

Chapter 10

North-East Pacific*Interactions on Intertidal Hard Substrata and Alteration by Human Impacts*

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10.1 | Introduction

The flora and fauna of the rocky intertidal zone are among the most biologically diverse on the planet – not in terms of species richness, but of the diversity and density of higher taxonomic categories. All of the major animal phyla can be found in the rocky intertidal, sometimes with representatives of each inhabiting a single rock or boulder. In addition to this phylogenetic diversity, the rocky intertidal may be one of the most ancient of habitats because it is a necessary and continual result of celestial mechanics set in motion prior to the diversification of life. When advising readers to ‘... look from the tide pool to the stars and then back to the tide pool again’, Steinbeck and Ricketts (1951) seemed to underline this point while advocating for a holistic approach to ecological research. A few years earlier, Ricketts and Calvin set out to comprehensively document what was then known about the ecology of the north-eastern Pacific (NEP) rocky intertidal in their classic book, *Between Pacific Tides* (Ricketts et al., 1985).

Since the first edition of *Between Pacific Tides* (1939), the NEP has become widely recognised as an ideal natural laboratory for experimental ecologists and as a platform for more observationally focussed ecologists seeking to

understand macroecological and biogeographical patterns. It is, of course, outside the scope of this chapter to attempt a comprehensive review of this extensive research. Rather, we focus on a couple of broad topics that are central to our current understanding of fundamental ecological, evolutionary and conservation topics that have benefitted from NEP rocky intertidal case studies. The first half of the chapter deals with recent work on the biotic and abiotic factors influencing patterns of range wide abundance and distribution of species, and how such patterns are being affected by human impacts. The second half reviews the latest research on the role of direct and indirect human impacts on top-down and bottom-up control of rocky intertidal community structure and functioning.

10.2 | Biogeographic Context

The NEP coast spans from the Baja California peninsula (Pacific coast) to Alaska (Figure 10.1). The southern boundary of the NEP is well defined by a biogeographic break at Magdalena Bay (~25°N). The region from 25°N to ~5°S (including the Gulf of California) constitutes the tropical eastern Pacific (TEP), while south of ~5°S (Paita, Peru) to Tierra del Fuego is the south-eastern

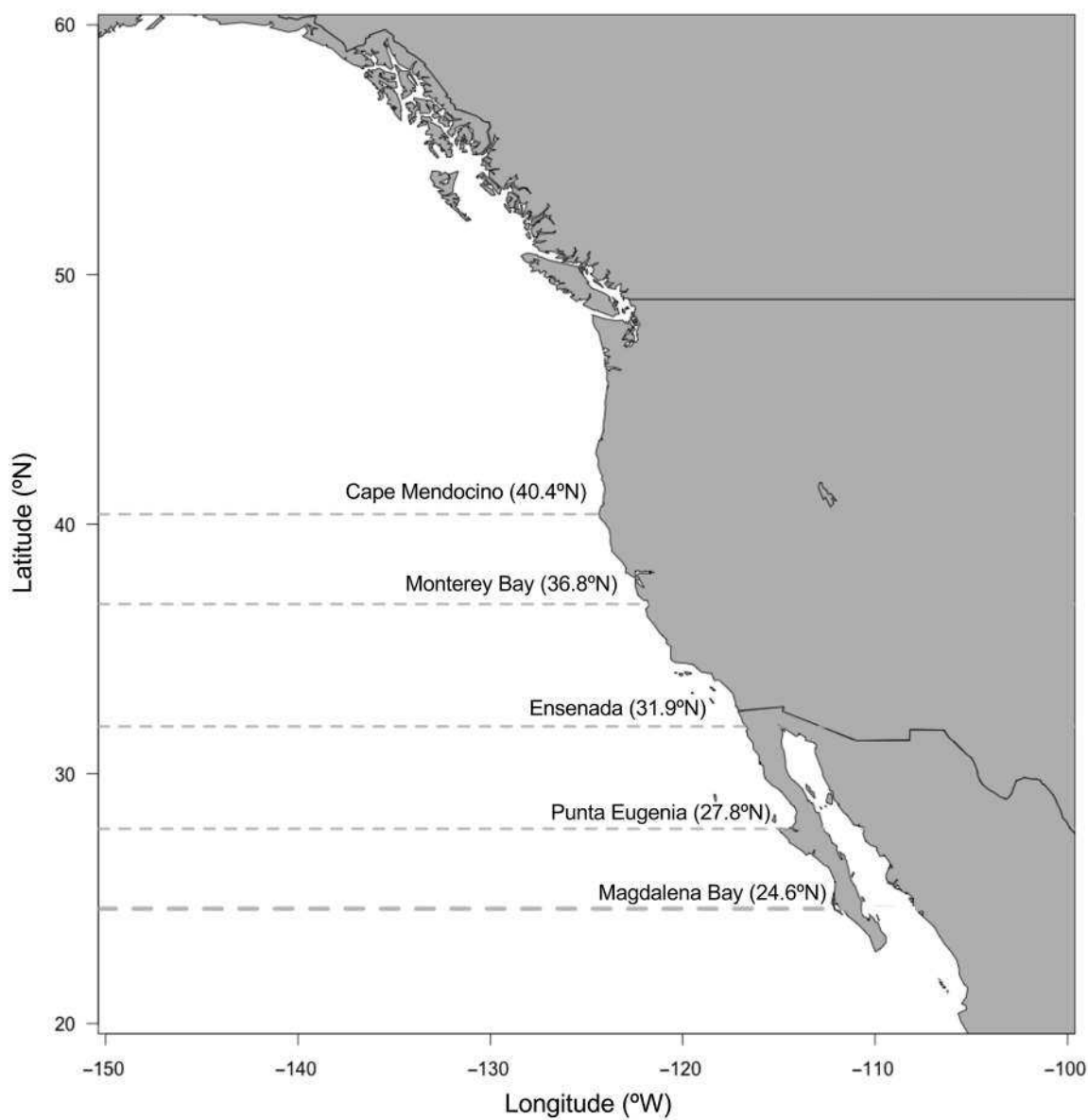


Fig. 10.1 Map of the NEP with latitudes of locations mentioned in the text. The thick dashed line at Magdalena Bay marks the southern edge of the NEP.

Pacific (covered in Chapter 12). Very few rocky intertidal species commonly found in the NEP or the south-eastern Pacific have ranges that extend into the TEP (and vice versa), giving the eastern Pacific rocky intertidal a well-defined biogeographic structure at this broadscale (Fenberg and Rivadeneira, 2019).

10.3 | Range-Wide Abundance Patterns

The largely north–south trending NEP coastline essentially means that species restricted to the intertidal zone have a linear, one-dimensional

geographic range, with single geographic locations representing their northern and southern limits and range centres (assuming there are no major range discontinuities). As a result, ecologists have utilised NEP rocky intertidal species to ask basic biogeographic questions that are more difficult to assess for species with relatively complex geographic ranges (e.g., birds and mammals or pelagic and deep-sea species). For example, Sagarin and Gaines (2002a) used NEP rocky intertidal species to test the hypothesis that individuals of a species are more common in the centre of their geographic ranges, commonly referred to as the ‘abundant centre hypothesis’ (ACH; Brown, 1984). Of the twelve species analysed throughout their ranges, only two had their highest abundances in their range centre. Prior to this study, the ACH was a common assumption in the ecology and evolution literature. Subsequent tests of the ACH of NEP rocky intertidal species have been also shown to be equivocal (Sagarin and Gaines, 2002b; Fenberg et al., 2014), and, at least in one case, an observed abundant centre is thought to be partly due to human impacts. This case is the owl limpet, *Lottia gigantea*, which is an ecologically important space occupier in the mid-/high-intertidal zone (Stimson, 1970; Lindberg et al., 1998; Fenberg and Rivadeneira, 2011; Fenberg, 2013). It ranges along the Pacific coast of central Baja Sur (26.05°N) to Mendocino County in northern California (39.25°N). Individuals are highly abundant towards the centre of its geographic range (southern California/northern Baja), where *L. gigantea* populations have experienced a long history of size-selective harvesting pressure (Kido and Murray, 2003; Sagarin et al., 2007; Erlandson et al., 2011; Fenberg and Roy, 2012). Females are highly territorial, defending their algal ‘garden’ from intraspecific (usually smaller males) and interspecific competitors (Stimson, 1970; Wright, 1989). Territory size (i.e., home range size) is highly correlated with shell size (Fenberg, 2013). Thus, the number of individuals physically able to occupy a given area will be higher for harvested populations because small- to medium-sized individuals have smaller home ranges/territories and are not generally harvested. Therefore, harvested populations (primarily in the range centre) should have a higher

density of individuals compared with populations that do not experience the effects of harvesting, contributing to the observed abundant centre pattern (Fenberg and Rivadeneira, 2011).

Regardless of whether species exhibit an abundant centre, a more meaningful question to ask is how range-wide abundance patterns are driven by biotic, abiotic and increasingly, anthropogenic factors (see earlier) over space and time (Sagarin et al., 2006). Understanding the causes of species’ abundance patterns will give us valuable insights to basic yet poorly understood concepts in ecology and evolution, such as: (1) what causes species range limits?; (2) how does the shape of a species’ range-wide abundance pattern influence probability of range expansion and/or contraction over time?; (3) do ecosystem processes (e.g., nutrient cycling, predator–prey interactions) vary across spatial gradients in concert with range-wide abundance patterns of keystone or foundation species? and (4), how do ecological and evolutionary traits such as body size, trophic level, dispersal potential and phylogenetic relationships interact with physical variables like sea surface temperature (SST) and habitat availability to shape range-wide abundance patterns?

Focussing such questions on species restricted to a single habitat type (e.g., rocky intertidal) across a large spatial gradient, such as the NEP, will provide ecologists with a useful model system to inform hypothesis testing across other habitat types and taxonomic groups. Indeed, much of the raw biological and physical data are already available from long-term monitoring and biodiversity survey projects, most notably from the Multi-Agency Rocky Intertidal Network (www.marine.gov) and the Partnership for Interdisciplinary Studies of Coastal Oceans (www.piscoweb.org). These consortia have surveyed (and resurveyed) over 100 rocky intertidal sites across the NEP, from central Baja to south-east Alaska. These ongoing surveys are used for monitoring species of conservation concern; (Miner et al., 2006; Sagarin et al., 2007; Crosson et al., 2014; Jurgens et al., 2015; Raimondi et al., 2015) and for providing the baseline information for large-scale biogeographic studies (Blanchette et al., 2008; Fenberg et al., 2015; Rivadeneira et al., 2015).

10.4 Northern Range Limits and Dynamics

Identifying the biological and physical factors that drive species range limits has been an ongoing focus of ecology and evolutionary biology (Sexton et al., 2009). This emphasis is partly because fundamental patterns of the biosphere, including global patterns of diversity and biogeographic structure are a function of the geographic distribution of species range limits. Thus, a general understanding of the factors that influence range limits are needed to explain these patterns and their macro-evolutionary origins. In a more contemporary sense, the causes of range limits are also needed to understand the susceptibility of species' ranges to alteration in response to modern climate change and other human impacts (e.g., habitat alteration). Given their relatively simple geographic ranges, NEP rocky intertidal species have become useful model organisms for such studies over the past decade, and some interesting patterns are beginning to emerge.

Broadly speaking, there are three causal mechanisms that may be used to explain range limits (Holt, 2003; Dawson et al., 2010): physical barriers to dispersal, genetic impoverishment and migration load. For NEP rocky intertidal species, physical barriers to dispersal are usually associated with habitat gaps (e.g., long stretches of sandy beach), areas of intense upwelling and/or abrupt SST changes (e.g., Point Conception and Cape Mendocino in California and Punta Eugenia in Baja). Some of these locations are well-known biogeographic and phylogeographic breaks, meaning that they often coincide with species range limits and population genetic divergence within species (Blanchette et al., 2008; Kelly and Palumbi, 2010; Fenberg et al., 2015). Whether these locations coincide with a species' border or phylogeographic break partly depends on its dispersal capability (Wares et al., 2001; Gaines et al., 2009; Pelc et al., 2009; Fenberg et al., 2015). Assessing the relative importance of which variables limit dispersal at the range edge (and, hence, set range limits) can be especially

challenging for species for which their ranges end in locations without obvious physical barriers. Range edge recruitment success (particularly for species with pelagic larvae) may be subject to a complicated set of species-specific interactions between nearshore oceanic processes and factors such as the density of source populations, ability for self-recruitment, coastal geography, habitat availability, thermal tolerances, season and post-settlement survival. Gaines et al. (2009) provide a nice overview of dispersal and geographic range limits with good examples from the NEP rocky intertidal (focussing on Point Conception). Therefore, we will build on their review by largely focussing on a few case studies published from 2010 onwards, particularly for species that have experienced dynamic northern range limits where there are no obvious physical barriers to dispersal.

The northern range limit of the barnacle *Tetraclita rubescens* has expanded by at least 200 km since the 1970s, from San Francisco (37.8°N) to the Oregon/California border (42°N; Dawson et al., 2010). During this period of expansion, individuals also increased in abundance within the expanded portion of its range (Dawson et al., 2010). Overall, however, this species is substantially more abundant in the central and southern portions of its range (Sagarin and Gaines, 2002a; Blanchette et al., 2008). Using these abundance and distribution data in combination with a population genetics and theoretical framework, Dawson et al. (2010) have inferred the most likely causes of the range limit and recent expansion. They argue that a physical barrier to dispersal is not the underlying cause of its range limit considering the recent range expansion, the largely uninterrupted extent of rocky intertidal habitat in the expanded range, the long dispersal potential (18–26 days), lack of genetic population structure and high genetic diversity. They also reject genetic impoverishment as a potential cause. Genetic impoverishment may cause range limits if immigration to the range edge population(s) is low and must therefore be sustained by self-recruitment. Populations sustained by self-recruitment may have limited genetic variance needed to adapt to novel conditions (i.e., beyond

the limit; Holt, 2003). In addition, range edges subjected to genetic impoverishment would be characterised by small peripheral populations with low genetic diversity and high genetic differentiation compared to more central populations. *T. rubescens* has high genetic diversity and lack of population structure found throughout its range, thus genetic impoverishment is thought to be an unlikely cause for the limit.

Rather, Dawson et al. (2010) suggest that migration load is the more likely candidate. If range edge populations are demographically dependent on immigration from range centre populations, then an influx of locally maladapted alleles may inhibit the opportunity for selection at the range edge, limiting the genetic scope for adaptation beyond the range edge. This genetic constraint is commonly referred to as 'migration load' (Dawson et al., 2010). Migration load would be observable if range edge populations are genetically diverse and weakly differentiated from the rest of the range. Range edge populations experiencing migration load would need to somehow overcome the flow of maladaptive alleles and attain the genetic capacity to adapt to the presumably harsh physical or biological environment beyond the range edge for expansion to occur. If, however, the environment beyond the range limit changes enough that adaptation is no longer needed, then range expansion is more likely.

The post 1970s range expansion of *T. rubescens* coincides with a SST warming of $\sim 0.8^{\circ}\text{C}$ along the California coast (Sagarin et al., 1999). Throughout its range, *T. rubescens* is most abundant in the relatively warm waters of southern California and Baja Mexico (Sagarin and Gaines, 2002a; Blanchette et al., 2008), suggesting that it is well adapted to warmer conditions. Thus, modern warming beyond the historical range edge would help facilitate a range expansion without the need to overcome any maladapted alleles that may have precluded populations to expand prior to the 1970s. If climate change relaxes the negative impacts of migration load (and migration load is a common cause of range limits), then, all else being equal, poleward range expansions are to be expected for NEP rocky intertidal species and generally across habitat types.

Although migration load is argued to be the primary cause of the northern range boundary for *T. rubescens*, a closer look at its range-wide abundance pattern reveals that there could also be at least one physical barrier to dispersal at play. A steep drop in the percentage cover of *T. rubescens* occurs at the northern end of Monterey Bay at Santa Cruz (36.95°N ; Figure 10.2). From Santa Cruz to the modern limit, *T. rubescens* individuals average a cover of 0.0004 per cent, compared to 0.01 per cent in the central and southern portion of its range (data courtesy of www.pacificrockyintertidal.org). Assuming a predominantly unidirectional flow of larvae from central to northern populations, then Monterey Bay could be a 'soft' barrier to dispersal – limiting, but not eliminating immigration towards the northern range edge. Migration load and the soft barrier may therefore act as a two-pronged cause for the range limit. Interestingly, *T. rubescens* (along with other 'southern' species) has increased in abundance at the southern end of Monterey Bay (at Hopkins Marine Station) in recent decades, presumably due to climate warming (Sagarin et al., 1999). This increase in adult abundance should also be mirrored by an increase in larval abundance around Monterey Bay; effectively increasing the chances for larvae to breach the soft barrier, providing more recruits for northern populations and increasing opportunities for range expansion.

Monterey Bay also appears to have an effect on the abundance and recruitment of northern populations of at least two other NEP rocky intertidal species. Like *T. rubescens*, the abundance (adults and juveniles) of the limpets *L. gigantea* and *Lottia scabra* drops sharply from Santa Cruz (at the northern end of Monterey Bay; Figure 10.2) to their respective northern limits (Gilman, 2006; Lehman, 2010; Fenberg and Rivadeneira, 2011; Shanks et al., 2014). Shanks et al. (2014) suggest that the drop in abundance and recruitment north of Monterey Bay is linked with a northern edge of where the kelp, *Macrocystis pyrifera*, form extensive beds. Sites associated with *M. pyrifera* beds (south of Santa Cruz) have higher juvenile and adult abundances compared to their northern ranges, a pattern mirrored by *L. gigantea* (Fenberg and Rivadeneira, 2011). Shanks et al. (2014)

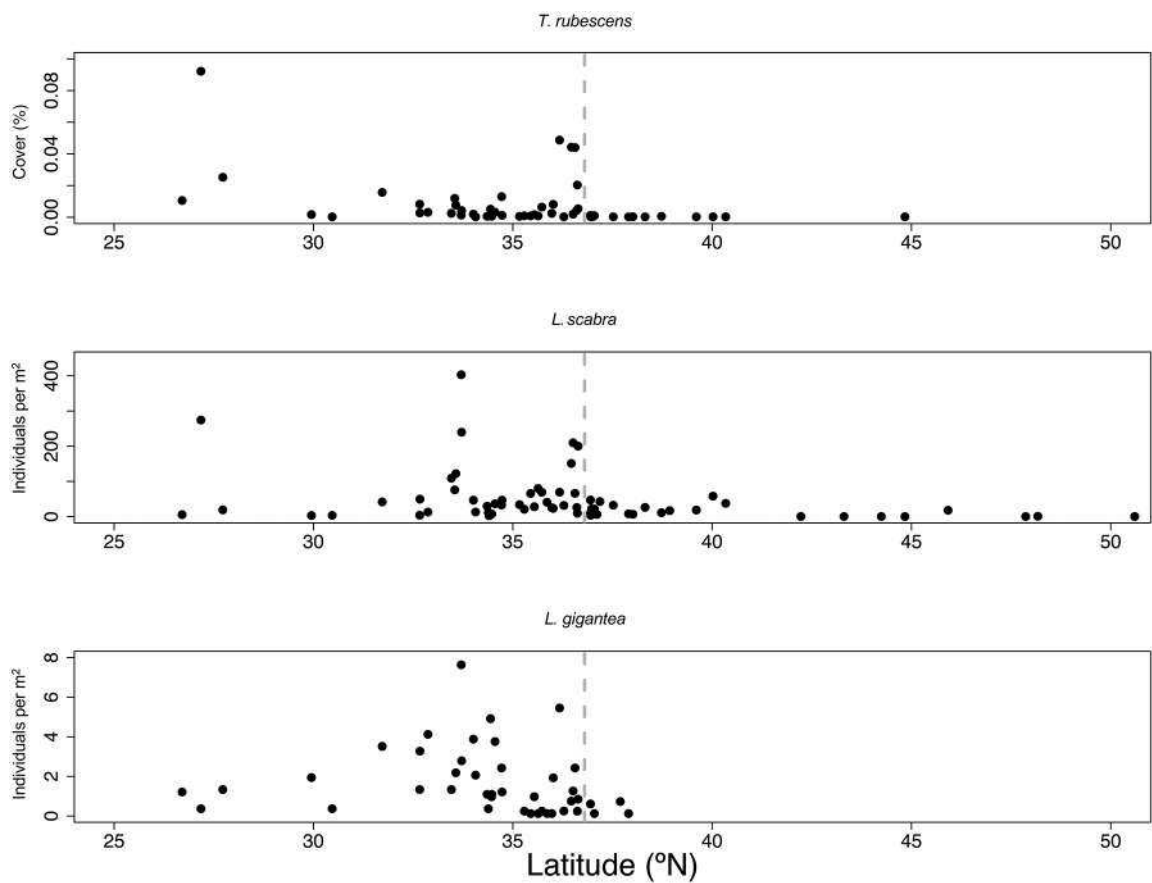


Fig. 10.2 Range-wide abundance patterns of *T. rubescens*, *L. scabra* and *L. gigantea* (data courtesy of www.pacificrockyintertidal.org). The dashed lines represent Monterey Bay (~36.8°N) where abrupt declines in abundance coincide for each species leading up to their respective northern range limits.

hypothesise that *M. pyrifera* beds act to limit alongshore flow (Gaylord et al., 2007, 2012; Nickols et al., 2012) and, therefore, help increase the local retention of larvae. Without these beds, larvae may be transferred away from suitable rocky shore habitat, leading to high larval wastage. The kelp *Nereocystis luetkeana* is more commonly found north of Santa Cruz, but Shanks et al. (2014) suggest this alga is less capable of restricting offshore flow of larvae because (1) it has only one stipe (compared to multiple stipes of *M. pyrifera*), (2) they generally form smaller beds closer to shore and (3) they almost completely die back during the winter (which, at least for *L. gigantea*, happens to coincide with the spawning season; Kido and Murray, 2003). If further study

supports this *M. pyrifera*/larval retention hypothesis, then it would suggest that the northern ranges of these NEP limpets (and possibly *T. rubescens* and other similarly ranging species) could be modulated, at least in part, by this biological interaction. Alternatively, the long sandy beach of Monterey Bay (~50 km) could act as a partial dispersal barrier for the limpets, which have relatively short pelagic larval durations (~6–14 days; Kay and Emler, 2002; Dawson et al., 2014).

Much of what we know about the potential causes of range limits of NEP species come from research on the northern limits of a handful of species that primarily range in the central and northern portions of the NEP (California, Oregon, Washington), where, not coincidentally, many of

the rocky shore ecologists tend to live. Far less is known about the drivers of northern limits of NEP species that primarily range into the southern part of the NEP along the Pacific coast of Baja California. For example, the historical range of the predatory gastropod *Mexacanthina lugubris* used to be entirely confined to Baja California, from Ensenada (31.9°N) to Magdalena Bay (24.6°N). Much like *T. rubescens* and other NEP species (e.g., *Kelletia kelletia*; Zacherl et al., 2003), the range limit of *M. lugubris* has expanded northwards by ~300 km into southern California (33.5°N) since the 1970s (Fenberg et al., 2014). While the range expansion could be a result of warming temperatures and individuals are simply following the edge of their thermal tolerance, other ecological, physical and anthropogenic factors also likely contribute to its recent northern range expansion.

Phylogeographically, the range of *M. lugubris* can be divided into well-defined northern and southern clades, separated by a break (estimated divergence time ~417 Kya) in the mid-peninsular region at Punta Eugenia (27.8°N). This well-defined genetic structure is thought to be due in part to its low dispersal potential (juveniles emerge directly from egg capsules attached to rock). Interestingly, the break is geographically concordant (although divergence times vary) with other phylogeographic breaks for a diverse set of marine and terrestrial species (see later, this chapter). For *M. lugubris*, the northern clade can be characterised by low haplotype and nucleotide diversity, especially in the expanded portion of its range (which is genetic evidence for the expansion) and high local abundances at the historical northern limit. Northern clade populations reside in a region of extensive rocky shore, especially in the vicinity around its historical northern limit, which coincides with a stretch of nearly 100 km of largely uninterrupted rocky shore. Moreover, its primary prey, the barnacle *Chthamalus fissus* is densely populated within the northern clade, again, particularly at the historical northern limit of *M. lugubris*. Fenberg et al. (2014) suggest that the wealth of habitat/food availability at the historic northern limit has helped to facilitate the high local abundance of *M. lugubris*, providing a strong source population that fuelled the northward expansion.

Much like *T. rubescens*, where high and increasing population densities towards its historical northern range edge may have facilitated the expansion, high abundances at the historic northern limit of *M. lugubris* in conjunction with a warming climate and bountiful habitat and food availability may have led to its range expansion. Importantly, however, warming temperatures alone will not necessarily cause a range edge expansion. Whether or not the range of a species expands will also depend upon its underlying meta-population dynamics, range-wide abundance patterns, and habitat and food availability, which can be highly species specific and geographically dependent (Fenberg et al., 2014). For example, intensive human size-selective harvesting of the highly competitive space occupier, *L. gigantea*, may have had an indirect positive effect on the abundance of *M. lugubris* at its historic northern limit. Size-selective harvest of *L. gigantea* could lead to competitive release, allowing other (non-harvested) space competitors like *C. fissus* to become more common. This increase in prey density might subsequently allow its predator, *M. lugubris*, to become more abundant. Thus, the anomalously high local abundances at its historic northern limit and even its subsequent range expansion may be an indirect and partial result of non-climate-related human impacts on species interactions.

The interaction between direct and indirect effects that result in the expansion of a species' range are likely to have ecological and evolutionary impacts for other species as well. These impacts may be particularly noticeable if the expanding species is abundant and a predator, like *M. lugubris*. For example, *C. fissus* alters the shape of its operculum openings when exposed to intense predation pressure by *M. lugubris* (Jarrett, 2009). Morphs with a narrow or bent operculum are more difficult for *M. lugubris* to prey upon. These defensive morphs are significantly more common at the historical northern range limit of *M. lugubris* where both species have high densities. This suggests that high densities of *M. lugubris* drives morphology of its prey. Accordingly, the defensive strategy is not common at a site in the expanded range, where *M. lugubris* abundance is not as high (Jarrett, 2009). But if *M. lugubris*

increases in abundance within its expanded range in the coming years as expected, then it would logically follow that the defensive *C. fissus* morphs will become more common as well. If selection is intense and geographically widespread enough, then this predator–prey interaction may select for microevolutionary change in *C. fissus* morphology within the co-distributed portion of their range.

To put into perspective what we have learned about northern range expansions, it is useful to contrast it with examples of northern range contractions (or local extinctions towards the range edge). For example, both the pelagically dispersing limpets, *L. gigantea*, and *L. scabra*, have very low adult and juvenile abundances towards their respective northern range edges (see earlier). The size structure of their northern populations (north of Monterey Bay) tend to be heavily skewed towards medium- to large-sized individuals at low densities. Similarly, populations within the central range of *Tegula funebris* (northern Baja California and southern California) consist of high densities of juveniles and adults, whereas more northerly populations (Oregon to Vancouver Island) have a patchy distribution, variable local abundances and recruitment appears to be more sporadic (Frank, 1975; Sagarin and Gaines, 2002a; Cooper and Shanks, 2011). Because individuals can live for twenty years or longer (Paine, 1969; Frank, 1975; Cooper and Shanks, 2011; Fenberg and Roy, 2012) and juveniles are rare, it is thought these northern populations are demographically unstable and prone to local extinctions. Studies of other NEP gastropods (e.g., *Haliotis* spp.) with similar reproductive life histories show that close proximity of reproductive individuals is key for successful fertilisation (Catton and Rogers-Bennett, 2013). Thus, low densities at the range edge should be related to low population fitness and increased probability of range contraction and localised extinctions due to Allee effects (Courchamp et al., 2008). Accordingly, the range of *L. gigantea* has contracted by a least two degrees of latitude in the last few decades and *L. scabra* has experienced a number of local extinctions at its northern range edge (Fenberg and Rivadeneira, 2011; Shanks et al., 2014).

10.5 Southern Range Limits and Dynamics

In stark contrast to what we know of northern range edge dynamics for some NEP species, there are very few case studies that have examined southern range edge dynamics. This is partly because climate change research generally predicts a northward range shift for NEP species, meaning that northern range edges have been more extensively monitored. In addition, many NEP species have their southern limits clustered within a relatively small and largely inaccessible region of the central/southern Baja coastline, between Punta Eugenia (27.8°N) and Magdalena Bay (24.6°N). For example, the ranges of *L. gigantea*, *L. scabra*, *T. rubescens*, *T. funebris* and *M. lugubris* (already discussed), and many others, end around Magdalena Bay. A review of the geographic ranges of NEP rocky intertidal gastropods (not including meiofaunal species, those primarily living subtidally or in multiple habitat types) reveals no species that range into the TEP and about half the species in the data set have southern range limits in the region between Punta Eugenia and Magdalena Bay (Fenberg and Rivadeneira, 2019). Among molluscs, Magdalena Bay tends to be more commonly associated with the southern range limits of rocky intertidal gastropods whereas Punta Eugenia (or Isla Cedros) is more often cited as a southern limit for bivalves (which tend to live in more soft-sediment habitats; Bernard et al., 1991). Interestingly, Punta Eugenia is also a well-known phylogeographic break for a number of rocky intertidal species, including isopods, fish and molluscs (Riddle et al., 2000; Bernardi et al., 2003; Riginos, 2005; Hurtado et al., 2010; Fenberg et al., 2014; Dolby et al., 2015). The region between Punta Eugenia and Magdalena Bay may therefore be described as both a biogeographic and phylogeographic transition zone across a diverse set of taxa, acting as a barrier to (1) the movement of individuals between populations of some species, leading to genetically distinct lineages (i.e., a phylogeographic break) and (2) the movement of individuals further south into the TEP.

Despite the concordance of these biogeographic and phylogeographic patterns, relatively little research has been dedicated to their causes. Biologically and physically, the Pacific coast of the Baja peninsula is a story of two halves, with the region near Punta Eugenia marking the dividing line. At this latitude, there is a transition from mid-latitude to tropical conditions, offshore flow of the southward-flowing California Current, cyclonic eddies north and south of Punta Eugenia, and variation in upwelling regimes (Hewitt, 1981; Zaytsev et al., 2003; Herrera-Cervantes et al., 2014). On average, SST is 3.5°C warmer along the southern half of Baja California compared to the northern half. But variation in oceanic conditions is not the whole story. Only 25 per cent of the coastline south of Punta Eugenia to the tip of the peninsula is habitable for rocky intertidal species compared to 51 per cent for the northern half (data from Fenberg et al., 2014). The rather abrupt transition from a cool (with multiple areas of upwelling) and mostly rocky coastline in the north to one with warm waters dominated by sandy beaches (including a 115 km uninterrupted stretch of sandy beach just north of Magdalena Bay) makes the Pacific coast of southern Baja challenging in terms of both thermal stress and dispersal opportunities for NEP rocky intertidal species. The combined effect of these physical factors should correspond to abrupt declines in adult and juvenile abundance for NEP species with their southern range edge in this region, as observed for *L. gigantea* (Fenberg and Rivadeneira, 2011).

Given this, we should not expect southern range limit expansions of NEP species with limits between Punta Eugenia and Magdalena Bay as a potential result of climate change. Rather, we would expect these limits to either be temporally stable or to contract northwards (Fenberg et al., 2014). On the other hand, if warm-adapted TEP rocky intertidal species from the south (and in the Gulf of California) can overcome the habitat barriers, then we might hypothesise a gradual northward shift of the boundary between tropical and temperate fauna over the next century as warming progresses. Indeed, some of the warm protected bays along the Pacific coast of southern and central Baja California already act as

northern refugia for some TEP species (Reid, 2002). This provides a source population from which to disperse when/if the outer coast becomes more thermally suitable (e.g., during El Niño years). But if TEP species are not able to overcome the habitat barriers, then we might expect a net loss of biodiversity at this northern edge of the tropics.

10.6 Range Dynamics over Paleontological Time Scales

This discussion has largely focussed on range dynamics over contemporary time scales. But we cannot make any general conclusions without taking into account processes occurring over much longer time scales. For example, classically it has been assumed that the poleward ranges of species from cool, temperate regions, such as those occurring in the northern part of the NEP, follow a basic ‘expansion–contraction’ (EC) model in response to respective interglacial and glacial periods. However, individualistic (i.e., species-specific) responses to environmental change may be more common than initially expected (Valentine and Jablonski, 1993; Stewart and Lister, 2001). Reliance on the fossil record alone to document NEP rocky intertidal range shifts over the Pleistocene can be problematic because (1) the relatively high-energy environment of the rocky shore is not ideal for preservation, (2) many Pleistocene records are biased towards relatively warm interglacial periods and (3) mixing of fauna from different time periods within individual fossil terraces may be more common than originally thought (Muhs et al., 2014). Rather, a combined approach that takes into consideration the fossil record, molecular phylogeography and other data sources is preferred. For example, Hellberg et al. (2001) use molecular, fossil and morphological evidence to support a late-Pleistocene northern range expansion in response to warming waters after the most recent glacial retreat for the direct-developing rocky intertidal gastropod, *Acanthinucella spirata*. While this supports the EC model (and climate change-mediated morphological evolution), subsequent tests of

other NEP rocky intertidal species are equivocal. Although only based on mtDNA markers, Marko et al. (2010) found that only 5 of their 14 sampled NEP rocky intertidal species showed molecular evidence of a postglacial northern range expansion. Interestingly, the mussel *Mytilus californianus* exhibits evidence of persistence in British Columbia and south-east Alaska during the last glacial maximum (LGM; ~20,000 years ago), while its main predator, the keystone species, *Pisaster ochraceus*, was likely absent from the region during this period (Marko et al., 2010). These contrasting histories must have had cascading effects for northern communities during the LGM. For example, without predation pressure setting its lower limit (Paine, 1966), *M. californianus* may have been able to exist lower on the shore and even subtidally (Paine, 1976; Marko et al., 2010). The subtidal refuge in turn would have helped ameliorate the undoubtedly cold/freezing aerial temperatures during the LGM and helped sustain its presence in the northern region. This scenario of an interaction between the physical environment (e.g., temperature/glaciation) differentially affecting the northern range histories of *M. californianus* and *P. ochraceus* in conjunction with the predation release facilitating a potential subtidal refuge for *M. californianus* highlights the complicated factors that shape NEP rocky intertidal communities over long time scales – which nicely sets up the next half of this chapter.

dominating the rocky intertidal. If *P. ochraceus* is removed, then *M. californianus* expands the cover of its beds to lower-intertidal levels, edging out individuals that predominantly live on rock. However, many of these species can also be found living on or within the mussel beds, usually as juveniles or small adults, albeit at different abundances (Lohse, 1993; Lafferty and Suchanek, 2016).

This pioneering research not only highlighted the utility of the NEP rocky intertidal as a natural laboratory for ecological research, but Paine’s ideas have since been confirmed for other keystone species in various marine and terrestrial systems (e.g., Mills et al., 1993; Power et al., 1996) – showing that single species (usually predators) can have an outsized effect on the overall structure and functioning of an ecosystem. This extensive body of research gives us a framework with which to make predictions on how direct or indirect human impacts on keystone species may have cascading ecological effects on the rest of the community. These days, the most worrisome indirect impacts on NEP rocky intertidal species are those associated with climate change and ocean acidification. Direct human impacts, on the other hand, usually take the form of size-selective harvesting. For the remainder of this section, we focus on how indirect and direct human impacts on species capable of top-down control have affected the NEP rocky intertidal.

10.7 Human Impacts on Top-Down Control of NEP Rocky Intertidal Community Structure

Robert Paine’s classic predator-removal experiments in northern Washington State showed that ecological communities can be structured, in part, by top-down control (Paine, 1966). As the original ‘keystone’ species, Paine showed that *P. ochraceus* can significantly affect the diversity, abundance and distribution of species in the community. As a voracious predator, *P. ochraceus* prevents the space occupier, *M. californianus*, from

10.8 Predator Responses to Altered Environments: Implications for Climate Change

The impacts of climate change on ecological communities are difficult to predict because indirect effects can generate ecological surprises resulting from complex webs of direct interactions (Gilman et al., 2010). However, ecological theory is available upon which to begin building a conceptual framework for expected change. Specifically, environmental stress theory makes predictions of how predators and prey should respond to

increases in, for example, thermal stress (Menge and Sutherland, 1987; Menge and Olson, 1990; Menge et al., 2002; Bruno et al., 2003). The consumer stress model (CSM) assumes that predators are more sensitive to stress than are prey, while the alternative Prey Stress Model (PSM) assumes the opposite, that prey are more sensitive than are predators. Both versions assume that consumers feed primarily on sessile prey. Thus, the CSM predicts that, with increasing stress, predator effects on prey will weaken, while, in the PSM, increasing stress should strengthen the effects of consumers on prey.

A primary effect of climate change will be through altered temperature regimes (IPCC, 2014), which can impose physiological stress on organisms. Coastal temperatures along the US west coast have increased by up to 3°C across the continental shelf (Mote et al., 2010), while inner shelf temperatures have decreased (Menge, unpublished data) due to intensifying upwelling resulting from increases in temperature over land (Iles et al., 2012). Thus, intertidal organisms face stress at both ends of the temperature gradient (Sanford, 2002). In the next section, we provide examples indicating how such temperature stresses may affect top-down and bottom-up processes in rocky intertidal communities.

10.9 | Temperature Stress

10.9.1 Effects on Whelks

Rocky intertidal species are exposed to both water and aerial temperatures on a daily basis, making them susceptible to the combined effects of oceanic and atmospheric climate change. But whether a particular species will respond differently to aerial versus water temperature may depend upon a number of factors, including vertical distribution on the shore, the timing of tidal cycles on a daily or seasonal basis, and behavioral and physiological response during periods of emersion/immersion. How water and aerial temperatures (and their subsequent influence on body temperature) affect species interactions, such as predation rates, will be a key step towards understanding how climate change

affects top-down processes in the rocky intertidal. A laboratory study by Yamane and Gilman (2009) found that the growth and feeding rate of the predatory gastropod, *Nucella ostrina*, was low for individuals with high emersed body temperatures. This is in contrast to the observed increased feeding and growth rates for individuals in warm immersion temperatures. This observation suggests that the primary prey of *N. ostrina*, the barnacle *Balanus glandula*, may suffer higher mortality during periods of warm immersion, but a respite from predation during periods of warm emersion (Yamane and Gilman, 2009).

Despite the often clear results, such studies often leave us wondering whether they correlate with more realistic temporal environmental fluctuations and extreme events. In other words, most laboratory studies test for the effects of constant temperature treatments while ignoring patterns of temperature variability (Thompson et al., 2013). Taking such systems into the field can directly address this issue. For example, a field study of *N. ostrina* in Oregon revealed that whelk feeding and metabolic rates were both elevated by increased temperatures (Dahlhoff et al., 2001). Thermal stress (low-tide air temperature), whelk body temperatures and biochemical indices of whelk conditions varied with site, wave exposure and prey abundance, indicating that physiological stress interacts with prey abundance to modify foraging activity of whelks.

Although Dahlhoff et al. (2001) showed that whelk foraging and physiology were responsive to environmental stress (warm temperatures), the extent to which this altered impacts on prey populations was unclear. In another field experiment, Menge et al. (2002) tested the effects of thermal stress on a whelk–barnacle interaction by modifying the local thermal climate. The technique used cages containing rocks with barnacles on them that were fastened to concrete blocks. Treatments included one cage without and two with whelks, one of which had a small shelter fastened to the concrete block inside the cage. The experiment was run twice, once during a warm, sunny summer and once during a cooler, rainy summer. Besides the provision of the small shelter, the CSM was tested by placing cages on sunny and shady sides of blocks, and on high

(more stressful) and low (less stressful) zones on the shore. Results showed that, as expected, whelk predation was reduced in the absence of shelter on the sunny side of the blocks. Surprisingly, height on the shore had no effect and predation rate was actually higher during the warmer summer than during the cooler summer, suggesting, as was observed by Dahlhoff et al. (2001), that, at least up to a point, whelk foraging activity is enhanced by warmer temperatures. In a simultaneous experiment, limpet grazing on algae showed identical, and even stronger effects of thermal stress on grazing rate (Menge et al., 2002).

10.9.2 Effects on Sea Stars

The ochre sea star *P. ochraceus* is a key top-down force in communities along the west coast of North America. Part of its dominant role is based on its relatively large size and its ability to adhere powerfully to rock surfaces and prey. Adults can reach large sizes, ranging up to several kilograms in wet mass, and, as a consequence of its apparent robustness, ecologists were slow to investigate its sensitivity to thermal stress. The first, and most surprising, study was that of Sanford (1999). Taking his cue from observations that *P. ochraceus* foraging activity and height on the shore appeared to cycle in concert with upwelling events, he carried out field and laboratory experiments to test the effects of water temperature on sea star feeding rates. Since upwelling brings cold water to the surface, he hypothesised that feeding intensity on transplanted clumps of mussels would decline during upwelling (cold) and increase during relaxation or downwelling (warm) events. Results supported his hypothesis. In both field and lab experiments, *P. ochraceus* fed slower in cold periods (or controlled cold sea water tables), faster in warmer periods (or warmer sea water tables) and, in the laboratory, shifted from fast to slow feeding rates as the water temperature was shifted from warmer to cooler. In a separate experiment, he showed an identical effect in whelks *Nucella canaliculata*. Based on these data, he proposed a conceptual model suggesting that feeding rate gains and metabolic rate losses with increasing

temperature led to an optimal range of 8–15.5°C for obtaining energy for growth and reproduction.

In a later study, Petes et al. (2008) tested the effect of height on the shore, and, thus, presumably, of thermal stress on *P. ochraceus* and *M. californianus*. Transplanted mussels were caged with and without sea stars, and survival, reproduction (mussels only), growth and heat-shock proteins (HSPs) were sampled in summer. Results indicated that, as predicted by the CSM, sea stars were stressed more than their prey. High caged sea stars all died, while low ones survived. Low caged sea stars without food had elevated Hsp70 relative to fed sea stars. In contrast, all mussels in sea star cages survived. Those in high cages reproduced earlier in summer, and had elevated Hsp70 relative to low caged mussels. Hence, although exposure to more stressful conditions high on the shore clearly stressed both predator and prey, prey survived while predators died, indicating that prey endured stress better than predators.

More recently, Monaco et al. (2016) examined the *P. ochraceus* vs *M. californianus* interaction using a physiological and behavioural approach. Using biomimetic sea stars and mussels (i.e., field-deployed models of each with thermistors embedded within them that mimicked thermal changes of living animals through time), they modelled thermal performance curves for air and water. They found that thermal ‘performance’ of *P. ochraceus* was higher than that of their main prey, *M. californianus*. That is, the sea star seemed to tolerate thermal stresses better than did the mussel. They suggested that this result was more consistent with the PSM than with the CSM, and that the difference between their result and Petes et al. (2008) was that the cages used in the latter prevented behavioural responses (e.g., moving to crevices for low tides) by the sea stars. This interesting result, however, did not involve a test of the relative ecological performances of sea stars and mussels. In a CSM scenario, the predicted outcome is that prey survival is better in stressful than in benign conditions, while in a PSM scenario prey survival is worse in stressful than in benign conditions (Menge and Olson, 1990). Previous tests of predation rates along a wave-stress gradient in one of the same sites used

by Monaco et al. (Strawberry Hill, Oregon; Menge et al., 1994) were consistent with the CSM model predictions. Thus, the Monaco et al. (2016) study suggests that the physiological mechanism proposed by the CSM (See Section 10.8) may be incorrect. Instead, the primary mechanism underlying the differences in CSM vs PSM may be that, unlike mobile consumers, sessile prey do not have a behavioural capacity (e.g., seeking low-stress sub-habitats) to avoid stress.

To what extent are predation rates (or other species interactions) affected by the level of temporal coincidence between aerial and water temperature values? That is, how are predation rates affected if physiologically stressful aerial and water temperatures occur during the same period (temporal coincidence) versus following in time but not overlapping (non-coincidence)? In a laboratory experiment, Pincebourde et al. (2012) found that per capita feeding rates of *P. ochraceus* were at their lowest if a period of warm aerial temperature was immediately followed by a period of warm water temperature (non-coincidence). They suggest that the negative physiological effect of warm aerial temperatures will last longer and recovery will be hampered if followed by a period of warm water. On the other hand, if a cold water period occurs after a period of aerial temperature stress, then individuals may be able to compensate or recover more quickly. Understanding the interaction of the timing of multiple stressors on individual species and their communities is especially important in the context of climate change.

In a field study, Szathmary et al. (2009) investigated the effect of aerial temperature exposure during low tide on foraging activity on succeeding days and found that the number of foraging *P. ochraceus* was inversely related to the average maximum temperature on the previous day. Thus, as suggested by Sanford's (2002) model, *P. ochraceus* foraging activity is inhibited by thermal extremes at both ends of the range, hot and cold. Consistent with this result, in laboratory experiments, Pincebourde et al. (2008) found that *P. ochraceus* growth rate also varied inversely with temperature. Clearly, this fearsome, robust predator is sensitive to the thermal climate. Since regional air temperatures are increasing and

water temperatures are cooling due to increased upwelling (Iles et al., 2012), it seems inevitable that sea star activity patterns will change, with overall declines in predation impact.

While these remarks suggest that, in the short term, *P. ochraceus* (and likely whelk) predation will decrease, the implication of these studies is that such changes will be subtle. However, some conditions could engender catastrophic changes comparable to those induced by Paine (1966, 1974) and others in removal experiments. Between 2013 and 2014, massive die-offs were documented in *P. ochraceus* populations (and other sea stars) at many NEP rocky intertidal sites (Stokstad, 2014; Jurgens et al., 2015; Menge et al., 2016; www.pacificrockyintertidal.org). Over the course of a few days, individuals developed lesions, lost the structural integrity of their limbs, changed their behavior and ultimately died. Field observations showed that larger individuals ('adults') developed wasting symptoms before juveniles, but, as the former disappeared, rates of disease increased in juveniles as well (Menge et al., 2016). Similarly, laboratory studies of individuals from the San Juan Islands in Washington indicate that larger individuals developed signs of wasting before juveniles, but that juveniles died at a faster rate once they showed symptoms (Eisenlord et al., 2016). This 'sea star wasting syndrome' (SSWD) has been linked to a virus called sea star-associated densovirus (Hewson et al., 2014). Although the ultimate cause of the outbreak is still unclear, some evidence implicates warming as a factor (Blanchette et al., 2005; Stokstad, 2014; Eisenlord et al., 2016). For example, previous outbreaks recorded in southern California were associated with warming events (e.g., the 1997 El Niño event; Blanchette et al., 2005). Eisenlord et al. (2016) found that individuals from a warm temperature treatment had higher mortality rates than those in cooler treatments, suggesting that the disease progresses faster in warm water (also observed by Kohl et al., 2016). On the other hand, field sites from Oregon through central California had cooler water temperatures during the peak of SSWD in 2014, making it somewhat difficult to confirm if temperature is a driver of the die-offs (Menge et al., 2016). Currently, researchers are

pursuing a multifactor explanation of SSWD, including temperature and possibly ocean acidification as possible factors interacting to produce this epidemic. Clearly, however, some factor altered the interaction between sea stars and what had previously been a benign microbe with disastrous consequences.

Regardless of how much temperature influences the prevalence of wasting, we can draw conclusions from Paine's research (and that of others: Menge et al., 1994; Robles et al., 2009) that the depletion of these voracious predators would cause significant cascading effects on local ecological communities. Without *P. ochraceus*, *M. californianus* beds would likely expand their vertical distribution towards the lower shore and potentially to the shallow subtidal in some cases. However, whether or not such a response will be universal, i.e., occur across the full biogeographic range of coexistence between *P. ochraceus* and *M. californianus*, is unclear. Some *P. ochraceus* removal experiments did not result in swift take-over of the lower intertidal by mussels (S. Gravem, personal communication; Menge, unpublished data). Such variable responses seem at least partly related to direct and indirect effects of ocean conditions, including upwelling strength and magnitude of prey recruitment (Menge et al., 2004). In southern California, where upwelling is weak, predation rates were low (Menge et al., 2004). North of Point Conception, predation rates varied among sites as a function of sea star abundance, density of mussel recruitment and the level of phytoplankton available as food for filter-feeding mussels and barnacles. Recruitment and phytoplankton blooms are strongly dependent on upwelling conditions, generally being greatest at sites of intermittent upwelling (Menge et al., 2011; Menge and Menge, 2013).

Studies of indirect human impacts on species capable of top-down control are often focussed on predators, but, of course, indirect human impacts on species at intermediate levels of the food chain may also affect community structure. A good example from NEP rocky shores is the community level impacts of withering syndrome (WS) on the black abalone, *Haliotis cracherodii*. WS is caused by a gastrointestinal prokaryote that

hinders digestion, which is known to occur in all five southern California abalone species (Friedman et al., 2002; Crosson et al., 2014). The primary symptom of infected animals is the shrinking and weakening of the foot, which can cause dislodgement from the substratum and death (Crosson et al., 2014). Like wasting disease in *P. ochraceus*, WS is thought to be induced, in part, by elevated water temperatures (Raimondi et al., 2002). Ben-Horin et al. (2013) measured the body temperatures of *H. cracherodii* individuals in the field and in the laboratory. They found that high daily temperature variability increased the susceptibility of individuals to infection, but that expression of WS only occurred during the warmest temperatures. The rocky intertidal thermal regime is highly variable at local and regional scales (Helmuth et al., 2006), meaning that transmission of the prokaryote will likely be widespread. However, the disease will only become symptomatic when temperatures exceed thresholds for triggering WS (Ben-Horin et al., 2013). For example, WS related die-offs of *H. cracherodii* in southern and central California seem to co-occur during El Niño years, at a site where warm water is discharged from a power plant and more often in the southern portion of its geographic range (Raimondi et al., 2002, 2015). These observations suggest that future El Niño years, other incidences of warm water discharge and climate change will increase the spread of WS in *H. cracherodii* and other susceptible abalone species. The combined effects of WS and harvesting in *H. cracherodii* have had such a negative impact that it is now listed as critically endangered by the International Union for Conservation of Nature (IUCN; Smith et al., 2003).

Community-level responses may be quite drastic following mass mortalities or local extinctions of keystone predators or grazers (or other functional groups). *H. cracherodii*, for example, are important grazers of drift algae, kelp and crustose coralline algae. Miner et al. (2006) conducted surveys before and after mass mortalities of *H. cracherodii* and found that community composition shifted from that dominated by bare rock and crustose coralline algae (good abalone habitat) to one consisting primarily of sessile invertebrates and sea urchins (poor

abalone habitat). This community shift may also hinder population recovery following the mortality event because high cover of bare rock and crustose coralline algae are thought to be favourable for juvenile settlement and growth (Miner et al., 2006). Thus, WS and its cascading ecological impacts act as compounding factors limiting the potential recovery of *H. cracherodii*.

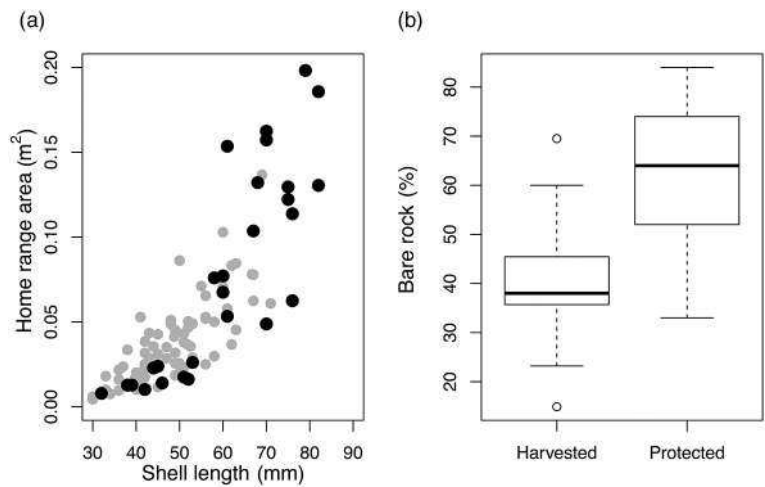
Besides humans (Butler et al., 2009), the primary predator of *H. cracherodii* and most observed source of mortality for individuals not affected by WS is the California sea otter (*Enhydra lutris nereis*), which is also listed as an endangered species by the IUCN (Doroff and Burdin, 2015). Such cases where both predator and prey are listed as threatened or endangered requires in-depth field studies quantifying how their interactions may affect their respective population dynamics. While these scenarios have been explored in a theoretical sense, the only empirical study to date has been conducted along the coast of California where *H. cracherodii* and *E. lutris nereis* are co-distributed. Raimondi et al. (2015) asked whether sea otter predation affects the demography and microhabitat distribution of abalone, potentially resulting in lower population density and/or greater usage of refuges where otters cannot easily reach (i.e., deep crevices in the rock). Indeed, they found that abalone did make greater usage of deep cracks and crevices at sites where sea otters were present, but, surprisingly, their population densities were also increased at such sites. Sea otter density may therefore have a positive effect on abalone populations, which is counter to a similar study of sea otter predation negatively impacting red abalone abundance (*H. rufescens*), which is co-distributed with *H. cracherodii* (Fanshawe et al., 2003). There are a few reasons why sea otters may have a positive effect on black abalone density, including the fact that both sea otters and abalone require rocky habitat, which are likely to include the microhabitats needed for abalone refuge. In addition, both sea otters and abalone require kelp, either as resting area and foraging habitat (otters) or as detritus for food (abalone). Moreover, we know from a classic trophic cascades case study (Estes and Duggins, 1995) that sea otter presence can increase kelp abundance (via predation control

of kelp eating urchins). Hence, sea otters can indirectly increase the overall amount of food for black abalone. Management policy for black abalone must therefore take into account multiple species, including sea otters and kelp. Of course, this study was only possible within the portion of the *H. cracherodii* range without high incidence of WS. Whether the same positive relationship between abalone and sea otter density will also occur if WS becomes more widespread requires further study (Raimondi et al., 2015).

10.10 | Harvesting

Thus far we have discussed how indirect human impacts (e.g., warmer or more extreme temperatures due to climate change) can affect species capable of top-down control of their community. But direct human impacts, like size-selective harvesting of such species has also been well studied. Limpets are ecologically important grazers and space occupiers of the NEP (Ricketts et al., 1985; Lindberg et al., 1998; Fenberg, 2013). *L. gigantea* is commonly size-selectively harvested within the central portion of its geographic range (~28–36°N) where it is one of the dominant space occupiers of the mid-upper-intertidal (Stimson, 1970; Lindberg et al., 1998; Fenberg and Rivadeneira, 2011; Fenberg, 2013). As individuals grow larger, they proportionally increase the size of their territories/home ranges (Fenberg, 2013). The larger individuals in a population are usually territorial females and can occupy up to 0.20 m² (Figure 10.3a). Territory holders defend their algal ‘garden’ from intraspecific (usually smaller males) and interspecific competitors (Stimson, 1970; Wright, 1989) by ‘bulldozing’ individuals off their territory using the anterior portion of their shell. Other space occupiers such as mussels, barnacles and macroalgae can be seen on the edges of territories, as well as small- to medium-sized *L. gigantea* individuals and other limpet species. After a population has been size-selectively harvested, sessile species and smaller-sized *L. gigantea* individuals can invade previously occupied territories (Lindberg et al., 1998). If harvesting is consistent enough, then the space

Fig. 10.3 (a) Home range scaling of *L. gigantea*. The black circles are individuals from sites where there is no size-selective harvesting. The grey circles are from sites where individuals are size-selectively harvested. (b) Box plots of the percentage of bare rock (suitable *L. gigantea* habitat) present in the mid-intertidal zone at harvested and protected sites. There is significantly more bare rock at protected sites ($P < 0.0001$).



occupancy of a site can shift from one dominated by large grazers (largely consisting of *L. gigantea* home range area) to one dominated by other functional groups, like filter feeders (barnacles and mussels) and macroalgae. Accordingly, Fenberg (2008) showed that the mid-intertidal zone of sites in southern and central California where individuals of *L. gigantea* are commonly size-selectively harvested have significantly less area available as potential *L. gigantea* grazing space (measured as bare rock) compared to sites where harvesting is minimal (Figure 10.3b).

10.11 Human Impacts on Bottom-Up Control of NEP Rocky Intertidal Community Structure

The NEP is an eastern boundary upwelling system, defined by variable cross-shelf circulation due to upwelling/downwelling forcing (Checkley and Barth, 2009). Viewed in cross-section, coastal circulation patterns resemble a reversing conveyor belt. When winds blow equatorwards, surface waters flow equatorwards and, due to the Coriolis force, offshore. The pressure gradient created by these flows draws water from depth,

bringing cold, high nutrient, low O₂ and high CO₂ water to the surface. When winds ‘relax’ (cease) or reverse, surface waters rebound coastwards and polewards, bringing warm, nutrient-depleted, high O₂ and low CO₂ water back to the coast. Between and within species patterns of geographic distribution and gene flow (i.e., biogeographic and phylogeographic breaks) often coincide with areas where upwelling is particularly strong, with predominantly equatorward currents (e.g., Cape Mendocino; Kelly and Palumbi, 2010; Fenberg et al., 2015). Recent research has demonstrated that, in addition to such large-scale patterns, seasonal and regional variation in upwelling/downwelling forcing are also strongly related to patterns of rocky intertidal community structure and functioning (Menge et al., 1997, 2003, 2004, 2015; Menge and Menge, 2013). Individual growth responses, species interactions and relative abundances of different trophic levels vary in response to the variation in upwelling cycles. Surprisingly, these life history and ecological responses are not necessarily at their highest in nearshore environments when upwelling is persistent.

Along a gradient from persistent downwelling to intermittent upwelling (i.e., alternating between upwelling and downwelling on ~7–10-day cycles) to persistent upwelling, Menge and Menge (2013) showed that ecological subsidies (phytoplankton

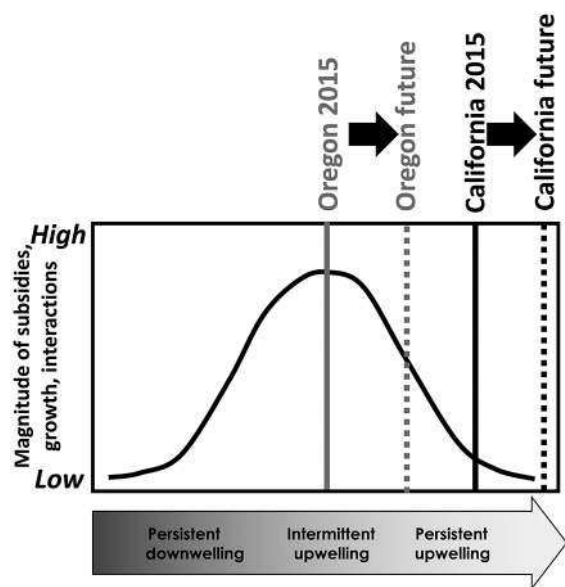


Fig. 10.4 IUH showing predictions for changes in magnitude of ecological subsidies, growth rates of predators and prey and intensity of species interactions for Oregon and California coasts at the present and in the future.

abundance, prey recruitment rates), prey response (barnacle settlement and mussel growth) and ecological interactions (competition and predation rates) are at their highest with intermittent upwelling. The mechanisms proposed to underlie these patterns were summarised as the intermittent upwelling hypothesis, or IUH (Menge and Menge, 2013; Figure 10.4). Specifically, with persistent upwelling, nutrient-fuelled near-surface phytoplankton blooms and propagules are transported offshore away from coastal habitats. Persistent downwelling produces the opposite pattern, where surface waters flow shoreward but the comparative lack of nutrients prevents phytoplankton blooms from forming. The intermediate condition occurs when upwelling causes high nutrients to form phytoplankton blooms, which typically form within three to five days. Wind cessation or reversal leads to ‘relaxation’ of offshore flow or onshore flow, respectively, causing shoreward transport of near-surface larvae and phytoplankton back to the shore. Marine invertebrate larvae can have a pelagic larval duration ranging from days to weeks (Shanks, 2009). Thus,

if larvae are developing during intermittent upwelling, then the frequent inshore and offshore movement could increase the odds that larvae are near rocky shore habitat when ready to settle. Indeed, sites associated with intermittent upwelling have increased phytoplankton/zoo-plankton abundance, recruitment and growth rates of invertebrates, and higher levels of competition/predation in rocky shore communities along the NEP, New Zealand and in other eastern boundary upwelling systems (Menge and Menge, 2013).

The IUH provides a well-supported mechanistic framework for how bottom-up processes can drive spatial and temporal variation in community structure in rocky intertidal systems, including along the NEP. Coupled with predictions of how climate change may affect upwelling/downwelling patterns, the IUH can also generate predictions about how ecosystem dynamics are likely to change in space. Future climate change projections predict that land temperatures will increase faster than coastal waters, creating a scenario favouring stronger upwelling-producing winds (Bakun et al., 2010; Di Lorenzo, 2015; Wang et al., 2015). In fact, there is evidence that upwelling has already intensified in most of the eastern boundary upwelling systems (Iles et al., 2012; Sydeman et al., 2014; Varela et al., 2015). Because upwelling brings cool water to the surface, increased upwelling may provide some refuge from SST warming in some locations. Generally, models predict that upwelling intensification will be particularly marked at higher latitudes, where coastal upwelling is generally less intense. This may cause homogenisation of upwelling-influenced habitats across latitudes and have cascading effects on the abundance and distribution of rocky intertidal flora and fauna (Wang et al., 2015). Specifically, the IUH predicts that under such poleward homogenisation of upwelling, the process rates that are high under intermittent upwelling will likely decrease as upwelling becomes more persistent and longer in duration. Along the west coast of North America, ecosystems that now typify much of the California coast would ‘move northward’, leading to reduced rates of recruitment, lower phytoplankton abundance, slower growth and weaker

competition and predation (Menge and Menge, 2013; Figure 10.4).

An increase in upwelling also may exacerbate other emerging threats to coastal ecosystems, such as ocean acidification and anoxia because deeper waters have lower pH and oxygen levels than at the surface (Chan et al., 2008; Bakun et al., 2015). For example, historical *M. californianus* shells from midden sites (~1,000–2,420 years ago) in Washington State have significantly higher shell calcification rates and shell thicknesses compared to modern shells, which Pfister et al. (2016) attribute to declining pH in modern times. If their shells become thinner as a result of ocean acidification and are compounded by an increase in upwelling intensity, then, all else being equal, predation rates on mussels would likely increase. But as already noted, upwelling intensity and other interacting environmental drivers of NEP community structure do not often have clear latitudinal trends (Helmuth et al., 2006; Menge and Menge, 2013). For example, substrate temperature influences the internal body temperature of mussels, which can often be very different from measurements based on air or SST alone (Helmuth et al., 2016). Furthermore, potential drivers of community structure and individual species' performance may form mosaic patterns along the coast; meaning that abiotic or biotic factors vary in a spatially non-monotonic or patchy manner, as opposed to a uniform gradient. Areas of overlap of these biotic or abiotic factors can either create locations of susceptibility or resilience to environmental change (Kroeker et al., 2016). For example, Kroeker et al. (2016) showed that *M. californianus* growth rates are lowered and predation vulnerability is highest in locations with an overlap of high body temperatures, low pH and inconsistent food availability.

10.12 | Conclusions

What is the relative influence of bottom-up/top-down control on the structure and functioning of ecological communities, and what physical and biological factors control the distribution and

abundance of species over space and time? Our understanding of these two fundamental questions in ecology have benefitted greatly from examples from the NEP rocky intertidal. But if we were to somehow pursue this basic research along an NEP untouched by human influence, we probably still would not have complete answers. The NEP and all other coastlines of the globe are affected by direct (e.g., harvesting) and indirect human impacts (e.g., climate change, disease dynamics) that we know can have measureable ecological effects. Applied and basic ecologists must now add these extra layers of complexity to our models for understanding the dynamics of rocky intertidal systems.

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