

Essay:

# **Anti-predation traits in marine bivalves along a latitudinal gradient**

## **Abstract**

From high to low latitudes, species richness tends to increase with striking universality. The mechanism explaining this latitudinal diversity gradient (LDG) remains elusive, but the LDG seems to arise from a complex combination of rates of origination, extinction, and dispersal of organisms. In the underlying evolutionary process, biotic interactions and especially predation pressure, play important roles. The relative importance of these various interactions also follow a latitudinal gradient. Along the gradient, environmental stability and available resources increase equatorward, allowing for an increasingly broad scope of possible ecological adaptations to predation combined with increased selective pressure. This creates increasing potential for evolutionary arms races enabling escalated development of anti-predation traits. In tandem, organisms at higher latitudes are more likely to adapt to abiotic conditions as the biotic environment becomes less rigorous and the abiotic environment more. This raises the question: "Does the expression of anti-predation traits follow the latitudinal richness gradient?" I investigated the marine LDG and using marine bivalves as a model system and shell traits (thickness, length, body mass to shell weight ratio and frequency of occurrence of drilling holes) as indicators for escalation. I found that escalation is not universally occurring at similar latitudes nor are there indications that escalation only occurs around the equator. Escalation is not predicted by the LDG, but is though most likely to occur around the equator and least likely at high latitudes. For escalation to occur highly selective predation pressure in a stable environment with high productivity is supposedly necessary to persist over long time scales. At high latitudes this would be disrupted by cycles of glaciations. I propose that as a result of glacial cycles, escalation occurring at higher latitudes is followed by de-escalation in cold periods. This resets the evolutionary arms race, which carries on around the equator.

# 1. Introduction

## 1.1. The latitudinal diversity gradient

From humble beginnings over 3 billion years ago, living organisms have colonized almost all marine and terrestrial environments on Earth. Life evolved since in myriad forms, physiologies, and life histories (Fine, 2015). This diversity is not evenly distributed around the planet. Instead, species richness seemingly universally increases from the poles to the equator. Such pattern is found in a wide range of functional groups, in both ectotherms and endotherms, in taxa that differ in body size, mode of dispersal, and trophic level (Hillebrand, 2004a; Kinlock *et al.*, 2018). This Latitudinal Diversity Gradient (LDG) has been called the most pervasive biotic pattern on Earth (Jablonski *et al.*, 2017) as well as the oldest one recognized (Hawkins, 2001). It is also the best studied biotic pattern, intriguing ecologists for over centuries now (Fine, 2015). The paradigm for the latitudinal gradient in species richness is that it is unimodal with a tropical peak (Chaudhary, Saeedi and Costello, 2016), but the detailed pattern of change with latitude “*depends on where one looks*” (Gaston *et al.*, 2000). This is demonstrated by differences in strength and steepness of the gradient dependent on for example the chosen diversity measure (such as Shannon diversity, local or regional species richness), geographical scale or area, and taxonomic level studied (Gray, 2001; Willig, Kaufman and Stevens, 2003; Hillebrand, 2004a, 2004b).

While the exact mechanism may remain elusive, so much is clear that the LDG seems to arise from a complex combination of origination, extinction, and dispersal of organisms (Mannion *et al.*, 2014). But what drives such events? The dozens of hypotheses that have been proposed over time (Willig, Kaufman and Stevens, 2003; Willig and Presley, 2018) can be roughly divided in three perspectives that are confounded with each other (Schoener, 2011; Vellend *et al.*, 2014; Fine, 2015): an ecological, and evolutionary and a geographical one. A fundamental principle in each is that latitude correlates with temperature and seasonality (Fine, 2015). From the ecological perspective this means that the tropics as a stable and highly energetic environment can sustain more life than the increasingly less productive and environmentally restrictive temperate and polar areas (Pianka, 1966; Hawkins, 2001; Willig, Kaufman and Stevens, 2003). From the evolutionary perspective (Rohde, 1992; Mittelbach *et al.*, 2007; Schluter and Pennell, 2017) stability and high energy allows for a higher diversification of species and traits in the tropics. The geographical perspective takes into account the effect of physical and physiological barriers and corridors affecting species richness (Rosenzweig, 1992, 1995), large scale oceanic currents for example are known to influence the geographical borders of tropical waters (Jablonski *et al.*, 2013; Valentine *et al.*, 2013).

## 1.2. Biotic interactions

Evolution and the resulting species diversity has long been viewed as a unidirectional process of adaptive responses to the environment (Schoener, 2011). This would result in traits enabling higher fitness, such as wider thermal tolerances in temperate organisms compared with tropical species (Compton *et al.*, 2007; Hawkins, 2010; Jetz and Fine, 2012). Development in traits is likely to affect the evolution of surrounding biota as well. For example, with increasing fitness a species may locally become a superior competitor, which may in turn lead to the extirpation of a fellow competitor. Such scenario might however also lead to the fellow competitor shifting to alternative resources and subsequently adapt. Either way, these changes continuously feedback to influence the subsequent evolution of the biota in a given community (Post and Palkovacs, 2009; Schoener, 2011). Biotic interactions play a critical role in these dynamics (Post and Palkovacs, 2009; Blois *et al.*, 2013; Louthan, Doak and Angert, 2015; Patzkowsky and Holland, 2016) and do so in three different ways (Vermeij, 2013): (1) by escalation, an evolutionary process in which enemies are the predominant agents of natural selection; (2) by coevolution in which two species or groups of species are important agents of selection for, and respond to, each other; (3) by the principle that improvement in one species causes deterioration in other species in a community. Over the course of time these interactions result in evolutionary trends in the morphology, behaviour, and distribution of organisms (Vermeij, 2005).

The importance of biotic interactions for evolutionary processes is not distributed evenly across the globe but instead, just as species richness, appears to follow a latitudinal cline (Schemske *et al.*, 2009). Seasonality along the latitudinal cline impacts organisms both directly, through the effects of light, temperature, precipitation, and other abiotic variables on their physiology, and indirectly, via biotic interactions (Williams *et al.*, 2017). At high latitudes the harsh and unstable environment with limited resources is considered the prevailing agent of selection resulting in a limited number of well-adapted species that can survive. At low latitudes in the relatively benign and stable tropics species richness increases and biotic interactions become an increasingly important agent of selection and speciation (Vermeij, 1994; Louthan, Doak and Angert, 2015, Schemske, 2009).

As for biotic interactions as a whole, it is well established that predation pressure increases from high to low latitudes (Mittelbach *et al.*, 2007; Schemske *et al.*, 2009; Freestone *et al.*, 2011; Moss *et al.*, 2016; Comita, 2017). Because of high predation pressure combined with a stable and rich environment natural selection by predators is considered to be the primary agent of selection at lower latitudes (Vermeij, 1994; Schemske, 2009; Moss *et al.*, 2016). As the physiological demands imposed by the environment generally decrease with latitude while predation pressure increases, organisms are allowed an increasingly broader ecological scope for adaptation combined with increased necessity for the evolution of anti-predation traits, which facilitates escalation (Vermeij, 2005; Vermeij, 2013). Predators with improved abilities able to withstand such anti-predation traits will be more successful than those without. This will lead to compensatory counter adaptations on the part of the prey, as any beneficial step forward by predator or prey must cost the other in a non-lethal way, so that evolutionary changes by one player increase selection on its opponent, causing a concomitant change (Brodie and Brodie, 1999; Bardhan and Chattopadhyay, 2003; Vermeij, 2013). This process, however, is not infinite: Escalated traits are energetically and ecologically costly (Vermeij, 1994; 2012), so when selective pressure by enemies is relatively low such escalatory processes are less likely to occur. Instead, a decrease in predation pressure allows for an increasing variation in life-history strategies (Moss *et al.*, 2016).

### 1.3 Research question

The distribution of species richness tends to follow a global pattern of increase from high to low latitudes and so does predation pressure. Both patterns are associated with gradients in temperature and seasonality. Along the gradient, environmental stability and available resources increase equatorward allowing for an increasingly broad scope of possible ecological adaptations to predation combined with increased selective pressure. In tandem, organisms at higher latitudes are more likely to adapt to abiotic conditions as the biotic environment becomes less rigorous and the abiotic environment more. This raises the question:

*“Does the expression of anti-predation traits follow the latitudinal richness gradient?”*

## 2. Marine bivalves

### 2.1. Marine bivalves as a model system

Marine bivalves are an excellent model system to study macroecological and macroevolutionary questions (Valentine *et al.*, 2006; Tomašových *et al.*, 2016; Jablonski *et al.*, 2017) and are considered representative for benthic communities as a whole (Valentine and Jablonski, 2015). They are widespread with a well-documented biogeography (Flessa and Jablonski, 1995) and exhibit relatively high taxonomic, phenotypic, and functional diversity. Almost all bivalves (except Pectinidae, scallops) are sessile or have such limited mobility (Gosling, 2015) that they are relatively easily studied *in situ* or extracted from the environment. Bivalves have a rich fossil record dating back over 540 mA which contains convincing evidence of an evolutionary history of escalation (Valentine *et al.*, 2006; Ponder and Lindberg, 2008; Moss *et al.*, 2016; Nagel-Myers, Dietl and Brett, 2009).

Not surprisingly perhaps, predation is considered to be the main natural cause of death for bivalves (Gosling, 2015) and bivalves probably constitute the dominant benthic prey community of today's marine environment (Bardhan and Chattopadhyay, 2003). Predators come from groups as diverse as fish, birds, mammals, crustaceans, echinoderms, flatworms and even other mollusks, especially gastropods (Gosling, 2015; Vermeij 2012).

Consumption of bivalve prey can be categorized in five different ways (Vermeij, 1994; Gosling, 2015): (1) Whole prey ingestion. This is considered the most ancient form of predation and employed mostly by birds and fish; (2) Insertion and extraction. Bivalves are opened with force by, for example, octopod cephalopods, sea stars and large *Cymbium* gastropods to extract the prey or consume it while still in its shell; (3) Pre-ingestive shell breaking. This is typically done by crustaceans such as crabs and lobsters, but also by mammals such as sea otters *Enhydra lutris* and shorebirds such as oystercatchers *Haematopus* sp. (4) Transport. Some birds and mammals are known to transport the prey to a place where it can be killed at a convenient time or place, for example larid gulls dropping bivalves on hard surface to break the shell; (5) Drilling, a highly specialized form of predation. Mostly gastropods such as moon snails and whelks drill a hole in the shell of their prey so that they can access the living tissue. Besides predation on the whole animal, bivalves are also partially preyed upon by syphon-nipping fish and shrimp (Zwarts and Wanink, 1989; Kvitek, 1991; Kamermans and Huitema, 1994). Syphon nipping is not necessarily lethal, but can force the bivalve to surface in response, leaving it more vulnerable for predation by for example shorebirds (De Goeij *et al.*, 2001)

## 2.2. Anti-predation traits

A bivalve predator will look to maximize energy gain by selecting prey that offers an optimal balance between the invested energy (through foraging, drilling and consumption) and energy gain (dependent on prey size and type) (Seitz *et al.*, 2001), so bivalves are expected to respond with adaptations that make this balance less profitable. Most commonly this resulted in adaptations that either increase handling time, foraging time, decrease the odds of encounter by a predator, or a combination of those.

Increased handling time reduces the profitability of the prey and prolongs the exposure of the predator to potential hazards. Handling time is commonly increased by increasing shell thickness, shell size or increased armor (Reimer and Tedengren, 1996; Nakaoka, 2000; Seitz *et al.*, 2001; Lord and Whitlatch, 2014). For example, predators such as eider ducks and shorebirds that consume the bivalve whole can only consume bivalves that do not exceed their gape width and prefer thin shelled bivalves over thick ones because energy can be extracted faster and at lower cost (Bustnes and Erikstad, 1990; Zwarts and Blomert, 1992). The sooner a size refuge is reached, the better the odds for survival of the bivalve, so in a high predation pressure environment shell growth speed is stimulated to increase (Vermeij, 1994; 2012). This does however come at a cost as fast growing shells are usually thinner than slow growing ones (Vermeij, 1994; Sherker, Ellrich and Scrosati, 2017), leaving them more vulnerable to shell crushing predators such as crabs.

Increased adductor muscles as in mussels (Reimer and Tedengren, 1996) or oysters (Lord and Whitlatch, 2014) are another way of increasing handling time and will reduce predation risk by for example octopods and sea stars. Forming dense aggregations is also a strategy known in mussels and oysters and likewise increases handling time as it makes it more difficult for the predator to isolate an individual (Seitz *et al.*, 2001; Gosling, 2015). In contrast bivalves may reduce the odds of encounter by doing the opposite: Residing in low density patches, which is suggested for the infaunal soft shell clam *Mya arenaria* and the Baltic tellin *Limecola balthica* (Seitz *et al.*, 2001). Both species are also known to occur though in very high densities (Powers *et al.*, 2002, 2006; Nazarova, Shunkina and Genelt-Yanovskiy, 2015; Ruthrauff *et al.*, 2018). Similarly in contrast, *Mya arenaria* predation survival has been suggested to be positively density-dependent instead of negatively (Beal, Parker and Vencile, 2001).

Alternatively, many bivalves have adopted an infaunal mode of living, which significantly reduces the risk of predation as most predators are epifaunal. Because burrowing deep comes at a cost, many bivalves have the ability to bury, or bury deeper, in response to predatory cues, such as *Limecola balthica* which is known to increase its burial depth in response to effluent from crabs feeding on conspecifics (Griffiths and Richardson, 2006; Maire *et al.*, 2010). However, burial does not offer protection against all predators. Syphons may be eaten by fish and shrimps (Zwarts and Wanink, 1989; Kvitek, 1991; Kamermans and Huitema, 1994) and shorebirds can probe the sediment several centimetres deep (Piersma, de Goeij and Tulp, 1993) to obtain their prey. Crabs can smell bivalves and dig them up if they are not burrowed deep enough (Gosling, 2015), while the moon snail *Neverita lewisii* is well adapted to burrowing and can hence follow infaunal prey into the sediment (Gosling, 2015). Syphon nipping may not always be lethal, but can lead to surfacing of the bivalve which increases the risk of predation (De Goeij *et al.*, 2001).

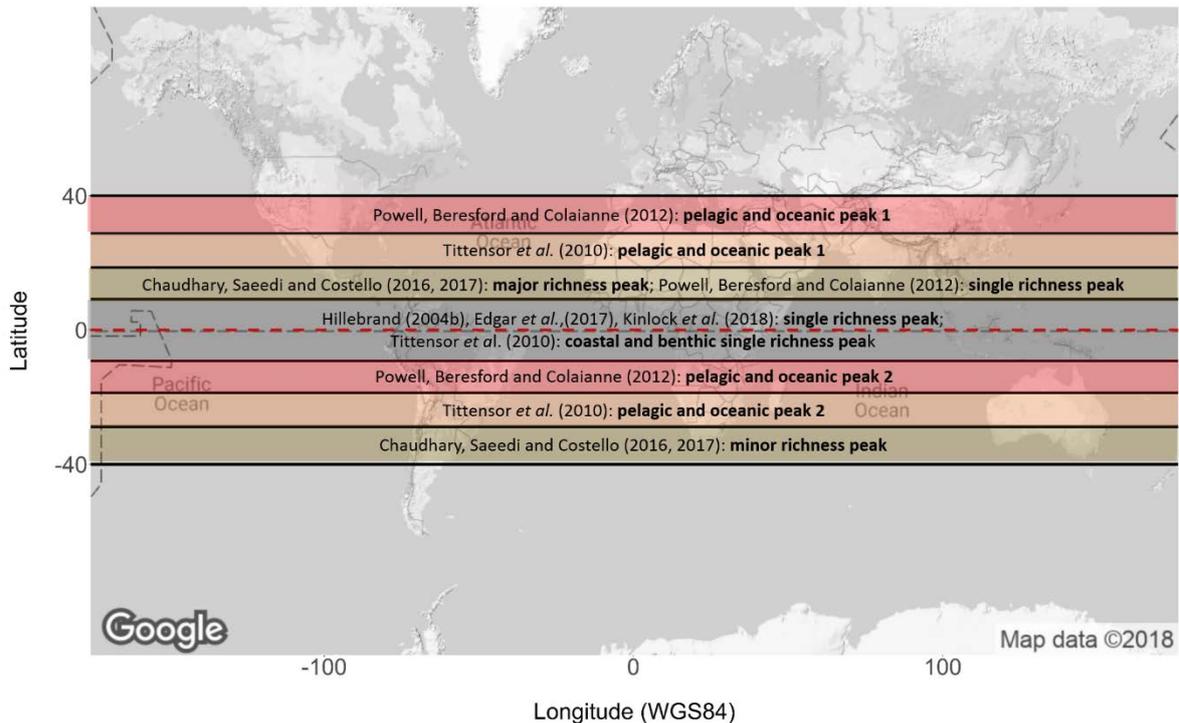
### 3. Macroecological patterns in marine bivalves

#### 3.1. Bivalve diversity and the LDG

When using marine bivalves as a model species to answer the question whether the expression of anti-predation traits follows the LDG, it is necessary to first investigate the marine LDG and the place of bivalves therein. If selective pressure for anti-predation traits were to consistently follow the LDG, a correlation between overall richness and bivalve richness can be expected.

In the marine realm the existence of the LDG has been well established, but there is no consensus as to where exactly diversity peaks, and if there is a single peak around the equator, or if there are two peaks at some distance from the equator on either side (figure 1). Hillebrand (2004b) in a comprehensive meta-analysis based on data from 600 published LDG's (198 of which marine) concluded that there is overall no difference between the marine and terrestrial LDG and that both show a unimodal gradient peaking around the equator. Using more advanced methods Kinlock *et al.* (2018) reanalyzed the original dataset as compiled by Hillebrand (2004b) with the addition of gradients from another 199 studies published since, confirming the broad conclusion that the marine as well as the terrestrial LDG is unimodal and peaking at the tropics. Edgar *et al.*, (2018) also propose the marine LDG to be unimodal peaking around the equator.

However, Tittensor *et al.* (2010) also concluded for oceanic and pelagic taxa that diversity peaks between 20°-30° on each side of the equator. Powell, Beresford and Colaianne, (2012) concluded from 149 LDG's that the generic marine LDG peaks not around the equator but further north, between 10° N and 20° N. This pattern is mostly explained by coastal benthic data which interestingly is largely comprised of the same data from the 'Census of Marine Life' project as analyzed by Tittensor *et al.* (2010), who in contrast concluded a peak for coastal benthic data close to the equator. For oceanic data Powell, Beresford and Colaianne (2012) found two peaks of diversity, the first between 30° N and 40° N and the second between 10° S and 20° S. A third, recently proposed variant is an LDG with two peaks, asymmetrically distributed and unequally high: A major diversity peak in the north in the between 20° N and 30° N with a second, less pronounced southern peak between 30° S and 40° S, thus showing a relative dip in the tropics (Chaudhary, Saeedi and Costello, 2016, 2017).



*Figure 1:* Latitudinal bands of peak species richness by different authors. Pelagic and oceanic richness bimodal peaks indicated in light red (Powell, Beresford and Colaianne, 2012) and orange (Tittensor *et al.*, 2010). Overall marine diversity asymmetrical bimodal peaks in olive (Chaudhary, Saeedi and Costello, 2016, 2017). Overall richness peaking at the equator indicated by grey band with the equator as dotted red line (Hillebrand, 2004b; Edgar *et al.*, 2017; Kinlock *et al.*, 2018). The same band also indicates highest coastal richness (Tittensor *et al.*, 2010). Overall richness peaking between 10°-20° N indicated with the top olive band (Powell, Beresford and Colaianne, 2012). Species richness is expressed as the number of unique species within a latitudinal band of 1°, 5°, or 10° depending on the studies. For results using other metrics please refer to the original publications.

Such different results can be attributed to sampling bias (Valentine *et al.*, 2013) or methodological issues (Gray, 2001; Powell, Beresford and Colaianne, 2012; Fernandez and Marques, 2017), but there are also other explanations. Along the western boundaries of ocean basins warm, poleward-flowing currents promote more prolific spreading of tropical species to higher latitudes while Eastern boundaries in contrast are characterized by cooler equatorward flows and more cool-water upwelling zones (Valentine *et al.*, 2013). As a result tropical conditions encompass ~51–52° of latitude along western coastlines, centered roughly on the equator, but only about ~36–38° along the East Pacific and East Atlantic, with a strong asymmetry about the equator (Jablonski *et al.*, 2013) and this may be reflected in the results.

An alternative explanation for a bimodal distribution (figure 1) is that this is an effect of global warming heating tropical waters above tolerance limits of local organisms (Chaudhary, Saeedi and Costello, 2016) as species that evolved in the tropics may suffer disproportionately from small increases in temperature (Vinagre *et al.*, 2018). Intriguingly the speculation by Chaudhary, Saeedi and Costello (2016) of global warming as an explanation for the bimodal pattern is consistent with the statement of Mannion *et al.* (2014) based on the marine fossil record, that throughout history the LDG has switched back and forth from a unimodal tropical peak pattern in icehouse climatic conditions to a bimodal peak with highest diversity in the temperate zones under greenhouse conditions. It should however also be recognized that any LDG may be subject to invasive or imported species weakening the gradient or altering the shape of the gradient.

For marine bivalves several authors (Valentine *et al.*, 2013; Berke *et al.*, 2014; Tomašových *et al.*, 2016) propose that the overall LDG is unimodal and northward skewed, peaking around 10°-20°N (figure 2a). The shape of the gradient may however be different according to the coastal shelf that was sampled (figure 2b). For example, a unimodal but asymmetric bivalve LDG was found along the East Pacific coast (Roy *et al.*, 2000), which is consistent with the observation of Jablonski *et al.* (2013) on the influence of oceanic currents on the variation in extent of the marine tropics. The dataset from Roy *et al.* (2000) however, was re-analysed and the LDG is now proposed to have a bimodal shape (Chaudhary, Saeedi and Costello, 2016; Jablonski *et al.*, 2017), as found for benthos in general (Chaudhary, Saeedi and Costello, 2016, figure not presented).

Bivalves from the Western Atlantic show such bimodal pattern as well (figure 2b). A bimodal gradient has also been identified for the Solenidae (razor clams) (Saeedi, Dennis and Costello, 2017). As in the overall marine LDG also in bivalves the LDG may be affected by anthropogenic activities such as introducing species (Gosling, 2015) and large scale aquaculture of clams (Yang *et al.*, 2016). Aside the shape of the gradient, actual diversity differs as well between oceanic regions, with the West Pacific having more than double the number of species compared to elsewhere (figure 2b; Jablonski *et al.*, 2017)

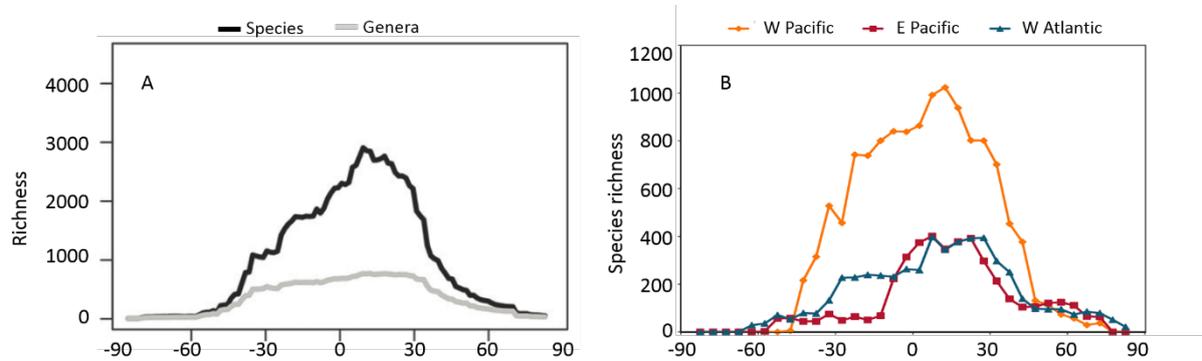


Figure 2: Marine bivalve LDG's. LDG by species and genera (A) as suggested by Tomašových *et al.* (2016); Three bivalve LDG's along the most studied coastal shelves (B) as summarized by Jablonski *et al.* (2017) based on the data used by Tomašových *et al.* (2016), which includes the re-analyzed data on the Eastern Pacific bivalve gradient originally published by Roy *et al.* (2000).

### 3.2. Historical explanations of bivalve distribution

If the LDG results from a complex combination of origination, extinction, and dispersal of organisms (Mannion *et al.*, 2014) an understanding of historical events may help to interpret the LDG and how escalatory traits may have developed stronger in one place than in the other. The current distribution of marine bivalves probably originated in deep time from the tropics (Jablonski *et al.*, 2013). According to the 'Out of the Tropics' hypothesis (OTT) (Jablonski, Kaustuv and Valentine, 2006) species lineages not only preferentially originated in the tropics but also persist there as they expand poleward. This does not preclude extratropical speciation (see also next paragraph), but predicts that most extratropical species belong to lineages that originated in the tropics. This makes the tropics both a cradle and a museum of diversity as also proposed by the niche conservatism hypothesis (Wiens and Donoghue, 2004) and means that geologic ages of bivalve genera at high and low latitudes, show deficiency of young molluscan taxa near both poles and a long tail of older taxa in all three regions (Jablonski *et al.*, 2013). It has also been proposed that marine bivalves had greater rates of origination at mid-latitudes than at low latitudes, and therefore also have atypical species richness maxima at mid-latitudes (Gillman and Wright, 2014) though this is not recognized in any of the bivalve LDG's discussed in this essay. (Jablonski *et al.*, 2017). Both theories are however not mutually exclusive and may have operated in tandem or vary regionally in importance.

The OTT furthermore implies that endemism in today's species should decrease with latitude and this is indeed found to be the case for present-day marine bivalves (Jablonski, Kaustuv and Valentine, 2006). In the marine realm the range sizes also increase towards the tropics, contrary to what is known from the terrestrial environment (Tomašových *et al.*, 2016 and references therein). If species in the tropics in general have large distribution ranges as show little endemism, it could mean that populations are large and connected over large geographical distances. If that is true, then adaptations are likely to become fixated in a population sooner compared to small populations with small ranges, thus it would facilitate the development of anti-predation traits exactly in the region where predation pressure is believed to be the highest (Vermeij, 1994). An exception though is the Southern Ocean where there may not be a strong correlation between latitude and endemism in bivalves (Briggs and Bowen, 2013). The highly latitude southern ocean in general is believed to have known a much longer period of geological stability compared to the northern high latitudes which according to some authors might explain atypical biogeographical patterns in that region (Gray, 2001; Göbbeler and Klusmann-Kolb, 2010).

A second important historical component shaping current bivalve distribution are cycles of periodic glaciation in the Pleistocene. These ice ages resulted in extinctions and species range shifts to lower latitudes, shaping species distribution by physiological tolerances and dispersal capabilities to north–south temperature gradients (Mannion *et al.*, 2014; Bowen *et al.*, 2016). Especially northern seas experienced greater extremes in temperature over the Pleistocene than tropical seas, and these ecosystems were periodically eradicated by glaciers encroaching onto continental shelves, whereas interglacial warming led to colonization and population expansions (Bowen *et al.*, 2016). This is indeed recognized in bivalves (Valentine *et al.*, 2013) and particularly the Last Glacial Maximum (LGM) approximately 18 000–20 000 years ago (Clark *et al.*, 2009) is believed to have resulted in the extirpation of many intertidal invertebrates, but not equally over taxonomic groups.

Ilves *et al.*, (2010) suggest that many western Atlantic intertidal invertebrates, including known bivalve predators such as sea stars and gastropods (Telford and Budd, 2011), were extirpated, while bivalves such as the blue mussel *Mytilus edulis*, the cold and cool water limited Baltic tellin *Limecola balthica* and the cosmopolitan *Hiatella* complex probably survived glaciation by range contraction and refugia (Luttikhuisen, Drent and Baker, 2003; Ilves *et al.*, 2010; Laakkonen, 2015; Layton, Martel and Hebert, 2016). This could imply that bivalves may have persisted without significant predation rendering them vulnerable to the predators later (re)colonizing the area. In addition, periods of cooling had a disproportional effect on species with well-developed anti-predation traits (Vermeij, 1994), probably because such traits are energetically costly in a colder environment. In a broader sense a consequence of these glacial cycles is that the tropics provide not only a stable climate annually, but also on a geological time scale experience much less disturbance compared to the poles (Mittelbach *et al.*, 2007). This would suggest that at low latitudes any evolutionary escalation process may occur continuously while at higher latitudes this process it would be periodically halted, thus resulting effectively in different evolutionary rates exhibiting different degrees of escalation.

### 3.3. Diversity and escalatory hotspots

In the marine realm today, a few significant hotspots of diversity and speciation are known and these are places where escalation may be more evident than elsewhere if escalation would be a function of species richness alone. Most famous is the tropical Indo-West Pacific, where both biodiversity in general and bivalve diversity are claimed to be the highest on the globe (Briggs and Bowen, 2013; Jablonski *et al.*, 2013). This is indeed also where most escalated marine species occur (Vermeij, 1994). An interesting example is provided by Bom *et al.* (2018) describing highly escalated molluscs, including bivalves, at the coast of the Arabian sea while at the same latitude in Mauritania (East Atlantic) molluscs showed much less signs of escalation. The other hotspots are the North Pacific, Western Atlantic and even the high-latitude Southern Ocean (Briggs and Bowen, 2013).

In the northern temperate Atlantic, there are significant differences in bivalves with escalated traits on either side of the ocean, while the environmental and geological history is considered rather equivalent. This difference is explained by the much higher presence of shell crushing and digging predators on the West side compared to the East (Jenkins, Burrows and Garbary, 2008; Vermeij, Dietl and Reid, 2008). This demonstrates that escalation does not necessarily correlate with latitude or does not correlate similarly in different regions. In the Southern ocean and on Antarctica rich intertidal communities include many bivalves (Aronson *et al.*, 2007; Göbbeler and Klussmann-Kolb, 2010; Griffiths and Waller, 2016), yet predation pressure appears low with common intertidal predators even being absent (Aronson *et al.*, 2007; Watson *et al.*, 2012), so high species richness alone does also not necessarily lead to escalation.

The locations of the hotspots are intriguing as the LDG suggests low species richness in the North Pacific and the Southern Ocean, while both other hotspots coincide with the absence of upwelling currents normally associated with high productivity and high species richness (Bakun, 1990; Sydeman *et al.*, 2014). It could be argued that around the equator where species are generally less tolerant to environmental fluctuations (Vinagre *et al.*, 2018) the periodic mixing of warm and relatively cool water may restrict the number of species that can persist there. All else being equal, tropical species richness will then be higher in areas without upwellings that are environmentally more stable.

The importance of stability for species richness is also suggested for the deep sea which can be even more diverse than shallow water seas, despite temperatures are always approximately 4°C. The common factor shared by species rich deep sea areas is continuity (not necessarily abundance) of resource availability (Valentine and Jablonski, 2015).

### 3.3. Latitudinal gradients in traits

In the paragraph on anti-predation traits the most common traits have been introduced. Not all of these are easily quantified in the field; finding literature to quantify the global trends in anti-predation trait expression along a latitudinal cline is challenging. An exception is a study by Piersma, de Goeij and Tulp (1993) on burrowing depth of bivalves over a latitudinal gradient. With their small sample biased to sites with intense shorebird predations, they, however, did not find any significant correlation. Most other studies address an aspect of the shell and as shell properties can indicate escalation those are discussed below.

Bergman's rule (1847) posits that body size in a species increases with latitude. This has been confirmed many times for many taxa including for example marine mammals (Torres-Romero, Morales-Castilla and Olalla-Tirragá, 2016). Interestingly, a converse trend is known in many terrestrial ectotherms such as insects and lizards. After analysis of mean shell length of marine bivalves on family level from a global dataset comprising 4845 species from 2277 shelf locations worldwide, Berke *et al.* (2013) found Bergmann as well as converse Bergmann trends with equal frequency, and a mean slope near 0 overall. Data was collected approximately from pole to pole at each major coastline except for East Africa. They concluded that the underlying mechanisms evidently differ and that latitudinal trends are most likely related to latitudinal trends in speciation and extinction rates.

Similarly heterogeneous results were previously found by Roy, Jablonski and Martien (2000) in bivalves (on a species level) from the North-Pacific coast. One can though question whether shell size is the appropriate metric to test for an increase in body size with latitude. Shell production requires energy and a sufficient amount of CaCO<sub>3</sub> saturation in the water, and both correlate negatively with latitude, and therefore a decrease in shell production is expected with increasing latitude (Watson *et al.*, 2012). This could hypothetically result in either smaller shells or thinner shells, thus containing relatively more living tissue mass. If the latter could also be used as a relative metric of 'body size', this might increase with latitude. Indeed, there is a global pole-to-equatorward increase in proportional shell (the proportion shell of total body mass) regardless whether this results from shell length or thickness as well as an increase in growth speed in mollusks in general (Watson, Morley and Peck, 2017). Clearly, thin and small sized shells put the bivalve at risk of predation, so such bivalves could only persist in places without high predation pressure. If at low latitudes either large or thick shells provide better protection against predators and predation pressure decreases with latitude, shells at or around the poles are expected to be thin or small. This hypothesis is supported by the weak calcification found in Antarctic invertebrates (Watson *et al.*, 2012) coinciding with absence of durophagous (shell-breaking) predators in Antarctica (Aronson *et al.*, 2007; Watson *et al.*, 2012). Similarly, in Alaska *Lemicola balthica* has been found to have a much higher body mass to shell mass ratio compared to individuals from more southern populations (Ruthrauff *et al.*, 2018).

A consistent feature across many taxa including marine bivalves is that longevity also correlates with latitude (Moss *et al.*, 2016), with the extreme example of the ocean quahog, *Arctica islandica*, a bivalve with a maximum reported life span of 507 (Butler *et al.*, 2013). In marine ectotherms such as bivalves, metabolic rate is positively correlated with temperature (Lord and Whitlatch, 2014) and it is this low metabolic that rate is believed to largely enable longevity at high latitudes (Fontana, Partridge and Longo, 2010; Moss *et al.*, 2016).

For the dominantly filter-feeding bivalves, food constitutes phytoplankton and other suspended particles and phytoplankton production is strongly tied to solar insolation, which is increasingly limited at high latitudes. This restricts metabolism (Moss *et al.*, 2016), which allows the organisms to withstand periods of scarcity, but also to co-exist in high densities (Vermeij, 1994). Alternatively, from an evolutionary perspective it is suggested that long life span may be instead be an adaptation to restrictive environments constraining the frequency of successful reproduction (Moss *et al.*, 2016).

It could however also be argued that with a decrease in predation pressure with latitude (as discussed in the introduction), mortality by predation simply become less frequent, as is supported by studies demonstrating a decrease in both drilling (Visaggi and Kelley, 2015) and skeleton-crushing (Bertness, Garrity and Levings, 1981) damage in bivalves over a latitudinal gradient.

## 4. Synthesis

To paraphrase Gaston *et al.* (2000) on the LDG, it does clearly “*depends on where one looks*”, and how one looks, whether a large scale pattern exists and how it can be described. To answer the question “*Does the expression of anti-predation traits follow the latitudinal richness gradient?*” a clear, unambiguous picture of the LDG is needed. Instead this is not the case as the marine LDG appears to occur in different varieties or may even undergo changes resulting from global warming and introduced species. Sampling bias, methodological concerns and the use of different metrics by different authors further complicates this.

“The” marine LDG is composed of observations from highly diverse and unevenly sampled datasets and one could argue whether such generic LDG allows the best insight in a possible correlation with the expression of anti-predation bivalves. Perhaps it might be more insightful to study only intertidal bivalves and its associated intertidal species richness gradient, however I did not manage to find publications that allowed me to cover this more specific topic in sufficient detail. Instead, a quantitative analysis with data from literature might be informative but that was outside of the practical scope of this essay.

I do not consider this problematic though, as my interest is ultimately in the mechanisms that determine species richness and how such mechanisms may relate to escalation in the form of the expression of anti-predation traits. Anti-predation traits in bivalves are most escalated in the Indo West Pacific (Vermeij, 1994; Vermeij, 2013), which is also a hotspot for speciation, overall species richness and bivalve richness (Briggs and Bowen, 2012, 2013; Jablonski *et al.*, 2017). However at similar latitudes elsewhere, escalation is less pronounced as demonstrated by Bom *et al.* (2018). Another, principally comparable difference in escalation is found when comparing the East- and Western Atlantic temperate coasts (Jenkins, Burrows and Garbary, 2008; Vermeij, Dietl and Reid, 2008), with the Western Atlantic also considered a biodiversity hotspot (Briggs and Bowen, 2013) and a higher degree of escalation. Both differences are explained by the authors by the absence of certain predators in the less escalated areas and thus not by latitude as a correlate of species richness or biotic interactions. This is supported by the high species richness but weak calcification found in Antarctic invertebrates (Watson *et al.*, 2012) coinciding with absence of durophagous predators (Aronson *et al.*, 2007; Watson *et al.*, 2012). It appears therefore that escalation occurs most likely at places with high species richness, but high species richness per se does not have to lead to escalation.

The general decrease in shell weight to body mass ratio from low to high latitude (Watson, Morley and Peck, 2017) combined with the observations of high densities (Powers *et al.*, 2002, 2006; Nazarova, Shunkina and Genelt-Yanovskiy, 2015) of bivalves such as *Limecola balthica* in arctic and subarctic regions containing relatively little shell weight (Ruthrauff *et al.*, 2018) suggests that at high latitudes it has not been necessary to invest in shell thickness. Sizes are small compared to conspecifics at lower latitudes (Powers *et al.*, 2002; Nazarova, Shunkina and Genelt-Yanovskiy, 2015; Ruthrauff *et al.*, 2018) suggesting a size refuge has also not been necessary. Furthermore there are indications that shell crushing and drilling frequency declines with latitude (Bertness, Garrity and Levings, 1981; Visaggi and Kelley, 2015) pointing towards low escalation at high latitudes. Arctic and temperate bivalves occurring in the intertidal without any marine predators can however be heavily predated upon by shorebirds (Escudero *et al.*, 2012; Ruthrauff *et al.*, 2015). This might be a result of bivalves living in a relative period of isolation during and shortly after the LGM. Considering the cold and variable weather the ecological scope for adaptations was narrow and aimed at surviving environmental conditions while predation pressure was low (Vermeij, 1994). If foraging by staging shorebirds is a relatively recent event, then there has been most likely insufficient evolutionary time for the bivalves to adapt accordingly. Following this logic, it could be expected that at lower latitudes bivalves would be better adapted to shorebird predation for example by burrowing deeper or increasing shell size. Yet, for both is no concrete evidence. This is perhaps explained if the bivalves in those areas have been exposed to heterogeneous modes of predation over a long time, which would inhibit the evolution of a specific anti-predation trait as such trait may provide an advantage against one predator but a disadvantage with another ( Vermeij, 2013).

In conclusion, I propose that escalation is promoted by a combination of factors: (1) Highly productive, warm seas, allowing for a high degree of specialization (Vermeij, 2013; Fine, 2015; Schluter and Pennell, 2017); (2) High species richness resulting in high predation pressure; (3) Geological and climatic stability (Gray, 2001; Valentine and Jablonski, 2015; Jablonski *et al.*, 2017) allowing for long term (co-) evolutionary processes as a result from (1) and (2). So escalation is not predicted by 'the' or 'a' LDG but is it however most likely to occur around the equator and least likely at high latitudes. As a result from glacial cycles, any escalation occurring towards higher latitudes is increasingly at risk of de-escalation in cold periods, setting the process back in development while it continues around the equator.

## References

- Aronson, R. B., Thatje, S., Clarke, A., Peck, L. S., Blake, D. B., Wilga, C. D. and Seibel, B. A. (2007) 'Climate Change and Invasibility of the Antarctic Benthos', *Annual Review of Ecology, Evolution, and Systematics*, 38(1), pp. 129–154.
- Bakun, A. (1990) 'Global climate change and intensification of coastal ocean upwelling', *Science*, 247(4939), pp. 198–201.
- Bardhan, S. and Chattopadhyay, D. (2003) 'the Mesozoic Marine Revolution: an Overview of a Biological "Arms Race"', *Indian Journal of Earth Sciences*, (1), pp. 1–28.
- Beal, B. F., Parker, M. R. and Vencile, K. W. (2001) 'Seasonal effects of intraspecific density and predator exclusion along a shore-level gradient on survival and growth of juveniles of the soft-shell clam, *Mya arenaria* L., in Maine, USA', *Journal of Experimental Marine Biology and Ecology*, 264(2), pp. 133–169.
- Bergmann, C. (1847) *Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse, Göttinger Studien*.
- Berke, S. K., Jablonski, D., Krug, A. Z. and Valentine, J. W. (2014) 'Origination and immigration drive latitudinal gradients in marine functional diversity', *PLoS ONE*, 9(7).
- Bertness, M. D., Garrity, S. D. and Levings, S. C. (1981) 'Predation Pressure and Gastropod Foraging: A Tropical-Temperate Comparison', *Evolution*, 35(5), pp. 995–1007.
- Blois, J., Zarnetske, P., Fitzpatrick, M. and Finnegan, S. (2013) 'Climate Change and the Past, Present, and Future of Biotic Interactions.', *Science*, 341(6145), pp. 499–504.
- Bom, R. A., de Fouw, J., Klaassen, R. H. G., Piersma, T., Lavaleye, M. S. S., Ens, B. J., Oudman, T. and van Gils, J. A. (2018) 'Food web consequences of an evolutionary arms race: Molluscs subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds', *Journal of Biogeography*, 45(2), pp. 342–354.
- Bowen, B. W., Gaither, M. R., DiBattista, J. D., Iacchei, M., Andrews, K. R., Grant, W. S., Toonen, R. J. and Briggs, J. C. (2016) 'Comparative phylogeography of the ocean planet', *Proceedings of the National Academy of Sciences*, 113(29), pp. 7962–7969.
- Briggs, J. C. and Bowen, B. W. (2012) 'A realignment of marine biogeographic provinces with particular reference to fish distributions', *Journal of Biogeography*, 39(1), pp. 12–30.
- Briggs, J. C. and Bowen, B. W. (2013) 'Marine shelf habitat: Biogeography and evolution', *Journal of Biogeography*, 40(6), pp. 1023–1035.
- Brodie, E. D. I. and Brodie, E. D. J. (1999) 'Predator – prey arms races, asymmetrical selection on predators and prey may be reduced when prey are dangerous', *BioScience*, 49(July), pp. 557–568.
- Bustnes, J. O. and Erikstad, K. E. (1990) 'Size selection of common mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*: energy maximization or shell weight minimization?', *Canadian Journal of Zoology*, 68(11), pp. 2280–2283.
- Butler, P. G., Wanamaker, A. D., Scourse, J. D., Richardson, C. A. and Reynolds, D. J. (2013) 'Variability of marine climate on the North Icelandic Shelf in a 1357-year proxy archive based on growth increments in the bivalve *Arctica islandica*', *Palaeogeography, Palaeoclimatology, Palaeoecology*, 373, pp. 141–151.
- Chaudhary, C., Saeedi, H. and Costello, M. J. (2016) 'Bimodality of Latitudinal Gradients in Marine Species Richness', *Trends in Ecology and Evolution*. Elsevier Ltd, 31(9), pp. 670–676.
- Chaudhary, C., Saeedi, H. and Costello, M. J. (2017) 'Marine Species Richness Is Bimodal with Latitude: A Reply to Fernandez and Marques', *Trends in Ecology and Evolution*. Elsevier Ltd, 32(4), pp. 234–237.
- Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S. W., McCabe, A. M., Mix, A. C., Bard, E., Schneider, R., Lambeck, K., Chappell, J., Cutler, K. B., Peltier, W. R., Fairbanks, R. G., Milne, G. A., Mitrovica, J. X., Yokoyama, Y., Lambeck, K., Deckker, P. De, Johnston, P., Fifield, L. K., Carlson, A. E., Stoner, J. S., Donnelly, J. P., Hillaire-Marcel, C., Clark, P. U., McCabe, A. M., Mix, A. C., Weaver, A. J., Steig, E. J., Brook, E. J., Price, S. F., Conway, H., Waddington, E. D., Heroy, D. C., Anderson, J. B., Bassett, S. E., Milne, G. A., Mitrovica, J. X., Clark, P. U., Schaefer, J. M., Licciardi, J. M., Clark, P. U., Brook, E. J., Elmore, D., Sharma, P., Weaver, A. J., Saenko, O., Clark, P. U., Mitrovica, J. X., Skinner, L. C., Shackleton, N. J., Waelbroeck, C., Schrag, D. P., Hampt, G., Murray, D. W., Lisiecki, L., Raymo, M. E., Bintanja, R., Wal, R. S. W. van de, Lea, D. W., Pak, D. K., Spero, H. J., Imbrie, J., Huybers, P., Feldberg, M., Mix, A. C., Martinez, I., Keigwin, L., Barrows, T. T., Yokoyama, Y., Southon, J., Stott, L., Poulsen, C., Lund, S., Thunell, R., Clement, A. C., Seager, R., Cane, M. A., Stott, L., Timmermann, A., Thunell, R., Huybers, P., Denton, G., Clark, P. U., Alley, R. B., Pollard, D., Chiang, J. C. H., Bitz, C. M., Bush, A. B. G., Philander, S. G. H., Briner, J. P., Miller, G. H., Davis, P. T., Finkel, R. C., Pahnke, K., Zahn, R., Elderfield, H., Schulz, M., Blunier, T., Brook, E. J., Wang, Y. J., Peltier, W. R., Edwards, R. L., Chappell, J., Bard, E., Hamelin, B., Fairbanks, R. G., Zindler, A., Hanebuth, T., Stattegger, K., Grootes, P. M., Shackleton, N. J., Hall, M. A., Vincent, E., Laskar, J., Robutel, P., Gastineau, M., Correia, A. C. M., Levrard, B., Ahn, J., Ahn, J., Brook, E. J. and Svensson, A. (2009) 'The Last Glacial Maximum.', *Science (New York, N.Y.)*, 325(5941), pp. 710–4.
- Comita, L. S. (2017) 'How latitude affects biotic interactions', *Science*, 356(6345), pp. 1328–1329.
- Compton, T. J., Rijkenberg, M. J. A., Drent, J. and Piersma, T. (2007) 'Thermal tolerance ranges and climate variability: A comparison between bivalves from differing climates', *Journal of Experimental Marine Biology and Ecology*, 352(1), pp. 200–211.
- Edgar, G. J., Alexander, T. J., Lefcheck, J. S., Bates, A. E., Kininmonth, S. J., Thomson, R. J., Duffy, J. E., Costello, M. J. and Stuart-Smith, R. D. (2017) 'Abundance and local-scale processes contribute to multi-phyta gradients in global marine diversity', *Science Advances*, 3(10).

- Escudero, G., Navedo, J. G., Piersma, T., De Goeij, P. and Edelaar, P. (2012) 'Foraging conditions "at the end of the world" in the context of long-distance migration and population declines in red knots', *Austral Ecology*, 37(3), pp. 355–364.
- Fernandez, M. O. and Marques, A. C. (2017) 'Diversity of Diversities: A Response to Chaudhary, Saeedi, and Costello', *Trends in Ecology and Evolution*, pp. 232–234.
- Fine, P. V. A. (2015) 'Ecological and Evolutionary Drivers of Geographic Variation in Species Diversity', *Annual Review of Ecology, Evolution, and Systematics*, 46(1), pp. 369–392.
- Flessa, K. W. and Jablonski, D. (1995) 'Biogeography of recent marine bivalve molluscs and its implications for paleobiogeography and the geography of extinction: A progress report', *Historical Biology*, 10(1), pp. 25–47.
- Fontana, L., Partridge, L. and Longo, V. D. (2010) 'Extending healthy life span-from yeast to humans', *Science*, pp. 321–326.
- Freestone, A. L., Osman, R. W., Ruiz, G. M. and Torchin, M. E. (2011) 'Stronger predation in the tropics shapes species richness patterns in marine communities', *Ecology*, 92(4), pp. 983–993.
- Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M. and Lawton, J. H. (2000) 'Abundance-occupancy relationships', *Journal of Applied Ecology*, 37(SUPPL. 1), pp. 39–59.
- Gillman, L. N. and Wright, S. D. (2014) 'Species richness and evolutionary speed: The influence of temperature, water and area', *Journal of Biogeography*, 41(1), pp. 39–51.
- Göbbeler, K. and Klusmann-Kolb, A. (2010) 'Out of Antarctica? - New insights into the phylogeny and biogeography of the Pleurobranchomorpha (Mollusca, Gastropoda)', *Molecular Phylogenetics and Evolution*, 55(3), pp. 996–1007.
- De Goeij, P., Luttkhuizen, P. C., Van Der Meer, J. and Piersma, T. (2001) 'Facilitation on an intertidal mudflat: The effect of siphon nipping by flatfish on burying depth of the bivalve *Macoma balthica*', *Oecologia*, 126(4), pp. 500–506.
- Gosling, E. (2015) *Marine Bivalve Molluscs: Second Edition*, *Marine Bivalve Molluscs: Second Edition*.
- Gray, J. S. (2001) 'Antarctic marine benthic biodiversity in a world-wide latitudinal context', *Polar Biology*, 24(9), pp. 633–641.
- Griffiths, C. L. and Richardson, C. A. (2006) 'Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*', *Journal of Experimental Marine Biology and Ecology*, 331(1), pp. 91–98.
- Griffiths, H. J. and Waller, C. L. (2016) 'The first comprehensive description of the biodiversity and biogeography of Antarctic and Sub-Antarctic intertidal communities', *Journal of Biogeography*, 43(6), pp. 1143–1155.
- Hawkins, B. A. (2001) 'Ecology's oldest pattern?', *Trends in Ecology & Evolution*, p. 470.
- Hawkins, B. A. (2010) 'Multiregional comparison of the ecological and phylogenetic structure of butterfly species richness gradients', *Journal of Biogeography*, 37(4), pp. 647–656.
- Hillebrand, H. (2004a) 'On the Generality of the Latitudinal Diversity Gradient', *The American Naturalist*, 163(2), pp. 192–211.
- Hillebrand, H. (2004b) 'Strength, slope and variability of marine latitudinal gradients', *Marine Ecology Progress Series*, 273, pp. 251–267.
- Ilves, K. L., Huang, W., Wares, J. P. and Hickerson, M. J. (2010) 'Colonization and/or mitochondrial selective sweeps across the North Atlantic intertidal assemblage revealed by multi-taxa approximate Bayesian computation', *Molecular Ecology*, 19(20), pp. 4505–4519.
- Jablonski, D., Belanger, C. L., Berke, S. K., Huang, S., Krug, A. Z., Roy, K., Tomasovych, A. and Valentine, J. W. (2013) 'Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient', *Proceedings of the National Academy of Sciences*, 110(26), pp. 10487–10494.
- Jablonski, D., Huang, S., Roy, K. and Valentine, J. W. (2017) 'Shaping the Latitudinal Diversity Gradient: New Perspectives from a Synthesis of Paleobiology and Biogeography', *The American Naturalist*, 189(1), pp. 1–12.
- Jablonski, D., Kaustuv, R. and Valentine, J. W. (2006) 'Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity Gradient', *Science*, 314(October), pp. 102–106. doi: 10.1126/science.1130880.
- Jenkins, S., Burrows, M. and Garbary, D. (2008) 'Comparisons of the Ecology of Shores Across the North Atlantic: Do Differences in Players Matter for Process?', *Ecology*, 89(April).
- Jetz, W. and Fine, P. V. A. (2012) 'Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment', *PLoS Biology*, 10(3).
- Kamermans, P. and Huitema, H. J. (1994) 'Shrimp (*Crangon crangon* L.) browsing upon siphon tips inhibits feeding and growth in the bivalve *Macoma balthica* (L.)', *Journal of Experimental Marine Biology and Ecology*, 175(1), pp. 59–75.
- Kinlock, N. L., Prowant, L., Herstoff, E. M., Foley, C. M., Akin-Fajiyi, M., Bender, N., Umarani, M., Ryu, H. Y., Şen, B. and Gurevitch, J. (2018) 'Explaining global variation in the latitudinal diversity gradient: Meta-analysis confirms known patterns and uncovers new ones', *Global Ecology and Biogeography*, 27(1), pp. 125–141.
- Kvitek, R. G. (1991) 'Paralytic shellfish toxins sequestered by bivalves as a defense against siphon-nipping fish', *Marine Biology*, 111(3), pp. 369–374.

- Laakkonen, H. (2015) *Phylogeography of amphi-boreal marine fauna*. PhD thesis.
- Layton, K. K. S., Martel, A. L. and Hebert, P. D. N. (2016) 'Geographic patterns of genetic diversity in two species complexes of Canadian marine bivalves', *Journal of Molluscan Studies*, 82(2), pp. 282–291.
- Lord, J. and Whitlatch, R. (2014) 'Latitudinal patterns of shell thickness and metabolism in the eastern oyster *Crassostrea virginica* along the east coast of North America', pp. 1487–1497.
- Louthan, A. M., Doak, D. F. and Angert, A. L. (2015) 'Where and When do Species Interactions Set Range Limits?', *Trends in Ecology and Evolution*. Elsevier Ltd, 30(12), pp. 780–792.
- Luttikhuizen, P. C., Drent, J. and Baker, a J. (2003) 'Population divergences predate last glacial maximum in Europe for a marine bivalve with pelagic larval dispersal', *DNA Sequence*, pp. 21–42.
- Maire, O., Merchant, J. N., Bulling, M., Teal, L. R., Grémare, A., Duchêne, J. C. and Solan, M. (2010) 'Indirect effects of non-lethal predation on bivalve activity and sediment reworking', *Journal of Experimental Marine Biology and Ecology*, 395(1–2), pp. 30–36.
- Mannion, P. D., Upchurch, P., Benson, R. B. J. and Goswami, A. (2014) 'The latitudinal biodiversity gradient through deep time', *Trends in Ecology and Evolution*. Elsevier Ltd, 29(1), pp. 42–50.
- Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., Harrison, S. P., Hurlbert, A. H., Knowlton, N., Lessios, H. A., McCain, C. M., McCune, A. R., McDade, L. A., McPeck, M. A., Near, T. J., Price, T. D., Ricklefs, R. E., Roy, K., Sax, D. F., Schluter, D., Sobel, J. M. and Turelli, M. (2007a) 'Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography', *Ecology Letters*, 10(4), pp. 315–331.
- Moss, D. K., Ivany, L. C., Judd, E. J., Cummings, P. W., Bearden, C. E., Kim, W. J., Artruc, E. G. and Driscoll, J. R. (2016) 'Lifespan, growth rate, and body size across latitude in marine bivalvia, with implications for phanerozoic evolution', *Proceedings of the Royal Society B: Biological Sciences*, 283(1836).
- Nagel-Myers, J., Dietl, G. P. and Brett, C. E. (2009) 'First report of sublethal breakage-induced predation on Devonian bivalves', *PALAIOS*, 24(7), pp. 460–465.
- Nakaoka, M. (2000) 'Nonlethal effects of predators on prey populations: Predator-mediated change in bivalve growth', *Ecology*, 81(4), pp. 1031–1045.
- Nazarova, S. A., Shunkina, K. and Genelt-Yanovskiy, E. A. (2015) 'Abundance distribution patterns of intertidal bivalves *Macoma balthica* and *Cerastoderma edule* at the Murman coast tidal flats (the Barents Sea)', *Journal of the Marine Biological Association of the United Kingdom*, 95(8), pp. 1613–1620.
- Parkhaev, P. Y. (2017) 'Origin and the Early Evolution of the Phylum Mollusca', *Paleontological Journal*, 51(6), pp. 663–686.
- Patzkowsky, M. E. and Holland, S. M. (2016) 'Biotic invasion, niche stability, and the assembly of regional biotas in deep time: Comparison between faunal provinces', *Paleobiology*, 42(3), pp. 359–379.
- Pianka, E. R. (1966) 'Latitudinal Gradients in Species Diversity : A Review of Concepts', *The American Naturalist*, 100(910), pp. 33–46.
- Piersma, T., de Goeij, P. and Tulp, I. (1993) 'An evaluation of intertidal feeding habitats from a shorebird perspective: Towards relevant comparisons between temperate and tropical mudflats', *Netherlands Journal of Sea Research*, 31(4), pp. 503–512.
- Ponder, W. F. and Lindberg, D. R. (2008) 'Phylogeny and Evolution of the Mollusca', *Bulletin of Marine Science*, 83(2), p. xi, 469 p.
- Post, D. M. and Palkovacs, E. P. (2009) 'Eco-evolutionary feedbacks in community and ecosystem ecology: Interactions between the ecological theatre and the evolutionary play', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1523), pp. 1629–1640.
- Powell, M. G., Beresford, V. P. and Colaianne, B. A. (2012) 'The latitudinal position of peak marine diversity in living and fossil biotas', *Journal of Biogeography*, 39(9), pp. 1687–1694.
- Powers, S. P., Bishop, M. A., Grabowski, J. H. and Peterson, C. H. (2002) 'Intertidal benthic resources of the Copper River Delta, Alaska, USA', *Journal of Sea Research*, 47(1), pp. 13–23.
- Powers, S. P., Bishop, M. A., Grabowski, J. H. and Peterson, C. H. (2006) 'Distribution of the invasive bivalve *Mya arenaria* L. on intertidal flats of southcentral Alaska', *Journal of Sea Research*, 55(3), pp. 207–216.
- Reimer, O. and Tedengren, M. (1996) 'Phenotypical Improvement of Morphological Defences in the Mussel *Mytilus edulis* Induced by Exposure to the Predator *Asterias rubens*', *Oikos*, 75(3), p. 383.
- Rohde, K. (1992) 'Latitudinal Gradients in Species Diversity: The Search for the Primary Cause', *Oikos*, 65(3), p. 514.
- Rosenzweig, M. (1992) 'Species diversity gradients : we known more and less than we thought', *Journal of Mammalogy*, 73, pp. 715–730.
- Rosenzweig, M. (1995) *Species diversity in space and time*, Cambridge University Press.
- Roy, K., Jablonski, D. and Martien, K. K. (2000) 'Invariant size-frequency distributions along a latitudinal gradient in marine bivalves', *Proceedings of the National Academy of Sciences*, 97(24), pp. 13150–13155.

- Roy, K., Jablonski, D., Valentine, J. W., Roy, K., Jablonski, D. and Valentine, J. W. (2000) 'Dissecting latitudinal diversity gradients : functional groups and clades of marine bivalves Dissecting latitudinal diversity gradients : functional groups and clades of marine bivalves', *267(1440)*, pp. 293–299.
- Ruthrauff, D. R., Dekinga, A., Gill, R. E., Gils, J. A. Van and Piersma, T. (2015) 'Ways to be different: foraging adaptations that facilitate higher intake rates in a northerly wintering shorebird compared with a low-latitude conspecific', *The Journal of Experimental Biology*, *218*, pp. 1188–1197.
- Ruthrauff, D. R., Dekinga, A., Gill, R. E. and Piersma, T. (2018) 'Energetic solutions of Rock Sandpipers to harsh winter conditions rely on prey quality', *Ibis*, *160(2)*, pp. 397–412. doi: 10.1111/ibi.12534.
- Saeedi, H., Dennis, T. E. and Costello, M. J. (2017) 'Bimodal latitudinal species richness and high endemism of razor clams (Mollusca)', *Journal of Biogeography*, *44(3)*, pp. 592–604.
- Schemske, D. (2009) 'Biotic interactions and speciation in the tropics', *Speciation and patterns of ...*, pp. 219–240.
- Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M. and Roy, K. (2009) 'Is There a Latitudinal Gradient in the Importance of Biotic Interactions?', *Annual Review of Ecology, Evolution, and Systematics*, *40(1)*, pp. 245–269.
- Schluter, D. and Pennell, M. W. (2017) 'Speciation gradients and the distribution of biodiversity', *Nature*, *546(7656)*, pp. 48–55.
- Schoener, T. W. (2011) 'The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics', *Science*, pp. 426–429.
- Seitz, R. D., Lipcius, R. N., Hines, A. H. and Eggleston, D. B. (2001) 'Density-dependent predation, habitat variation, and the persistence of marine bivalve prey', *Ecology*, *82(9)*, pp. 2435–2451.
- Sherker, Z. T., Ellrich, J. A. and Scrosati, R. A. (2017) 'Predator-induced shell plasticity in mussels hinders predation by drilling snails', *Marine Ecology Progress Series*, *573*, pp. 167–175.
- Sydeman, W. J., García-Reyes, M., Schoeman, D. S., Rykaczewski, R. R., Thompson, S. A., Black, B. . A. and Bograd, S. J. (2014) 'Climate change and wind intensification in coastal upwelling ecosystems', *Science*, *345(6192)*, pp. 77–80.
- Telford, M. J. and Budd, G. E. (2011) 'Invertebrate evolution: Bringing order to the molluscan chaos', *Current Biology*. Elsevier Ltd, *21(23)*, pp. R964–R966.
- Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. Vanden and Worm, B. (2010) 'Global patterns and predictors of marine biodiversity across taxa', *Nature*, *466(7310)*, pp. 1098–1101.
- Tomašových, A., Kennedy, J. D., Betzner, T. J., Kuehne, N. B., Edie, S., Kim, S., Supriya, K., White, A. E., Rahbek, C., Huang, S., Price, T. D. and Jablonski, D. (2016) 'Unifying latitudinal gradients in range size and richness across marine and terrestrial systems', *Proceedings of the Royal Society B: Biological Sciences*, *283(1830)*.
- Torres-Romero, E. J., Morales-Castilla, I. and Olalla-Tiarraga, M. (2016) 'Bergmann's rule in the oceans? Temperature strongly correlates with global interspecific patterns of body size in marine mammals', *Global Ecology and Biogeography*, *25(10)*, pp. 1206–1215.
- Valentine, J. W. and Jablonski, D. (2015) 'A twofold role for global energy gradients in marine biodiversity trends', *Journal of Biogeography*, *42(6)*, pp. 997–1005.
- Valentine, J. W., Jablonski, D., Kidwell, S. and Roy, K. (2006) 'Assessing the fidelity of the fossil record by using marine bivalves', *Proceedings of the National Academy of Sciences*, *103(17)*, pp. 6599–6604.
- Valentine, J. W., Jablonski, D., Krug, A. Z. and Berke, S. K. (2013) 'The sampling and estimation of marine paleodiversity patterns: implications of a Pliocene model', *Paleobiology*, *39(01)*, pp. 1–20.
- Vellend, M., Lajoie, G., Bourret, A., Múrria, C., Kembel, S. W. and Garant, D. (2014) 'Drawing ecological inferences from coincident patterns of population- and community-level biodiversity', *Molecular Ecology*, *23(12)*, pp. 2890–2901.
- Vermeij, G. (2013) 'On Escalation', *Annual Review of Earth and Planetary Sciences*, *41(1)*, pp. 1–19.
- Vermeij, G. J. (1994) 'The Evolutionary Interaction Among Species : Selection , Escalation , and Coevolution', *Ecology*, *25(1994)*, pp. 219–236.
- Vermeij, G. J. (2005) 'From phenomenology to first principles: toward a theory of diversity', *Proceedings of the California Academy of Sciences*, *56(2)*, pp. 12–23.
- Vermeij, G. J. (2013) 'On Escalation', *Annual Review of Earth and Planetary Sciences*, *41(1)*, pp. 1–19.
- Vermeij, G. J., Dietl, G. P. and Reid, D. G. (2008) 'The Trans-Atlantic History Of Diversity And Body Size In Ecological Guilds', *Ecology*, *89(11)*, pp. S39–S52.
- Vinagre, C., Mendonça, V., Cereja, R., Abreu-Afonso, F., Dias, M., Mizrahi, D. and Flores, A. A. V. (2018) 'Ecological traps in shallow coastal waters-Potential effect of heat-waves in tropical and temperate organisms', *PLoS ONE*, *13(2)*, pp. 1–17.
- Visaggi, C. C. and Kelley, P. H. (2015) 'Equatorward increase in naticid gastropod drilling predation on infaunal bivalves from Brazil with paleontological implications', *Palaeogeography, Palaeoclimatology, Palaeoecology*, *438*, pp. 285–299.

- Watson, S. A., Morley, S. A. and Peck, L. S. (2017) 'Latitudinal trends in shell production cost from the tropics to the poles', *Science Advances*, 3(9).
- Watson, S. A., Peck, L. S., Tyler, P. A., Southgate, P. C., Tan, K. S., Day, R. W. and Morley, S. A. (2012) 'Marine invertebrate skeleton size varies with latitude, temperature and carbonate saturation: Implications for global change and ocean acidification', *Global Change Biology*, 18(10), pp. 3026–3038.
- Wiens, J. and Donoghue, M. (2004) 'Historical biogeography, ecology and species richness', *Trends in Ecology & Evolution*, 19(12), pp. 639–644.
- Williams, C. M., Ragland, G. J., Betini, G., Buckley, L. B., Cheviron, Z. A., Donohue, K., Hereford, J., Humphries, M. M., Lisovski, S., Marshall, K. E., Schmidt, P. S., Sheldon, K. S., Varpe, Ø. and Visser, M. E. (2017) 'Understanding Evolutionary Impacts of Seasonality: An Introduction to the Symposium', *Integrative and Comparative Biology*, 57(5), pp. 921–933.
- Willig, M. R., Kaufman, D. M. and Stevens, R. D. (2003) 'Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis', *Annual Review of Ecology, Evolution, and Systematics*, 34(1), pp. 273–309.
- Willig, M. R. and Presley, S. J. (2018) *Latitudinal Gradients of Biodiversity: Theory and Empirical Patterns, Encyclopedia of the Anthropocene*. Elsevier Inc.
- Yang, H. Y., Chen, B., Piersma, T., Zhang, Z. and Ding, C. (2016) 'Molluscs of an intertidal soft-sediment area in China: Does overfishing explain a high density but low diversity community that benefits staging shorebirds?', *Journal of Sea Research*. Elsevier B.V., 109, pp. 20–28.
- Zwarts, L. and Blomert, A. M. (1992) 'Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available', *Marine Ecology Progress Series*, 83(2–3), pp. 113–128.
- Zwarts, L. and Wanink, J. (1989) 'Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves', *Marine Biology*, 100(2), pp. 227–240.