 treatments used during this study, providing both pulse and press disturbances, and a combination of the two. Boulders numbered 1-5 had 20 purple topshells (*Steromphala umbilicalis*) added and 20% of the Green Algae present scraped off (both press and pulse). Boulders numbered 6-10 had 20 Purple topshells added (press only). Boulders numbered 11-15 had no manipulation and acted as a control treatment. Boulders 16-20 had 20% of the green algae present scraped off, but no

topshells added (pulse only). While availability of topshells meant the exact size could not be standardised, they ranged in size between 7-13mm (maximum shell length).

Boulders were monitored every 2 weeks (exact dates determined by timing of low water) from June to September to assess seasonal change. Flora and fauna were recorded at every survey to monitor community change.





Figure 3a and b: Shows boulder photographed at Swanage. Controls included 20% Green algae scrapped and 20 Purple Topshells added. Numbered with blue aquatic paint.

Interactions of highly mobile species at high tide

As this is an intertidal area, fish may play an important role in the ecosystem and must be taken into consideration when looking at how the system responds to change (Gibson and Yoshiyama, 1999; Raffaelli and Hawkins, 2012; Barrett et al, 2016). Across all three locations underwater imagery was used to identify which fish species use the intertidal zone, as well as to compare biodiversity and abundance between each community state.

Remote Underwater Video (RUV) is a surveying technique commonly used in marine environments (King et al., 2018) as it is considered to be a cost effective, safe and non-destructive method (Folpp et al., 2013). However, within intertidal habitats, even low levels of wave action made traditional RUV deployment impossible as units were moved and tipped over by direct impact with waves. To address this, three GoPro Hero 3 HD underwater cameras were fixed onto boulders at the location sites using a masonry hammer drill. The RUV units were then screwed in the mid-shore intertidal zone at 1.5m ~ above Chart datum, facing a surveyed boulder. Recordings were 30 minutes in duration, allowing for an initial 5minute settlement period and 25 minutes of analysis time (as per Boakes et al. 2022). Samples were taken only on clear days with small/no waves and little/no wind to ensure good underwater visibility between 2-3 metres. Three cameras were deployed at each of the sites once a month, on days with good conditions throughout the season, giving a total of 27 footage samples.



Figure 4a: RUV installation process. Equipment: Masonry hammer drill, screwdriver and GoPro Hero 3.

Ethics statement

All data collection and experimental manipulations were conducted following ethical and health and safety approval from Bournemouth University.

Data Analysis

Establishing natural community states

Community structure was examined using NDMS plots using the R package –Vegan (Oksanen et al., 2020). Differences in communities were determined from visual analysis of the data since different ecological communities had not been predetermined. NDMS plots were produced separately for April and September.

Experimentally manipulating community states

An analysis was also performed on the manipulation results. The data displayed changes in species abundances or percentage cover over the survey period. This was in terms of total number of grazers including topshells, *Fucus* and green algae corresponding to the four treatments. Data was analysed using generalised mixed effect models in R (package lme4) using a Poisson link function (Bates et al., 2015) where species counts of grazers or percentage cover of algae were the dependent variable with treatment, date and the interaction between them being the fixed factors. The rock (a repeated measure) was treated as a random factor.

Interactions of highly mobile species at high tide

Several fish identification guides were used to identify the species that entered the intertidal zone during the ROV deployment (Wheeler, 1969; Muus and Dahlstrom, 1974; Hayward and Ryland, 1995; Howson and Picton, 1997; Dipper, 2001; Sterry and Cleave, 2012). Species composition and abundances were entered into Excel to create a standard table of results.

Results

Establishing natural community states

NMDS plots generally showed separation into three community states. Stress values were relatively high, but just within acceptable limits of <= 0.2 (Dixon, 2003; Oksanen, 2007; Zorz, 2019). Regardless of the location, a barnacle dominated community, a prominently green algae community and a mature (brown and red) algae and grazer community could be found. While some community types were more prevalent in some sites, all community types were present in each site.

In April, Osmington shows many boulders with a mature algae and grazer community, whereas Swanage shows more boulders with a green algae community (Fig 2a). Yet both natural sites still have evidence of boulders that fall into all three defined community types. In contrast the data for Sandbanks, the only man-made site, seems to show no dominance of a single state, with data points widely spread across all three community types. The September data analysed by NMDS plots (Figure 2b) seems to show slightly less defined trends than April. However, it is still clear that Osmington (natural site) has a higher proportion of boulders that fall into the mature grazer/algae community group. Swanage (natural Site), similar to the findings in April, has a majority of boulders within green algae state. Once again Sandbanks (mad-man site) shows no specific state with boulders recorded in all communities.

Experimentally manipulating community states

Both the number of grazers and the coverage of green algae on the boulders varied over time and between the different experimental treatments (interaction term of mixed model p < 0.001 in both cases). For *Fucus* cover, the model would not converge using a Poisson link function so a standard mixed model was used. The interaction term was not significant (p = 0.074). However, differences did occur between treatments (p = 0.006).



Figure 5a: Data collected from Sandbanks, Swanage, and Osmington in April. NMDS Plots represent community structures on boulders from the three study locations. Stress = 0.19



Figure5b:Data collected from Sandbanks, Swanage, and Osmington in September. NMDS Plots represent community structures on boulders from the three study locations. Stress = 0.20

In terms of grazers, there was an initial fall in grazer numbers following the initial manipulation in the treatments with grazers added, but the number then remained steady for the remaining monitoring period (Figure 6a). While it is likely that these grazers are the experimentally added species (as few grazers were present prior to the manipulation) this cannot be confirmed as the additional grazers were not marked. Green algae cover fell in all treatments over the course of the summer. However, this was much more pronounced in the treatments with additional grazers present. The initial removal of green algae appeared to have little long-term effect on its abundance – either in isolation, or when combined with the addition of grazers (Figure 6b). The abundance of *Fucus* did increase in some treatments However, no clear trend with grazers could be seen, as the increases were seen in treatments with grazers added and green algae removed (Figure 6c).



Figure 6a: Mean percentage cover of Grazers recorded for each of the four different treatments represented by error bars over the manipulation period (June – September) surveyed at Swanage. Mean Values (+/- 95% confidence intervals based on mixed effect models) for time and for the different experimental treatments (a) Green algae cover (b) Grazer number (c) Fucus percentage cover.



Figure 6 b: Figure 6a: Mean percentage cover of green algae recorded for each of the four different treatments, represented by error bars, over the manipulation period (June – September) surveyed at Swanage. Mean Values (+/- 95% confidence intervals based on mixed effect models) for over time and for the difference experimental treatments (a) Green algae cover (b) Grazer number (c) Fucus percentage cover.



Figure 6a: Figure 6a: Mean percentage cover of Fucus recorded for each of the four different treatments represented by error bars over the manipulation period (June – September) surveyed at Swanage. Mean Values (+/- 95% confidence intervals based on mixed effect models) for over time and for the different experimental treatments (a) Green algae cover (b) Grazer number (c) Fucus percentage cover.

Interactions of highly mobile species at high tide

Family	Common name	Scientific	Osmington	Sandbanks	Swanage	Total Individuals
Labridae	Corking Wrasse	Crenilabrus melops	3	0	0	3
Labridae	Goldsinny Wrasse	Ctenolabrus rupestris	2	0	2	4
Gadidae	Bib/Pout	Trisopterus luscus	4	0	2	6
Labridae	Ballan Wrasse	Labrus bergylta	2	0	1	3
Ammodytidae	Lesser Sand eel	Ammodytes tobianus	20	0	4	24
Blenniidae	Blenny/Shanny	Lipophrys pholis	7	0	3	10

Table 1: Total number of individuals recorded across 27 videos deployed within survey locations.

A total of six fish species were observed entering the intertidal area during high tide. Libridae was the most common fish family observed with three separate species identified: Corking Wrasse (*Crenilabrus melops*), Goldsinny Wrasse (*Ctenolabrus rupestris*) and Ballan Wrasse (*Labrus bergylta*). Yet the highest abundance of a single individual species was the Lesser Sand Eel (*Ammodytes tobianus*) noted at twenty-four individuals.

Discussion

Establishing natural community states

Between April and September there was no change in the types of community state present on the three rocky shores studied. Space occupying species (either barnacles, green algae or brown algae) appear to determine the community state present on the rocky shore.

Osmington presents more boulders in the mature brown algae and grazer community state pointing towards a slightly more developed succession habitat with the wider variety and density of species. Whereas Swanage shows more boulders with an early successional or highly disturbed green algae community. Sandbanks shows a variety of community states with no clearly dominating community state.

Experimentally manipulating community states

The results show that when topshells are added to the system we can see a drop in the percentage of green algae present. This is because the topshells graze on the algae (Raffaelli and Hawkins, 2012), potentially leaving room for new colonization. This grazing of green algae could allow for the observed increase of *Fucus*, though the results were not conclusive as this increase was only seen on some boulders. This increase of slower growing or later succession seaweed ultimately provides refuge for grazers (Benson, 2002). This could potentially result in positive feedback and determination of more stable alternative states.

When topshells are added in combination with the removal of green algae we see similar results to when topshells only were added. It seems topshells have the most significant effect on the system as a long-term pressure (press pressure) rather than the short-term pulse pressure of removing seaweeds. Therefore this study suggests that topshells (*Steromphala umbilicalis*) could be important in the development of more complex communities on rocky shores in the UK.

Alternative states and tipping points on Rocky Shores

As previous research suggested, rocky shore species are easy to study and manipulate (Barnes & Hughes, 1999; Raffaelli & Hawkins, 2012). Moreover, Luchencos' (1978) theories have been confirmed - that moderate grazing allows biodiversity to increase as dominant species like green algae were kept at bay. This study highlights that alternative states can be induced on rocky shores by carrying out small scale manipulations in key marine fauna abundance.

Following the addition of grazers to a very simple, green algal dominated community, the community composition changed rapidly within the course of two weeks. Significant reductions of green algae were found, and the added grazers continued to inhabit the boulders they were added to. While the community structure of these boulders would still have been dominated by green algae, there was considerable bare rock, potentially available for colonisation, with some evidence of increases in *Fucus* over the time of the study. Colonisation of new species on rocky shores is dependent on 'supply side ecology' or recruitment, most often from planktonic sources (Menge and Sutherland, 1987; Chambers and Trippel, 2012), with recruitment being highly seasonal in UK waters (Brunel et al., 2007; Chambers and Trippel, 2012). As such, the creation of bare rock by the grazers may facilitate the colonisation of new species once the supply of those species become available in the area This could be considered an essential part of a tipping point between community states. While falling outside the formal study period for this thesis, it has been noted that the site of the manipulations conducted in 2021 has altered significantly in summer 2022, being dominated by Fucus and with considerably more grazers of multiple species. While on some boulders, these changes could have been facilitated by the manipulations in this study, factors such as storm disturbance or sand scour during the winter months could also have removed green algae, allowing more room for colonisation (Bertocci et al., 2005; Vaselli et al., 2008).

The study suggests that tipping points begin to occur as soon as the alteration is induced, in this case the grazers became dominant over the green algae. Over a longer period, this would result in room for a wider diversity of space occupying species, as demonstrated by the increase in alternative seaweed species e.g. *Fucus*. The experimental manipulation evidently created a new alternative state by adding a low diversity of grazers therefore this rocky shore system exhibits a relatively low ecological resilience (Scheffer et al., 2012). However, if they were to be removed again, it is speculated that algae would quickly recolonize. If this was the case this system would have high adaptive capacity (Chambers et al., 2019), and the states created by the experiments would not be considered stable alternative states but a mechanism through which a regime shift could potentially occur.

Implications of the study for conservation and restoration of marine systems

While the links between biodiversity and ecosystem resilience are inconclusive, the weight of evidence suggest that increased biodiversity creates more complex and resilient systems (Loreau and De Mazancourt, 2013). While protected areas are typically of high biodiversity value, more emphasis is being placed on ecosystem restoration, especially in marine and coastal environments (e.g. seagrass, saltmarsh – Bayraktarov et al., 2016; Bayraktarov et al., 2020), with most of the work focussed on restoring the habitat forming species (e.g. planting seagrass). While not directly investigating ecosystem restoration, it is clear from this study that increasing the complexity of a system (e.g. by ensuring grazers are present) can alter the development and community structure of a system, and thought could be given to the need for important 'companion species' in restoration projects (e.g. algal grazers in seagrass restoration). Equally, the role of invasive species can be highly detrimental to marine communities (Bax et al., 2003; Bellwood, 2004). Rocky shores with a poor species diversity (such as those found on man-made structures, often dominated by green algae) can

be hotspots for invasive species, and aid in their dispersal (Dafforn et al., 2009; Geburzi et al., 2018). Consideration of improving these habitats would not only involve consideration of the provision of microhabitats (e.g. Hall et al. 2018), but also the direct addition of species which may increase the complexity of the system, and its resilience to invasive species colonisation.

Interactions of highly mobile species at high tide

From this study it is evident that a variety of fish utilise the intertidal zone, a total of 6 different species were observed and overall, 51 individuals. Ecological studies of intertidal fish are important because fish are often bio-monitors of ecosystem health. Interestingly, no fish were observed at Sandbanks in the RUV footage, although observational data has shown there is evidence of fish. Sandbanks is a man-made habitat and suffers from a very busy summer period, during which visitor numbers drastically increase. Barrett et al., (2016) suggests the absence of such fish indicates an environment has been subjected to disturbance or stress. Investigations on the influence of human presence on rocky shores globally found that fish abundances in all species are reduced in the more heavily visited areas (Addessi, 1994; Brosnan and Crumrine, 1994; Deepananda and Macusi, 2013). Swanage and Osmington are natural sites with a more complex offshore habitat. This, in combination with less disturbance, provides a more desirable environment for fish.

In terms of the role these fish play in the food chain, few studies have assessed the diets of intertidal fish. Evidently, there is a large knowledge gap in this area (Barrett et al., 2016). Past research suggests that the main prey species of many intertidal fish is green seaweed and barnacles (Horn et al., 1998), both of which were found on all of the surveyed rocky shores in this study and formed community states.

Blennies (*Lipophrys pholis*) were found abundantly at both natural sites. They are considered a predatory fish feeding the limbs of barnacles (Neal, 2005). Past studies suggest that *Lipophrys pholis* are most often found in shallow rock pools and prefer areas with substantial amounts of coralline algae (Dipper, 2001; Neal, 2005) which is found at these sites. Pouting is also thought to be predatory, although some studies suggest they are mainly scavengers (Wheeler, 1969; Muus and Dahlstrom, 1974; Dipper 2001). Again, this species was found at both sites.

The Labridae family was observed at Swanage and Osmington's rocky shores. These wrasse species are thought to be omnivores, feeding mostly on molluscs, including limpets and mussels, crustaceans and algae (Wheeler, 1969; Muus and Dahlstrom, 1974; Dipper 2001). Research suggests they prefer shallow rocky areas with an abundance of seaweed (Ager, 2008). This concept was reinforced by the evidence found at the two natural locations (Swanage and Osmington) in this research.

Sand eels (*Ammodytes tobianus*) were only found at Swanage. This species is known to swim in schools. They bury themselves 20-50 cm deep in the sand during the winter and dart for sand at any sign of danger (Rowley, 2008). Their diet consists of zooplankton and some large diatoms as well as worms, small crustaceans and small fish (Wheeler, 1969; Muus and Dahlstrom, 1974; Dipper 2001). Swanage has an abundance of sand bottom patches and in combination with availability of food this makes an ideal habitat. Although, as a common UK species it is probable that they are present at the other two sites which similarly have expanses of sand bottom.

As footage was captured from 3 viewpoints, the entire habitat, is not taken into consideration. More-over It is important to consider that deploying cameras may cause minor disturbance (Cappo et al., 2003). Accordingly, it is likely that real abundances of fish populations were underestimated, higher densities and species abundances are probable (Cappo et al., 2003; Zarco-Perello and Enríquez, 2019).

Conclusions

Evidence has suggested the fragile nature of the UK's most common shallow marine ecosystem. Through experimental treatments of keystone species, alternative states can be achieved. From the results 3 relatively stable states can be identified on these UK rocky shores, some more complex than others. Additionally, rocky shores in a simple system, demonstration that the press disturbances in this case adding the grazer purple topshell to the system is more important than the pulse disturbances of removing green algae. This study indicates that adding grazers to a shallow marine environment will cause the biodiversity to increase over time. Therefore, in the bigger picture this research opens up the idea that manmade structures in the marine environment have the opportunity to become more biodiverse by adding grazers to the system.

This research may be viewed as the first evaluation of UK intertidal fish via RUV, highlighting the important role fish play in the rocky shore community. This proves that community state, complexity and human presence significantly influence fish abundance and diversity. However, it is apparent that further research is needed to assess their diet and examine their position in the food chain.

This study can be used as a UK example of the potential regime shifts to come, as projected to globally affect all marine habitats as anthropogenic and climatic stresses increase (Jackson et al., 2001; Hulme et al., 2002; Few et al., 2007; Brashares et al., 2014). There is a current knowledge gap in how rocky shores will respond to anthropogenic changes and what changes will affect them most. Furthermore, research is needed to develop a greater understanding of where tipping points will occur, what alternative states could be induced and how this could affect ecosystem services.

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