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VERTICAL FAUNAL EXCHANGE IN THE OCEAN AND THE DEEP SOURCE-SINK HYPOTHESES: A REVIEW FROM THE PERSPECTIVE OF PRESSURE TOLERANCE STUDIES

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Abstract Faunal exchanges between shallow-water and deep-sea environments, throughout geological times, have resulted in the broad colonization of oceanic depths we see today. Attempts have been made to explain the current distribution of benthic animals by the submergence (shallow to deep) hypothesis or the high-latitude emergence (deep to shallow) hypothesis. More recently, discussions of bi-directional exchanges have emerged. Here we aim to summarize and explore empirical support for the various hypotheses by reviewing over 130 studies on the tolerance (survival) of adults and larvae of ~260 species following compression or decompression. Secondarily, we attempt to tease out the importance of ontogeny (comparing tolerance of adult and larval life stages), phylogeny (comparing tolerance among major phyla) and geographic location of collection (looking for latitudinal trends). Overall, empirical evidence supports the formalization of a bi-directional exchange hypothesis as the most parsimonious explanation for current bathymetric patterns of biodiversity and highlights the pressure tolerance of benthic animals occupying bathyal depths. No clear ontogenetic patterns emerged, but comparison of pressure tolerance between adult and larval stages remains tentative due to the limited number of species for which this was assessed across life stages (nearly all under decompression scenarios). Pressure tolerance varies across and within phyla, and more basal taxa do not show consistent patterns of lower mortality (or longer survival) upon pressure shifts, although organismal simplicity and protective features (e.g. calcified exoskeleton) seem to increase tolerance. Adults of deep-sea species collected at lower latitudes appear to survive to pressure in equal or higher proportions, but for much shorter durations than those collected from higher latitudes, partly supporting suggestions that bathymetric transitions may be favoured in isothermal water columns (closer to the poles). Globally, this synthesis highlights technical and conceptual gaps offering a framework for further investigation of vertical movements of marine species across depths, which will be particularly useful in predicting ecosystem shifts in response to climate change.

Keywords: Barotolerance, bathymetric distribution, biodiversity, compression, deep sea, emergence, faunal exchanges, hydrostatic pressure, submergence, vertical movements

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Introduction

Evolving views of the deep sea

A fundamental division in the world ocean involves the distinction between shallow-water and deep-sea environments (Webb et al. 2010). The transition between the two is not universally defined, but it is often considered to occur at ~200 m, which typically marks the depth of the continental shelf break (Thistle 2003, Ramirez-Llodra et al. 2011) or the lower limit of light penetration in the water column (Yancey 1991). Oceanic depths have long exerted great fascination on humans. Some believed them to be devoid of life and proposed the azoic theory (Forbes 1844), yet deep dwelling marine fauna had already been discovered, and Risso (1810, 1820) had reported that the vertical distribution of certain fishes extended 500 m below the sea surface. Eventually, there was broad recognition that fauna occurred at all ocean depths, but the deep sea continued to be depicted as a harsh environment, exhibiting lower biodiversity than shallow water (Sanders 1968). Paradigms regarding the low biodiversity and productivity of the deep sea were revised when hundreds of benthic macrofaunal species were recovered from deep-sea trawls for the first time (Hessler & Sanders 1967, Gage & Tyler 1991) and exceptional ecosystems such as those occurring at hydrothermal vents were discovered (Corliss & Ballard 1977). Over the last few decades, hotspots of biodiversity in the deep sea have been highlighted (e.g. seamounts, coral and sponge gardens, hydrothermal vents and cold seeps), which rival some of the most diversified environments on the planet. In fact, recent extrapolations suggest that deep-sea habitats could host over 10 million species (Ramirez-Llodra et al. 2011), more than the total number of species currently known to populate Earth (Mora et al. 2011).

The realization that the deep-sea fosters high levels of biodiversity, and the fact that depths >200 m cover more than 60% of the surface area of the globe, prompted contrasting hypotheses regarding the origin of extant deep-sea species. These hypotheses proposed either that deep-sea taxa evolved *in situ* with representatives subsequently colonizing shallow waters, or that deep-sea species evolved from shallow-water species following range extension into deep waters (Locket 1977, Gage & Tyler 1991). Studies focusing on deep-sea and shallow-water colonization developed during the 1960s and 1970s (Menzies & Wilson 1961, Kussakin 1973, Menzies et al. 1973, Hessler & Thistle 1975, Hessler et al. 1979), although hypotheses were postulated a few decades earlier (Dahl 1954, Wolff 1960). While deep-sea research has intensified during the past 50 years, the role of the deep ocean as a biodiversity source or sink remains obscure (Gage & Tyler 1991, Miglietta et al. 2011). Resolving this is complicated by ongoing uncertainty regarding the importance of specific depths as biodiversity sinks or sources at different geological times (Rex et al. 2005, Bik et al. 2010).

Hypotheses on ocean colonization and bathymetric ranges

Shallow to deep

The submergence hypothesis postulates that taxa from shallow waters extended their bathymetric range downwards following climate-driven extinction events in the deep sea (related to oxygen depletion), and radiated at bathyal (>200–2000 m) and abyssal depths (>2000–6000 m) (Kussakin 1973, Jablonski & Bottjer 1991, Jablonski 2005). This hypothesis relies in part on phylogenetic and taxonomic evidence that deep-sea species are derived from shallow-water species, together with ancestral state reconstructions (extrapolation back in time to common ancestors from measured characteristics of individuals or populations) based on current biogeographic distributions (Brown & Thatje 2014). Fossil evidence suggests that higher taxonomic levels predominantly originated in nearshore environments whereas lower taxonomic levels originated in offshore environments where radiation occurred subsequently (Jablonski & Bottjer 1991). Deep-sea colonization by shallow-water taxa is suggested to have occurred throughout geological history, especially during the late Mesozoic and early Cenozoic periods, when the water column was isothermal across low latitudes (Menzies et al. 1973, Jablonski et al. 1983, Wilson 1999). Jacobs and Lindberg (1998) provided support for this hypothesis, suggesting that onshore to deep-sea diversification predominated in the Mesozoic prior to the Turonian stage of the Cretaceous. Extinct deep-sea fauna identified in fossil records from these periods have been linked to extant shallow-water animals whose ancestors may have colonized the deep sea (Kussakin 1973, Cottin et al. 2012). In fact, it is argued that the colonization of the deep sea by shallow-water animals may be continuous in isothermal water columns, such as in regions of deep (cold) water formation (Wolff 1960, Tyler & Young 1998, Tyler & Dixon 2000, Oliphant et al. 2011). Smaller temperature differences between shallow water and deep sea are thought to greatly reduce the physiological barrier to bathymetric range extension (Gage & Tyler 1991, Raupach et al. 2009), but shallow-water species still must acclimatize or adapt to increasing pressure conditions to migrate downwards (Clarke et al. 1992, Hall & Thatje 2009, Brown & Thatje 2014, Gaither et al. 2016, Lemaire et al. 2018).

Shallow-water organisms that colonize the deep sea may possess sufficient physiological (and possibly developmental) plasticity to directly invade the deep sea and thrive under relatively extreme conditions, which include high hydrostatic pressure, constant low temperature, complete darkness and minimal nutrients from primary production (Hessler & Wilson 1983, Pradillon et al. 2004). Alternatively, if acclimatization to these conditions is beyond the physiological scope of invading shallow-water organisms, indirect invasion through adaptation may occur. Subsequent reproductive isolation from shallow relatives (Hessler & Wilson 1983) may lead to speciation and radiation (Brown & Thatje 2014). Adaptation to more specialized habitats such as hydrothermal vents and cold seeps is thought to happen subsequently (Kiel & Little 2006, Kiel 2016, Sun et al. 2018), although direct colonization of other chemosynthetic deep-sea environments such as whale falls has also been suggested (Distel et al. 2000). The movement of taxa from shallow to deep waters may occur in response to catastrophic events (Speijer & van Der Zwaan 1996), giving rise to the concept of the deep-sea refuge (Cavin 2001, Guinot et al. 2013). The deeper dwelling populations of taxa with broad bathymetric ranges are proposed to have allowed these species to survive surface-water mass extinction events, becoming the source populations for subsequent recolonization and repopulation of shallow waters (see examples in Cavin 2001, Friedman & Sallan 2012, Guinot et al. 2013).

Deep to shallow

The opposing emergence hypothesis proposes that modern deep-sea invertebrates evolved from ancestors that already occupied deep water (Hessler & Thistle 1975), subsequently migrating upwards and populating shallow depths at high latitudes (Hessler & Thistle 1975, Hessler et al. 1979, Wägele 1989, Wilson 1999). This hypothesis suggests that the high extant deep-sea biodiversity could not be a product of small colonization events from shallow waters (Birstein 1963, Hessler & Sanders 1967, Hessler & Thistle 1975). The vast majority of species diversity in many deep-sea families without primitive or less evolved shallow-water representatives is restricted to deep bathymetric ranges, which is proposed to challenge the possibility that these lineages migrated from shallower waters (Hessler & Wilson 1983). For example, some deep-sea isopod lineages evolved *in situ*, within the deep sea, before colonizing shallow water, based on the deep-water occurrence of the most primitive genera or species and the occurrence of shallow-water taxa that lack eyes (Hessler & Wilson 1983). This pattern of origination was reportedly reversed during periods of the Cretaceous and Cenozoic in response to changing environmental conditions, such as increasing oxygenation in the deep benthic environment, extinction of taxa associated with low-oxygen conditions, and increased oxygenation of sediments by bioturbation with the expansion of deep burrowing species into offshore environments (Jacobs & Lindberg 1998).

Bi-directional movement

Although not a formal hypothesis, recent evidence suggesting bi-directional transitions between shallow-water and deep-sea environments within some lineages provides an alternative to unidirectional shallow-deep and deep-shallow colonizations. For example, foraminiferan microfossils from shallow-water populations and deep-sea populations have been discovered to derive from a range of depth strata, evoking an active exchange of fauna (Lipps & Hickman 1982). Similarly, a combination of early-derived and late-branching lineages are found in deep-sea populations of nematodes, hinting at dynamic exchanges between fauna from different depths (Bik et al. 2010). Clade structures showing recent close relationships between deep-water and shallow-water nematode species suggest interchanges between deep-sea and intertidal zones are common in this group (Bik et al. 2010). In addition, a study of the echinoderm class Ophiuroidea revealed complex macro-evolutionary patterns of bathymetric movement (Bribiesca-Contreras et al. 2017). Notably, researchers found that no hypotheses pertaining to "uniform onshore or offshore origins" could be directly supported since there was "a long history of multiple transitions between deep and shallow water lineages" (Bribiesca-Contreras et al. 2017). These studies provide valuable insight into the origin and evolution of many species and their bathymetric distribution. However, despite gathering evidence for bi-directional exchange (see also Hall & Thatje 2009, Strugnell et al. 2011, Riehl & Kaiser 2012), strong support for this view has yet to be presented.

Exploring colonization theories through the pressure tolerance lens

The bathymetric distribution of species in the ocean is constrained by their tolerance and adaptation to many factors, on the whole dominated by the combined effects of temperature and hydrostatic pressure gradients (Menzies et al. 1973, Wilson et al. 2007, Mestre et al. 2009, Brown & Thatje 2011, Cottin et al. 2012, Kiel et al. 2012, Brown & Thatje 2014). Since all environmental factors (i.e. temperature, illumination, food supply, substrate type) except pressure are affecting other ecosystems of the globe, hydrostatic pressure is perhaps the most fundamental characteristic of the deep sea. Yet, compared to our knowledge of thermal biology and of the influence of temperature on deep-sea biodiversity (Yasuhara & Danovaro 2016), the contribution of hydrostatic pressure is understudied. This is largely because the study of pressure as an experimental factor is much more recent than the study of temperature (Rivalain et al. 2010), even though the physiological action of pressure on immersed cells, tissues and whole metazoans has been the subject of laboratory investigations since the late nineteenth century (Regnard 1884, Regnard 1885, Regnard 1891, Fontaine 1930, Cattell 1936). Incomplete knowledge of the specific role of pressure is limiting our global understanding of bathymetric adaptations, which is something that has been highlighted as a major gap in knowledge for a long time (Cattell 1936, Schlieper 1968, Macdonald 1997, Pradillon & Gaill 2007).

Fundamental characteristics and effects of pressure

The basic definition of pressure as a thermodynamic parameter is the force per unit area applied on a surface in a direction perpendicular to this surface. Hydrostatic pressure exhibits a linear gradient from the surface to the bottom of the ocean (Tyler & Young 1998, Pradillon & Gaill 2007), increasing steadily by ~1 MPa (~10 bar or ~10 atm) with every 100 m depth (Macdonald 1997, Pradillon et al. 2004). It must be specified that our knowledge of pressure effects centres largely on the outcome of compression (exposure to a higher pressure than that of the natural state or native habitat), by exposing animals or biological systems normally adapted to atmospheric (surface) pressure to increasing hydrostatic pressure. Decompression (exposure of deep-adapted life forms to surface pressure) and recompression (when deep-adapted lifeforms are brought to the surface and recompressed to the pressure of their native habitat) are not equally well understood. This is not surprising since compression studies of shallow-water taxa predate decompression studies of deep-water taxa, which have until very recently been thought to be incapable of surviving at atmospheric pressure (Pradillon & Gaill 2007).

The complex effects of hydrostatic pressure at the various levels of biological organization (genes, molecules, cells, organisms) will not be detailed here since they have previously been reviewed independently and in relation to temperature (Pradillon & Gaill 2007, Yancey 2020, Macdonald 2021). Pressure primarily produces changes in energy, volume and chemical reactivity (Rivalain et al. 2010): in water, the energy conveyed by pressure is small compared to the energy conveyed by temperature; compressibility means that volumes under high pressure are smaller than under lower pressure (with cascading effects on various processes at different organizational levels); and pressure typically improves solubility and enhances chemical reactivity.

Given these properties, changes in pressure (from outside the natural range of an organism) affects molecular, cellular, biochemical and physiological processes, which can be reflected at the level of the whole organism through loss of motor function and other sub-lethal effects, all the way to mortality (Macdonald & Teal 1975, Morris et al. 2015). Even if dysfunctions are temporary, they may jeopardize basic ecological behaviours such as foraging and escaping from predators, which are essential to survival (Oliphant et al. 2011, Munro et al. 2015, Ammendolia et al. 2018). Overall, the full range of biochemical and physiological effects of shifts in hydrostatic pressure and how they differ among marine phyla is incompletely understood (Pradillon & Gaill 2007), in part because experimental approaches face technological challenges, as discussed below.

Experimental equipment and approaches

Our ability to assess the impacts of hydrostatic pressure on marine organisms essentially revolves around the availability of suitable laboratory facilities and equipment, the choice of appropriate response variables and the selection of representative study systems/organisms.

The evolution of technologies and experimental approaches has been decisive in developing our understanding of pressure impacts (i.e. compression) on aquatic species. There are numerous types of pressure systems of different sizes (from tiny chambers to large vessels) with various corresponding fixtures (e.g. temperature controls, viewing ports, gas extractors) described in reviews by Pradillon & Gaill (2007) and by Macdonald (2021). For the most part, the equipment used for compression studies with macrobenthic animals regulates pressure through a piston and vessel design (Schlieper 1968, Childress 1976, Pradillon & Gaill 2007, Shillito et al. 2014, Macdonald 2021). Generally speaking, there are: (1) large systems used to test pressure tolerances and maintain adults organisms (e.g. Macdonald & Gilchrist 1980, Quetin & Childress 1980, Pradillon et al. 2001, 2004); (2) smaller systems to test pressure tolerances on embryonic and larval stages of organisms (e.g. Marsh et al. 2001, Pradillon et al. 2001, 2004), and; (3) isobaric systems for *in situ* collection of organisms at native pressure (e.g. Yayanos 1981, Koyama et al. 2002). While early systems were surprisingly ingenious, including glass windows and attempts at flow-through (Schlieper 1968), the experimental study of hydrostatic pressure was revolutionized by the development of a large-volume flow-through pressure system called IPOCAMP (Incubateur Pressurisé pour l'Observation et la Culture d'Animaux Marins Profonds) (Shillito et al. 2001, 2014). With built-in temperature control, this system enables the study of thermo- and barotolerance of macrofauna for durations ranging from hours to weeks. In some cases, pressure aquaria have been outfitted with specialized features to maintain chemosynthetic species (Shillito et al. 2015). However, approaches that expose animals from chemosynthetic habitats are relatively novel and have been limited by additional technical constraints in terms of volume and trial duration. Systems designed to mimic the chemically complex hydrothermal vent environment can either be maintained at surface pressure (e.g. LabHorta;

Miyake et al. 2007, Bettencourt et al. 2010) or native deep-sea pressures (e.g. AbyssBox; Sarradin et al. 2007, Shillito et al. 2015).

In the most fundamental way, the pressure tolerance of a species (i.e. the ability to survive changes in pressure) can be assessed by measuring survival (often in study-specific terms rather than standard terms such as LD_{50}) to pressures beyond the known bathymetric range, following compression or decompression (Villalobos et al. 2006, Oliphant et al. 2011, Brown & Thatje 2015, Ammendolia et al. 2018). In addition, various non-lethal responses can be measured, which may rely on shifts in behaviour (Wilcock et al. 1978, Shillito 2006, Thatje et al. 2010, Brown et al. 2017, Ammendolia et al. 2018, Pallareti et al. 2018, Brown et al. 2019), developmental anomalies (Young & Tyler 1993, Tyler & Dixon 2000, Villalobos et al. 2006, Sumida et al. 2015), physiological processes (Childress 1976, Childress & Thuesen 1993, Ravaux et al. 2009, 2013, Brown et al. 2017, Pallareti et al. 2018, Brown et al. 2019, 2020) and genetic markers (Dixon et al. 2002, Barros et al. 2015, Morris et al. 2015, Brown et al. 2017).

Another layer of complexity resides in the fact that the measurable effects of pressure may vary both across taxa (Brown & Thatje 2015) and across life stages of a given species (e.g. Tyler & Dixon 2000, Aquino-Souza 2006, Villalobos et al. 2006, Yoshiki et al. 2006, 2008, 2011, Munro et al. 2015, Brown et al. 2017). Beyond the choice of model animals (or life stages), procuring them may present additional challenges. While obtaining shallow-water organisms for experimental studies is straightforward, there are technical difficulties surrounding the collection and holding of deep-sea organisms (Shillito et al. 2001, 2015, Pallareti et al. 2018). Offshore expeditions are costly and logistically complex, thereby limiting opportunities for collecting animals at depth and potentially introducing geographic and habitat-based sampling bias. For instance, chemosynthetic environments, such as hydrothermal vents and cold seeps, have been and remain a focus of cross-disciplinary oceanographic expeditions (Gaill et al. 1997, Tyler & Dixon 2000, Marsh et al. 2001, Martinez et al. 2001, Pradillon et al. 2001, Shillito et al. 2001, Dixon et al. 2002, Lee 2003, Pruski & Dixon 2003, Shillito et al. 2004, Shillito 2006, Ravaux et al. 2009, 2013, Smith et al. 2013, Bettencourt et al. 2017). While high pressure is typical of both non-chemosynthetic and chemosynthetic environments (Ravaux et al. 2009), the latter are also characterized by high sulphide concentrations (Ravaux et al. 2003) and hydrothermal vents present high and potentially extreme temperatures (Shillito et al. 2001). Hence, pressure tolerance in deep-sea taxa collected from chemosynthetic environments may not necessarily be representative of this tolerance in species from the wider deep sea.

Experimental results are informative as long as the test subjects are well acclimated, and the factor of interest is the only applied change. Long delays associated with ascent and retrieval generate stress in deep-sea organisms during collection, and subsequent maintenance on the ship under minimally suitable conditions (for days or weeks) brings additional space-related and technical challenges. Fortuitously, most marine invertebrates do not have internal gas spaces that result in damage from gas expansion during decompression, meaning that adult animals of most marine taxa can be used for laboratory investigations if there is no cell or tissue damage (Dixon et al. 2004). However, the risk of internal and external injuries associated with sampling apparatuses (e.g. claws or suction devices of remotely operated vehicles, trawl nets, box cores) remains fairly high.

Rationale and objectives of the review

Some 95% of the marine biosphere lies below 200 m depth (Jaenicke 1983, Jannasch & Taylor 1984, Somero 1992, Danovaro et al. 2014, Brown et al. 2017), and climate-driven increases in ocean surface temperatures are predicted to drive vertical range shifts in benthic organisms over relatively short timescales (Brown & Thatje 2015, Morris et al. 2015, Brown et al. 2017, Pallareti et al. 2018). These movements of marine species across depths could potentially alter existing ecosystems, emphasizing the importance of developing our understanding of colonization theories in the face of anticipated climatic shifts.

The last synthetic contributions aiming to evaluate responses to hydrostatic pressure and tease out their role on the vertical distribution of benthic megafauna through an experimental lens were presented in the 1960s (Menzies & Wilson 1961, Rice 1964, Schlieper 1968). As outlined in these reviews, early experiments were tentative, and their methodologies were poorly described for the most part. Since then, technologies have evolved, and studies involving compression and/or decompression have bloomed, yet no recent assessment of the pressure tolerance literature has been conducted to determine how it may feed into the hypotheses of ocean colonization. The objective of the present synthesis is to fill this gap by summarizing and exploring experimental and observational evidence from the past 60 years that provide insight into the pressure tolerance of extant macrobenthic taxa. The challenges associated with pressure studies (briefly outlined in the previous section) have given rise to a diversity of experimental approaches that make results difficult to compare directly, precluding a formal meta-analysis. However, an exhaustive qualitative analysis is long overdue, which might help provide directions for future studies in this field. Our goal is to build a first comprehensive dataset and attempt to ground truth the various conceptual propositions with the empirical information currently available.

Pressure tolerance is often viewed as one of the predictors of vertical migration in marine species (Young et al. 1997, Tyler & Young 1998, Tyler et al. 2000, Aquino-Souza 2006, Villalobos et al. 2006, Smith & Thatje 2012, Sumida et al. 2015). Based on this assumption, we evaluate whether empirical data of pressure tolerance (as per cent survival and survival duration; see Appendix) provide support for shallow-deep or deep-shallow transitions, or whether bi-directional colonization may offer a more parsimonious explanation. This assessment includes general comparisons between compression and decompression studies, as well as an examination of the effect of depth zone of origin (bathyal vs. abyssal) in the latter. In addition, we attempt to tease out trends in pressure tolerance based on the most probable modulators: ontogeny (comparing tolerance of adult and larval life stages), phylogeny/taxonomy (comparing tolerance among major phyla) and geographic location of collection (looking for latitudinal trends). In line with the colonization hypotheses, this review focuses on macrobenthic species; therefore, pelagic and planktonic animals, and unicellular organisms, are not considered. Where possible, efforts are made to distinguish the responses of deep-water representatives from chemosynthetic and non-chemosynthetic environments, given that the former must additionally cope with habitat-specific gradients in temperature and water chemistry.

Review of pressure tolerance studies

Overview

We have compiled and organized the findings of over 130 studies conducted between 1961 and 2020 (see Appendix method and Table 1). Within this full dataset, some form of empirical measure of pressure tolerance exists for at least 262 species of metazoans across nine phyla. Of these, 244 (93%) have been recorded as having survived pressure shifts, regardless of type and duration of exposure and proportion (or life stage) of survivors. Globally, more species have been exposed to decompression than compression scenarios, but both types of exposure have yielded high proportions of minimal survivorship in early and/or later (adult) life stages (Figure 1).

Importantly, empirical evidence of pressure tolerance is heterogeneous in nature, ranging from acute hour-long pressurization trials of a single life stage in a selected species to long-term holding of decompressed species for months to years. Some species have only been exposed to one stable pressure level, whereas others have been tested under a suite of pressure conditions, including incremental or stable compression/decompression and recompression, and others yet have concurrently

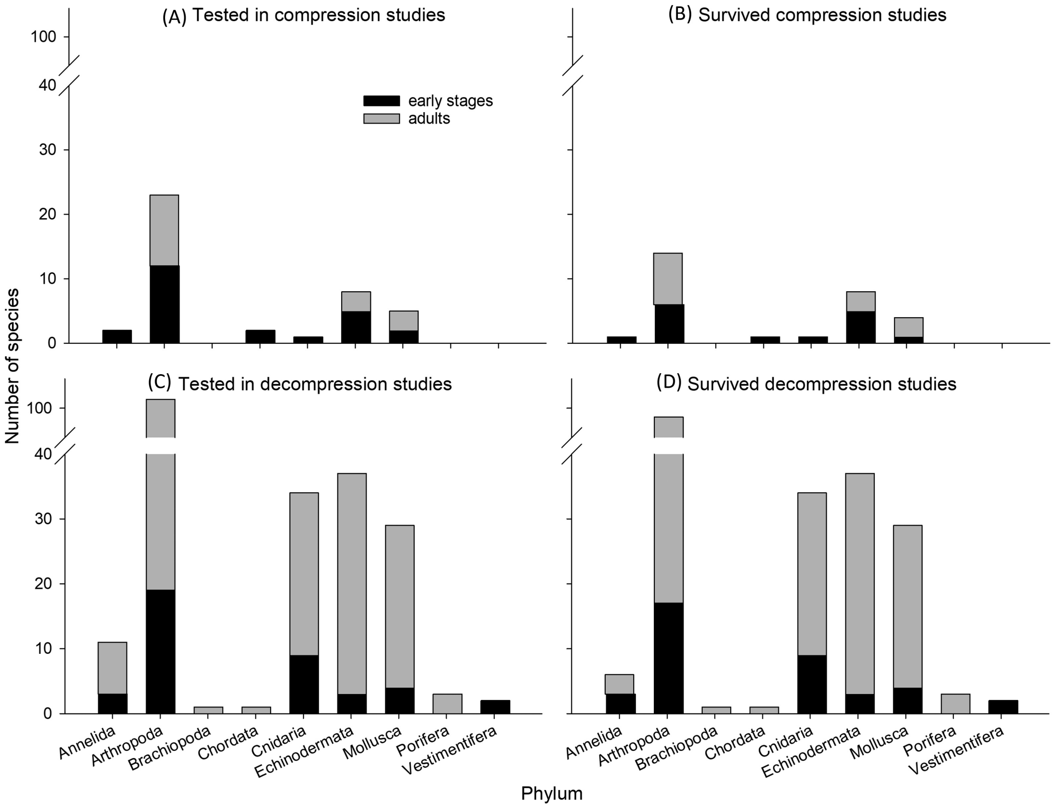

Figure 1 Overview of available empirical evidence of pressure tolerance separated into metazoan phyla, type of study (compression, decompression) and life stage (early stages or adults). (A) Number of benthic species that have been the subject compression studies, of which (B) survival was demonstrated in one way or another. (C) Number of benthic species that have been the subject decompression studies, of which (D) survival was demonstrated in one way or another.

been exposed to a range of pressures and temperatures in multifactorial designs (Appendix Table 1). Depending on the study objectives, the outcomes are also reported using various descriptive and quantitative metrics. Unfortunately, standard measures such as LD_{50} have typically not been used. The simplest, most universal means of assessing pressure tolerance involves measuring per cent survival inside a group of animals exposed to compression or decompression, with or without a complementary measure of survival duration (or inversely). Except in cases of long-term holding, the measure of momentary survival makes abstraction of the state of the survivors, which does not guarantee that fitness was maintained or that the exposure was not ultimately lethal. Therefore, teasing out the meaning of the findings shown in Figure 1, and how they can be compared is challenging. In an attempt to extract further information, we have adopted a two-stage approach: first we try to draw generalizations where possible, notwithstanding the caveats mentioned above; and second, we present case studies inside each phylum to provide a more detailed understanding of the state of knowledge.

Combining a subset of compression and decompression studies that provide clear survival rates and durations (see criteria in Appendix, and selected records in Appendix Table 2), the nine major metazoan phyla are still represented, including 45 species tested at early life stages (embryos and larvae) and 144 species tested at later life stages (juveniles and adults), some of which may be the

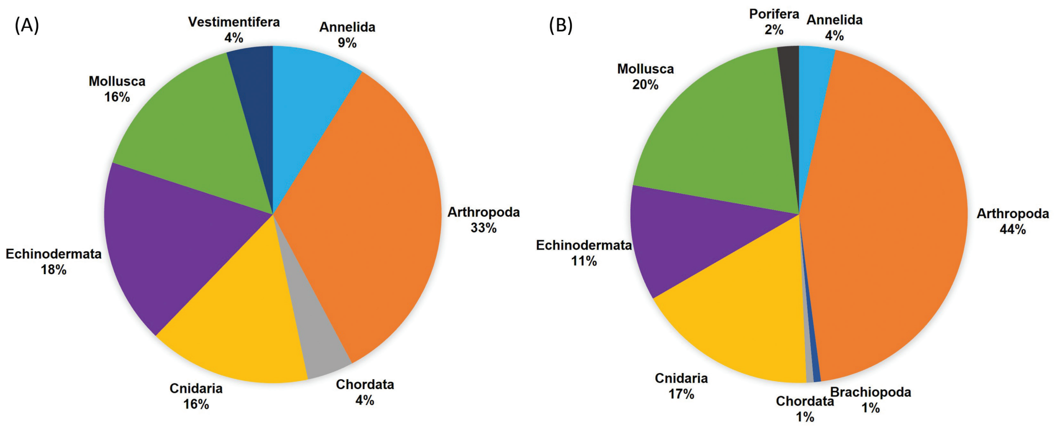

Figure 2 Taxonomic distribution of macrobenthic species used in studies of pressure tolerance (compression or decompression) that examined (A) early life stages (embryos or larvae, $N = 45$ species) and (B) late life stages (juveniles or adults, $N = 144$ species) and for which per cent survivors and duration of survival (until mortality or end of study) were both provided. Refer to Appendix for a description of studies included.

same species. In each of these two groups, most species belong to Arthropoda (33%–44%), followed by Cnidaria, Echinodermata and Mollusca (11%–20%), and the rest (Annelida, Chordata, Foraminifera, Porifera, Vestimentifera) each represent 1%–9% (Figure 2). Looking at the type of tolerance in this subset reveals that three of the most studied phyla (Arthropoda, Echinodermata and Mollusca) provide fairly balanced assessments, with both life stages having been submitted to compression and decompression scenarios (and a slight predominance of decompression studies conducted with adults). In contrast, assessments are more biased for Cnidaria, which have only been the subject of decompression studies at both life stages.

Regardless of the type of exposure (compression or decompression), most species survived exposure of ~1.5 to >26,000 hours to pressure that differed from their native pressure by at least 2 MPa (~200 m), suggesting some level of tolerance. Maximum proportion of survivors ranged broadly from as little as 2%–7% and up to 100% of exposed individuals. There was considerable variability, but average per cent survival was more commonly higher in decompression than compression studies in phyla where both metrics were available, i.e. across 9 species of Annelida, 79 species of Arthropoda, 24 species of Echinodermata and 36 species of Mollusca (Figure 3). The only exception was reported in a single invertebrate Chordata species where compression of larvae for 24 hours was highly successful.

Ontogeny

An overview of the subset shown in Figure 3A does not reveal any clear trend in per cent survival (regardless of exposure duration) between studies conducted on adults or larvae of different taxa within a phylum. The survival duration (Figure 3B) cannot be readily compared between life stages inside a phylum because studies are always of shorter duration for embryos and larvae (≤500 hours; constrained by developmental tempo). However, we found 21 species across six phyla for which survival rates were provided for the early and late life stages of the same species (Figure 4). All but one of these were tested under decompression scenarios (deep-water species exposed to atmospheric pressure) and, as stated above, duration of exposure was not necessarily equivalent for both stages. The only compression study was conducted with an arthropod and resulted in 100% survival for both life stages tested. In the decompression studies, per cent survival was the same or was similar

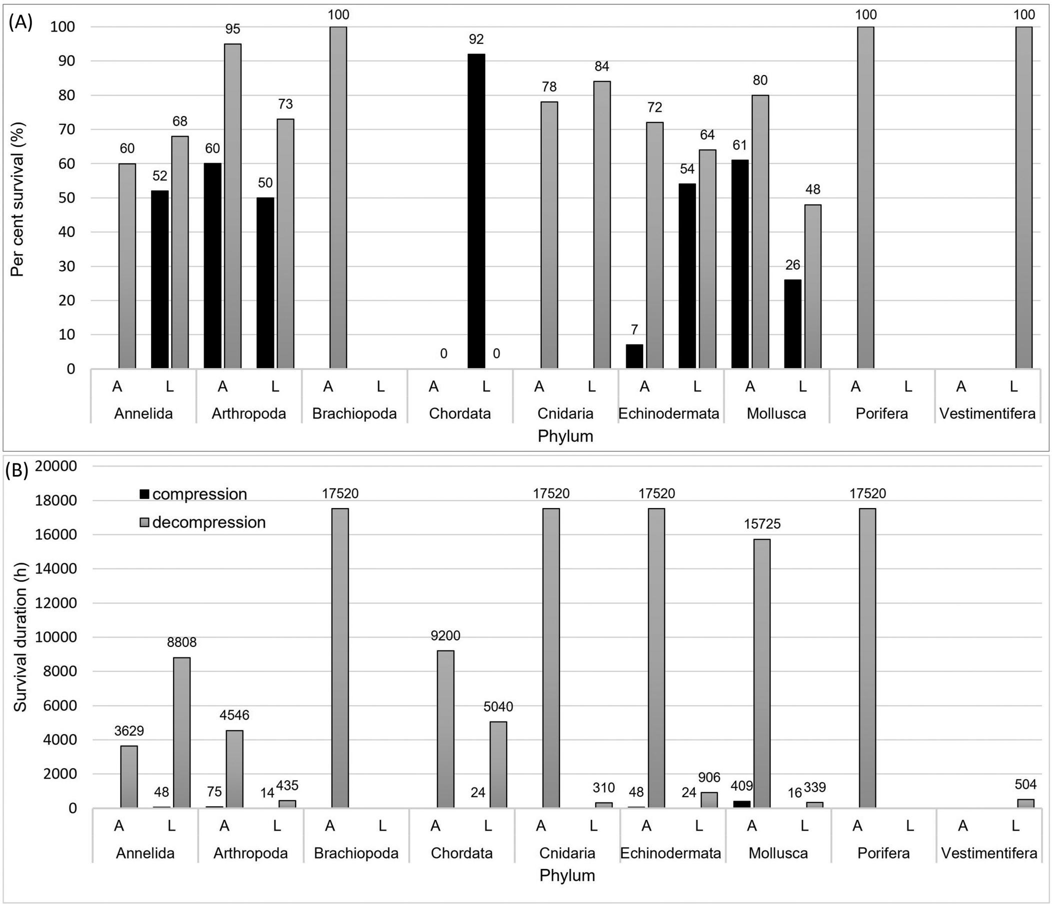

Figure 3 (A) Mean per cent survival and (B) mean survival duration (until mortality or end of study) reported following compression and decompression studies conducted with juvenile or adult stages (labelled A) and early life stages, mostly larvae (labelled L) of benthic species belonging to the major metazoan phyla (*N*=9 Annelida, 79 Arthropoda, 1 Brachiopoda, 1 Chordata, 32 Cnidaria, 24 Echinodermata, 36 Mollusca, 3 Porifera, 2 Vestimentifera). Bars without values are subgroups for which data are not available. See dataset in Appendix Table 2.

(within 5%) between life stages in roughly half the species (Figure 4). Survival was lower for the early life stages than for the adults in one of two annelids, two of four arthropods, the only chordate, one of seven species of cnidarians, one of three echinoderms, and in the single mollusc; conversely, it was only lower for the adults in one of the two annelids.

Taxonomy

Based on the compiled data for the main metazoan phyla, per cent survival and survival duration did not display any clear phylogenetic trend. The recorded survival of adults to pressure shifts (regardless of sample size and exposure duration) was commonly ≥50% and often as high as 100% in many taxa, and results varied markedly both across and within phyla (Figures 3 and 4). During maintenance, the longest surviving taxa were typically Cnidaria, Echinodermata, Mollusca and Porifera, while Arthropoda survived the shortest duration, but still well above 100 days (to over a year for some studies).

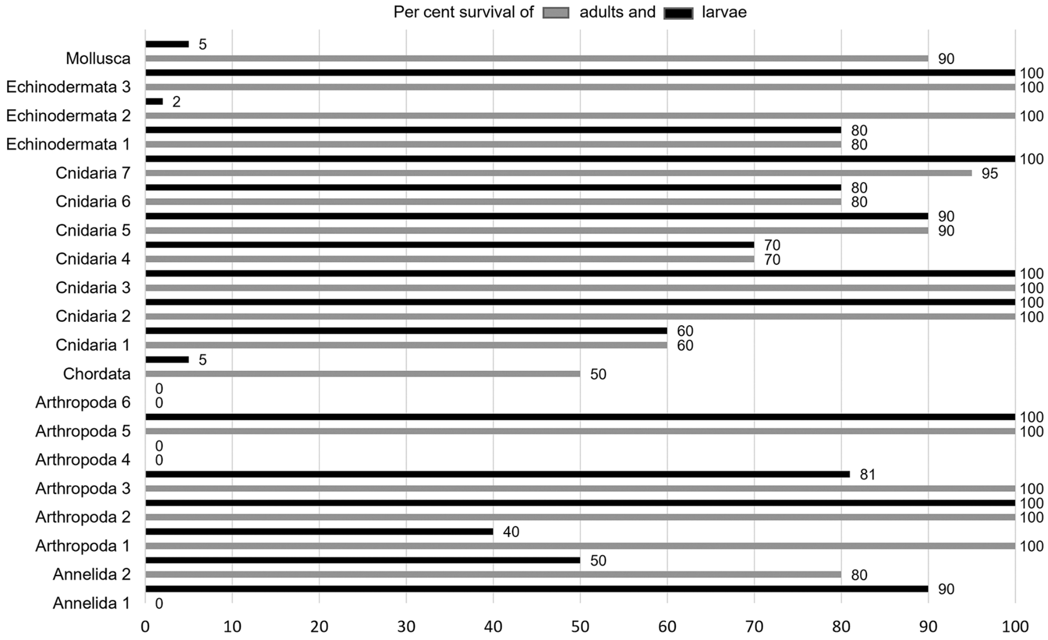

Figure 4 Exploration of per cent survival in adults and early life stages (mostly larvae) of the same deep-sea species following decompression to atmospheric pressure (grouped per phylum). Each pair of bars represents a species. See details of dataset in Appendix Table 3.

Depth zone and geographic region of origin

Based on the compiled subset, per cent survival and survival duration were highest/longest for decompressed adult individuals collected from bathyal depths, compared to both compression of taxa from shallower zones and decompression of taxa from deeper zones (Figure 5A). When considering only decompression of adults originating from the bathyal zone (minus those from chemosynthetic habitats such as vents and seeps), per cent survival was slightly higher, but survival duration much shorter for studies conducted at lower latitude (Gulf of Mexico, Mediterranean Sea, Tropical Indian and Pacific Oceans) compared to higher latitudes (Northwest/Northeast Atlantic and Pacific Oceans) (Figure 5B).

Apart from the high/low latitude trend, no pattern emerged from comparisons among geographic regions, and the influence of the habitat of origin (i.e. including or excluding chemosynthetic environments) was minimal (Figure 6). Worth mentioning is the fact that studies at higher latitudes were chiefly conducted in the Atlantic and studies at lower latitudes were chiefly conducted in the Mediterranean, creating a bias where ocean basins are not equally represented. With respect to taxonomy, the top four phyla identified at the onset still dominate.

Case studies of decompression

Adults and juveniles from deep chemosynthetic environments

Organisms from chemosynthetic habitats have been reported to survive decompression quite well (often >70%) from a substantial number of studies (Appendix Table 1) (Mickel & Childress 1982, Childress et al. 1984, 1991, Gaill et al. 1997, Shillito et al. 2001, Dixon et al. 2002, Ravaux et al. 2003, Shillito et al. 2004, Shillito 2006, Cottin et al. 2008, Kádár et al. 2008a, Boutet et al. 2009,

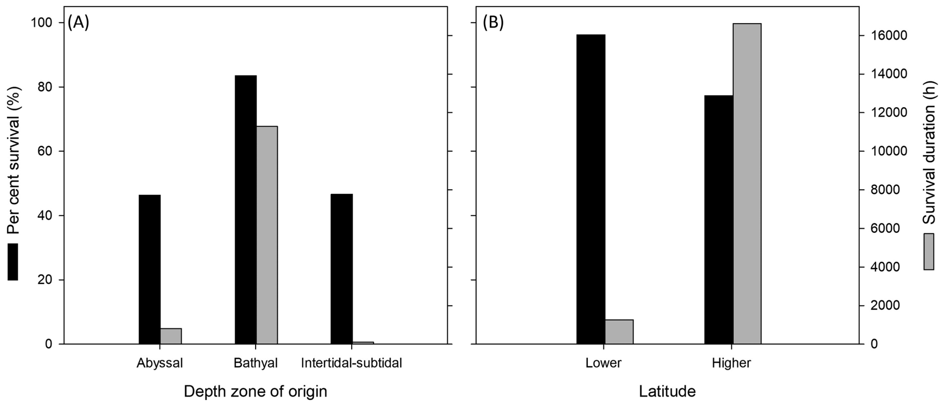

Figure 5 Exploration of per cent survival (left axis) and survival duration (right axis) from case studies of adults of the main phyla exposed to compression or decompression. (A) Comparison among depth zones of origin, regardless of habitat and exposure type ($N = 142$, including 6 Annelida, 62 Arthropoda, 1 Brachiopoda, 1 Chordata, 16 Echinodermata, 25 Cnidaria, 28 Mollusca and 3 Porifera). (B) Comparison among latitudes for bathyal taxa (from non-chemosynthetic habitats) exposed to decompression ($N = 104$, including 2 Annelida, 43 Arthropoda, 1 Chordata, 25 Cnidaria, 12 Echinodermata, 18 Mollusca and 3 Porifera). See details of dataset in Appendix Table 4.

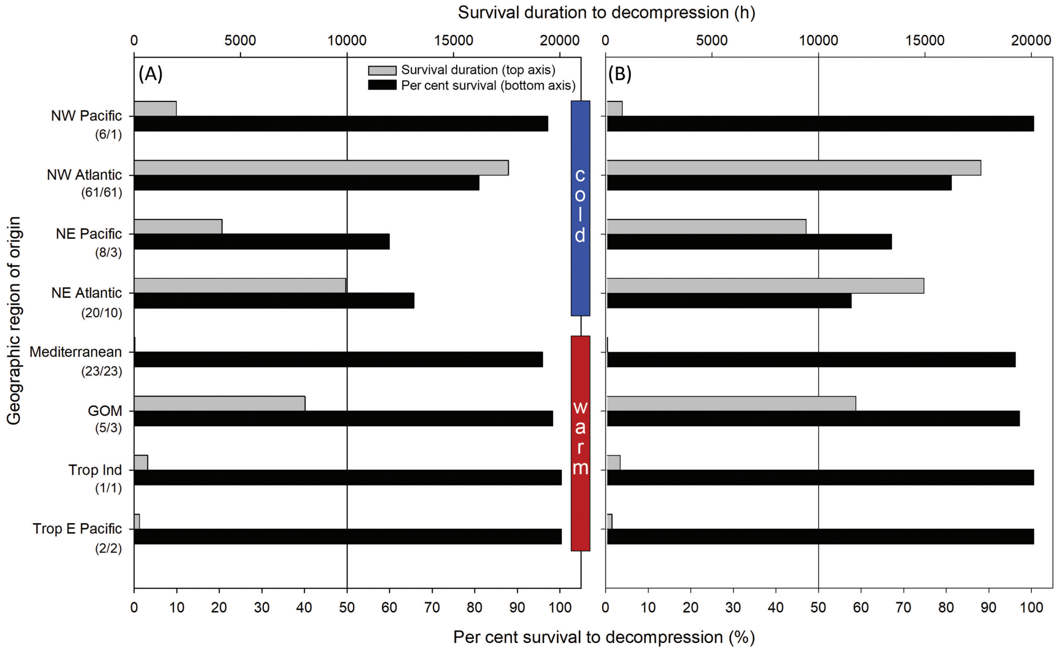

Figure 6 Exploration of per cent survival (bottom axis) and survival duration (top axis) among geographic regions from case studies of adults of the main benthic phyla collected at bathyal depths exposed to decompression. (A) Studies of chemosynthetic and non-chemosynthetic taxa; $N = 126$ species (6 Annelida, 55 Arthropoda, 1 Chordata, 25 Cnidaria, 12 Echinodermata, 24 Mollusca and 3 Porifera). (B) Studies of non-chemosynthetic taxa only; $N = 104$ with taxonomic distribution as in Figure 4B. The top four regions are higher latitudes (blue rectangle), and the bottom four regions are lower latitudes (red rectangle). The number of records per region is shown in parentheses (as panel A/panel B). NW, Northwest; NE, Northeast; GOM, Gulf of Mexico; Trop, Tropical; E, East. See details of dataset in Appendix Table 4.

Cottin et al. 2010, Durand et al. 2010, Ravaux et al. 2013, Shillito et al. 2015). Phylum-specific examples are outlined below.

Annelida. There are relatively few examples of chemosynthetic Annelida successfully maintained at surface pressure, but the hydrothermal vent tubeworm *Lamellibrachia luymesi* was collected and held for 1–15 months in laboratory conditions (Dattagupta 2006). It was noted that most individuals survived despite physical damage to the base of the tube sustained during the collection process. By contrast, multiple species of chemosynthetic Annelida did not survive decompression (Childress et al. 1984, Pradillon 2005). This inability to survive long exposures to decompression was also noted in unpublished work with the species *Paralvinella palmiformis* held at surface pressure (Lee, pers. comm).

Arthropoda. Survival of vent/seep arthropods at surface pressure is generally >50% (only one experiment resulted in 0% survival; Appendix Table 1), and individuals have been found to survive for sustained periods. The vent shrimp *Mirocaris fortunata* collected from 1617 m was maintained at atmospheric pressure for >12 months, although it was not made clear how much mortality occurred (Smith et al. 2013). The shrimp *M. fortunata* was also collected from the Northeast Atlantic while five species of crab and shrimp were collected from the Northwest Pacific off the coast of Japan: all were maintained for over a year at atmospheric pressure (Miyake et al. 2007, Hamasaki et al. 2010, Smith et al. 2013).

Mollusca. Molluscs collected at vents and seeps that were brought to the surface exhibited 100% survival to decompression for durations ranging from 12 hours to a year (Martinez et al. 2001, Kádár et al. 2005, 2006, Bettencourt et al. 2008, Kádár et al. 2008b, Colaço et al. 2011). The mussel *Bathymodiolus azoricus* was collected from the Northeast Atlantic at Menez Gwen and Rainbow vent fields from depths of 840, 850 and 2300 m. Individuals survived anywhere from 10 to 365 days (e.g. Pruski & Dixon 2003, Dixon et al. 2004, Kádár et al. 2008b, Bettencourt et al. 2010, Martins et al. 2014, Barros et al. 2015, Bettencourt et al. 2017). Likewise, the cold seep mussel *Bathymodiolus childressi* was collected from the Gulf of Mexico and survived decompression to surface pressure conditions for periods ranging from 15 to 365 days (Arellano & Young 2009).

Adults and juveniles from deep non-chemosynthetic environments

Macrobenthic species collected from the deep Northwest Atlantic have shown a consistent ability to survive and thrive at surface pressure for years (Appendix Table 1). Furthermore, several species have also reproduced, some persisting through multiple generations (see details below). Reports from many other regions indicate that a diversity of deep-sea taxa from non-chemosynthetic environments survive at surface pressure for days to months and beyond (Appendix Table 1). Notably, 13 species of Arthropoda and 14 species of Echinodermata were collected from 250 to 1000 m depth in the Tropical West Pacific Ocean and maintained in the laboratory for 120 days (Wilson et al. 2013). Some phylum-specific examples are provided below.

Annelida. Annelid species collected from the Northwest Atlantic survived differently when decompressed to atmospheric pressure under very similar settings (in the same laboratory). For instance, the polychaete *Neopolynoe acanellae* collected from depths of 466 to 1406 m exhibited 100% survival (Hamel et al. 2015), whereas *Ophryotrocha* sp. collected from 60 to 730 m exhibited 50% survival (Mercier et al. 2014, Verkaik et al. 2017). Despite lower survival, the latter was maintained for several generations.

Arthropoda. Generally, arthropods tolerated decompression well, but there was variability across studies. An amphipod from the Northeast Atlantic, *Stephonyx biscayensis*, survived decompression from 1528 to 1765 m depths over acute exposure periods (0.17 hour) without exhibiting any mortality, and was subsequently held for 60 days at surface pressure (Brown & Thatje 2011). Similarly, the Lophogastrida *Gnathophausia ingens* collected from 400 to 900 m tolerated acute decompression to surface pressure (for 4–6 hours), with some specimens surviving for 45 days post-experimentation (Mickel & Childress 1982). In the case of collections from deeper abyssal depths down to 3900 m in the Indian Ocean, survival rates to decompression varied among species (Treude et al. 2002). Specimens of the amphipods *Paralicella* spp. and *Abyssorchomene abyssorum* did not survive at surface pressure while *Abyssorchomene distinctus* survived for 21 days (Treude et al. 2002). In the case of *Paralicella* aff. *alberti,* individuals were collected from two different depth zones, bathyal and abyssal; the individual collected from the former survived for 26 days whereas the individual collected from the latter died shortly after being brought to surface (Treude et al. 2002). Several pycnogonids (*Nymphon hirtipes*), collected from depths of 1350 to 1450 m in the Northwest Atlantic off eastern Canada not only survived long-term holding, but laid eggs and yielded juveniles (Mercier et al. 2015). Moreover, several species of barnacles, shrimps and amphipods from the bathyal Northwest Atlantic survived for years at atmospheric pressure in mesocosms.

Cnidaria. Some 22 different species of cnidarians originating from a range of depths in the North Atlantic, down to 2500 m, were maintained for over 2 years at surface pressure with some of them spawning (sea anemones and corals) and producing offspring (e.g. Mercier & Hamel 2009a, Sun et al. 2009, Hamel et al. 2010, Sun et al. 2010, Mercier et al. 2011b, 2011d, Baillon et al. 2014, Mercier et al. 2017). One of them, the deep-sea scleractinian coral *Flabellum alabastrum*, exhibited growth between 1 and 5 mm/year over 2 years (Hamel et al. 2010). Two other scleractinian coral species collected from the Mediterranean Sea at depths of 214–218 m were held at surface pressure for 517 days to study their growth (Orejas et al. 2008). The commensal sea anemone *Allantactis parasitica* from the Northwest Atlantic, living in association with large deep-water gastropods, survived also for several years at atmospheric pressure; some individuals spawned, and interactions with the hosts were characterized (Mercier & Hamel 2008b, 2009b, Mercier et al. 2011a).

Mollusca. Under similar decompression conditions, only 50% of the bathyal mollusc species, including *Frigidoalvania brychia* (Weinberg 1990), survived for 772 days. Several species from the Northwest Atlantic, e.g. the gastropod *Buccinum scalariforme*, were seen to mate and lay egg masses that produced surviving offspring (Montgomery et al. 2017).

Porifera. Three species of demosponges from the bathyal Northwest Atlantic fed and exhibited growth over years of holding at atmospheric pressure; some individuals were used in experimental trials to estimate their filtration rates under various environmental conditions (Robertson et al. 2017).

Echinodermata. Several species of sea stars, brittle stars and sea urchins collected from deep waters off eastern Canada survived for months to years under atmospheric pressure. Among them, the brooding sea star *Henricia lisa* (Mercier & Hamel 2008a) and *Hippasteria phrygiana* fed and reproduced (Stuckless et al. 2021). Others sea stars were used in series of experimental trials over a period of several months, including *Ceramaster granularis* (Stuckless et al. 2021).

Embryos and larvae from chemosynthetic environments

Relative to the number of studies that investigated the pressure tolerance of adults, there were fewer studies of decompression in early life stages (eggs, embryos and various larval stages) of species from chemosynthetic environments (Appendix Table 1), which can be largely attributed to logistical challenges (Pradillon et al. 2001, Pradillon 2005, Cottin et al. 2008, Ravaux et al. 2009). Very few investigators obtained larvae directly from chemosynthetic environments and reported their development. Among them, Arellano et al. (2014) collected eggs and veligers of vent gastropods and Epifanio et al. (1999) collected megalopa larvae of vent crabs (see findings below). More reports exist of deep-sea species from chemosynthetic environments having spawned at surface pressure with successful larval development, as exemplified below.

Arthropoda. The deep-water barnacle *Neoverruca* sp. demonstrated greater survival in treatments that exposed larvae to lower pressures (surface pressure) than treatments that compressed larvae (born in the laboratory from decompressed genitors) to native pressure conditions (Watanabe et al. 2004). Survival at surface pressure decreased slightly from 100% to 97% over the course of

14–17 days. Many deep-sea arthropods sampled from the Nikko Seamount vents of the Northwest Pacific successfully spawned, including the vent crab *Austinograea yunhana* and vent shrimp *Opaepele* spp. (Miyake et al. 2007). However, the larvae of the latter did not continue development post-hatching and those of the former experienced early mortality, which investigators suggested was unrelated to pressure issues (Miyake et al. 2007). A similar suggestion was made when larvae of *Gandalfus yunohana* were obtained in the laboratory and successfully metamorphosed into megalopal stages, but died without moulting into juveniles after 104 days (Hamasaki et al. 2010). It was proposed that chemical cues from the natural environment were required for moulting to juvenile and that pressure was not the immediate limiting factor. Wantanabe et al. (2004) offered similar conclusions when adults of hydrothermal vent barnacles *Neoverruca* from the Northwest Pacific spawned larvae under surface pressure, and none successfully metamorphosed/settled before dying after 183 days. In a rare study of larvae obtained from the deep, Epifanio et al. (1999) collected megalopa stages of the hydrothermal vent crab *Bythograea thermydron* from 2500 m, which survived only until their third stage of development (while juveniles collected at the same time were maintained at surface pressure for a period of 201 days).

Mollusca. Generally, larvae of deep-sea vent species of molluscs (obtained following spawning of adults collected at depth) survived well (>58%) when decompressed and exposed to surface pressure (Arellano & Young 2011, Arellano et al. 2014). Arellano et al. (2014) also collected eggs of the gastropod *Bathynerita naticoidea* and veligers of *B. childressi* in the Gulf of Mexico, which were said to have successfully hatched and developed at surface pressure, but the maximum survival duration was not assessed.

Embryos and larvae from non-chemosynthetic environments

Propagules that resulted from the reproduction of deep-water adults collected from non-chemosynthetic environments generally survived well under various experimental conditions (Appendix Table 1).

Annelida. The deep-water polychaete *Ophryotrocha* sp., collected from the Northwest Atlantic, reproduced several times under mesocosm conditions at atmospheric pressure, with offspring reaching maturity and reproducing themselves over successive generations (Mercier et al. 2014). The reproductive output of this species was later used in an investigation of the impact of ocean acidification (Verkaik et al. 2017).

Arthropoda. Several individuals of the deep-sea pycnogonid *Nymphon hirtipes* collected at 700–1450 m depths in the Northwest Atlantic laid egg masses at atmospheric pressure, which underwent embryonic, larval and juvenile development until their release by the brooding males (Mercier et al. 2015). Survival rates remained 100% over 9 months of monitoring. In a series of pressure experiments on the early life stages of copepod species that reproduce in high-pressure environments (*Neocalanus cristatus, N. flemingeri* and *N. plumchrus*), which were collected at 1000–1500 m depths in the Northwest Pacific, development and hatching success were not affected by pressure (Yoshiki et al. 2011).

Cnidaria. Larvae produced by deep-sea corals, including *Drifa* sp., *Drifa glomerata, Flabellum angulare* and by the sea anemone *Urticina* sp. had high survival rates (>70%) to the planula and juvenile stages (Sun et al. 2009, 2010, Mercier et al. 2011b,c,d), but their ability to survive to later stages was not evaluated due to logistical constraints. Moreover, propagules (embryos, larvae) of the sea anemone *Allantactis parasitica* developed into juveniles that grew over several months at atmospheric pressure (Mercier & Hamel 2009a).

Echinodermata. Progeny of two deep-water sea stars (*Hippasteria phrygiana* and *Henricia lisa*) from the Northwest Atlantic were reported to develop from fertilized oocytes to gastrulae and fertilized oocytes to fully developed juveniles, respectively. In the case of *H. lisa*, the brooded offspring had a survival rate of 100% (Mercier & Hamel 2008a).

Mollusca. The deep North Atlantic gastropod *Buccinum scalariforme* developed from egg to juvenile inside egg masses laid during holding at atmospheric pressure; juveniles emerged after 120 days of development, with a survival rate of ~5% (Montgomery et al. 2017). Low survival is likely part of the reproductive strategy of this species, whereby most oocytes are used as nurse cells by a limited number of developing offspring.

Case studies of compression

Adults and juveniles

Shallow-water species submitted to compression generally did not survive as long as decompressed deep-sea species outlined above (Appendix Table 1). Nevertheless, many species demonstrated an ability to withstand pressure beyond that prevailing inside their native distributions, as shown in the phylum-specific examples below.

Arthropoda. The shallow-water shrimp *Palaemonetes varians* demonstrated 70% survival at 10 MPa after 28 days of exposure (Cottin et al. 2012). The authors of the study suggested that mortalities may have been associated with cannibalism resulting from the absence of feeding rather than from compression itself. In a series of experiments on the subtidal crab *Lithodes maja*, survival at the end of 240 hours of exposure was 100% at 7 MPa and down to 0% at 12.5 MPa (Brown et al. 2017). In another shallow-water crab, *Maja brachydactyla*, 100% of individuals survived 90 hours of exposure to 15.2 MPa (Thatje and Robinson 2011). Similarly, all (100%) of the hermit crabs *Pagurus cuanensis* survived 1-hour compression to 5 MPa (Thatje et al. 2010).

Echinodermata. The survival of sea urchins *Strongylocentrotus droebachiensis* and sea cucumbers *Cucumaria frondosa* collected from the Northwest Atlantic decreased from 100% to 0% with increasing duration (24 vs. 72 hours) of compression corresponding to depths beyond their natural range, i.e. 2–3 times the deepest depth of natural occurrence (Ammendolia et al. 2018). As for the sea star *Leptasterias polaris*, it survived compression well for 24–48 hours (83%–100%), but there was 100% mortality after 9 days of exposure at the same pressure, demonstrating decreased tolerance over prolonged experimental durations.

Mollusca. The same trend of decreasing tolerance with exposure duration was noted for the shallow-water bivalve *Mytilus edulis,* with mortality occurring after 216 hours of compression at 22 MPa (Ammendolia et al. 2018). Menzies and Wilson (1961) had also found that *M. edulis diegensis* could cope with acute compression up to 23.3 MPa for 5.8 hours, whereas no individuals were able to survive to 35 MPa for 8 hours, suggesting that barotolerance was met at depths beyond ~3500 m. In another species, *M. galloprovincialis* collected from 0 to 10 m, compression to 46.5 MPa for 144 hours resulted in 0% survival while compression to slightly lower pressures (15.5 MPa) for 1656 hours resulted in 38% survival (Galgani et al. 2005).

Embryos and larvae

A limited number of studies have tested the compression of early life stages because long-term investigations require appropriate holding facilities and continuous monitoring over more or less extended developmental periods. Globally, there were trends of decreasing survival with increasing pressure beyond the scope of natural bathymetric range in larvae of shallow-water species.

Annelida. After 48 hours of pressure exposure, survival of the larvae of the annelid *Pomatoceros lamarcki* decreased from 69.1% at 10.1 MPa to 41.4% at 20.3 MPa and 19.3% at 30.4 MPa (Vevers et al. 2010).

Arthropoda and Cnidaria. George & Marum (1974) tested the effect of experimental compression (6.1–65.5 MPa) for 1 hour on the survival of larvae of some species of shallow-water Arthropoda and Cnidaria from either the Caribbean or Northwest Atlantic, with variable survival from 0% to 100%. In short compression experiments that lasted ~4 hours, no difference in survival was found among development stages of the crab *Lithodes maja* (Munro et al. 2015).

Chordata. In the Caribbean ascidian *Polyandrocarpa zorritensis,* survival rates of tadpole larvae increased with exposure to pressure, from 62% at 5 MPa to 92% at 20.3 MPa (Sumida et al. 2015). However, survival of juveniles was not in line with this trend, suggesting there was limited capacity to adapt fully to these high-pressure conditions (Sumida et al. 2015).

Echinodermata. Species of shallow-water echinoderms (sea stars and sea urchins) collected from the Northeast Atlantic and Antarctica had high survival (mostly >80%) when compressed for 24–48 hours to pressures characteristic of depths greater than their natural occurrence (Tyler & Young 1998, Aquino-Souza 2006, Villalobos et al. 2006). Other experiments tested the larvae of sea cucumbers *Apostichopus japonicus* from the western Pacific for as little as 7 minutes and found that survival reduced as pressure increased (Ding et al. 2007). Embryos of the sea urchin *Sterechinus neumayeri,* collected from Antarctica, survived compression better than later prism and 4-arm pluteus larval stages (Tyler et al. 2000). Specifically, survival at 25.3 MPa was 91%, 18% and 4%, for the three stages, respectively. Similar trends were observed with another sea urchin (*Psammechinus miliaris*) from the Northeast Atlantic in which survival to compression diminished as development progressed, i.e. gastrulae survived more than late prism stages (Aquino-Souza et al. 2008). This was also reflected in a shallow-water sea star, *Asterias rubens,* collected from the Northeast Atlantic where the late bipinnaria generally survived more than the early bipinnaria when compressed over 48 hours (Villalobos et al. 2006).

Mollusca. Survival of the mollusc *Crepidula fornicata* exposed for 24 hours to various compression levels decreased from 100% at 20 MPa to 75% at 30 MPa and 52% at 40 MPa (Mestre et al. 2013). Interestingly, pressure tolerance varied between different larval stages, whereby late veligers of *C. fornicata* survived slightly better under elevated pressure than early veligers (Mestre et al. 2013).

Discussion

Pressure tolerance and the hypotheses of ocean colonization

Many short-term compression studies have proposed pressure tolerance (survival for a relatively brief duration) to be a predictor of deep-sea invasion by shallow-water species (Young et al. 1997, Tyler & Young 1998, Tyler et al. 2000, Aquino-Souza 2006, Villalobos et al. 2006, Smith & Thatje 2012, Sumida et al. 2015). The present review aimed to use a similar lens to take a broader look at currently available results from both compression and decompression studies, exploring how they might inform vertical colonization patterns. Evidence of tolerance to higher or lower pressures was overall quite widespread in the studies of macrobenthic species compiled here. Strictly based on the number of records demonstrating higher per cent survival and/or longer survival duration following decompression of deep-water species than compression of shallow-water species, we globally found stronger support for the deep-shallow than the shallow-deep hypothesis. Generally, the survival of adults after exposure to compression and/or decompression was higher for deep-sea than shallow-water taxa. Furthermore, adults of many deep-sea species seem to possess the capacity to withstand shallow-water pressure conditions for prolonged periods, whereas evidence of adult shallow-water organisms surviving high pressure remains limited. For instance, studies of numerous deep-sea species (from a range of phyla) have reported survival at surface pressure over months to years (e.g. Weinberg 1990, Miyake et al. 2007, Mercier et al. 2011d), both in laboratory chemosynthetic conditions (e.g. Colaço et al. 2006, Miyake et al. 2007, Colaço et al. 2011, Miyake et al. 2012, Matabos et al. 2015, Shillito et al. 2015) and non-chemosynthetic cold-water conditions (e.g. Mercier & Hamel 2008a, 2009a, Sun et al. 2009, Mercier et al. 2014, 2015). While more limited, good examples also exist of shallow-water taxa surviving long-term compression, e.g. 69 days for the mussel *Mytilus* *galloprovincialis* maintained in sea cages at depths to 1550 m (Galgani et al. 2005) and 28 days for the shrimp *Palaemonetes varians* maintained in vessels pressurized to 10 MPa, or ~1000 m (Cottin et al. 2012). However, this review found many reports of survival to pressure in shallow-water taxa decreasing both as a function of pressure level and exposure duration.

Beyond survival rates, several long-term studies observed key behaviours such as feeding, growth, spawning and larval development in deep-sea species at surface pressure, indicating that those species acclimatized successfully to surface pressure under appropriate holding conditions. The ability of deep-sea species to survive at surface pressure may not even be fully captured within the available literature because information on total survival duration beyond experimental trials was often absent. For example, Brown & Thatje (2011) assessed tolerance to compression in the deep-sea crustacean *Stephonyx biscayensis* following 60 days acclimation to decompression and surface pressure, and reported that survival at surface pressure exceeded the acclimation period.

Interestingly, the length of post-collection survival of deep-sea adults at surface pressure was generally longer for taxa collected from bathyal (>200–2000 m) than abyssal depths (>2000–6000 m). This trend was evidenced for both chemosynthetic (i.e. coming from deeper depths, but the same thermal regime) and non-chemosynthetic species, suggesting that species from bathyal depths could more easily acclimatize to surface pressures than those from abyssal depths. In fact, bathyal species also exhibited high survival at pressure greater than that experienced in their natural distribution, suggesting that their adults have the physiological capacity to acclimatize to abyssal depths too. While more limited, there is still evidence that abyssal taxa can survive decompression, which is at odds with early (and persisting) assumptions that animals collected from depths below 1500 to 2000 m would be largely incapable of surviving at surface pressure (Pruski & Dixon 2003, Dixon et al. 2004, Pradillon & Gaill 2007). It may be that the numerous cases of abyssal species showing shorter survival at surface pressure result from physical/physiological damage incurred during collection, rather than from an innate physiological barrier. For instance, animals collected deeper may undergo more severe/acute temperature and/or pressure shocks during recovery, causing damage to nervous tissue at both transcriptional and cellular levels, potentially leading to serious injuries and death (e.g. Morris et al. 2013). Hence, bathymetric thresholds in decompression tolerance may be weaker or non-existent under more isothermal regimes, as exemplified by deep-sea corals of the genus *Flabellum* surviving equally well after being collected from bathyal or abyssal zones of the Northwest Atlantic (Hamel et al. 2010, Mercier et al. 2011d). The fact that genetic and individual pressure resistance was found to be highest at the optimum temperature of a given intertidal species (Schlieper 1968) brings support to enhanced pressure tolerance (and greater potential for vertical migrations) in isothermal water columns (see also the discussion of latitudinal trends).

The tolerance of deep-sea species to decompression was confirmed when looking at the frequency of successful development, from oocytes to late larvae, settlement and survival to advanced juvenile stages. Spawning events at surface pressure leading to propagule cultures that reached metamorphosis and settlement were documented in several deep-sea species across various phyla. At least one deep-sea species (the annelid *Ophryotrocha* sp.) underwent multiple generations at surface pressure in flow-through laboratory conditions (Mercier et al. 2014). Furthermore, adult sea stars, sea anemones and octocorals collected from as deep as 2500 m produced larvae that were reared to juvenile stages at surface pressure (e.g. Mercier & Hamel 2008a, Sun et al. 2010, Mercier et al. 2015, 2017) (see discussion of ontogeny for details). Even adult tonguefish larvae developed at surface pressure, forming eyes and actively feeding at 7 days old (Miyake et al. 2007), which is intriguing because deep-sea fish do not typically survive under surface pressure conditions (Pradillon 2005). Many investigative teams have argued that the ability for deep-sea larvae to survive under laboratory conditions may be underestimated, as mentioned for adult stages in the earlier discussion. Studies do not typically sample larvae directly from the deep sea (though some did); rather, most eggs, embryos and larvae come from the reproduction of genitors collected at depth. Even where propagules are subsequently extracted or released naturally under laboratory conditions, the extent of the trauma that gametes or brooded larvae experience during sampling and recovery of adults has yet to be determined. Ultimately, collection methods, including rapid decompression or use of sampling technologies that may inflict physical damage, may negatively affect the reproductive health/fitness of animals. Other factors susceptible to undermine the survival of early life stages include the absence of natural chemical cues required for metamorphosis and settlement of deep-sea larvae (Watanabe et al. 2004, Hamasaki et al. 2010), and poor water quality (Colaço et al. 2006). For example, many deep-sea ascidian larvae (Chordata) developed until juvenile stages and demonstrated adequate feeding, but died after 7 months because of what was described as a ciliate infestation (Havenhand et al. 2006). Numerous factors are known to similarly prevent full development to juvenile in cultures of shallow-water species (Hodin et al. 2019).

While there is substantial evidence that deep-sea adults and larvae are able to tolerate shallow-water pressures (present dataset), and that deep-sea larvae may undergo extensive vertical migrations all the way to the surface (Young et al. 2018), many of these decompression-tolerant species are nevertheless absent from habitats found at shallow depths. Other pre- and post-settlement processes may affect the survival of deep-water taxa at shallow-water pressures. For example, a field study that transplanted deep-sea Antarctic acorn barnacles (*Bathylasma corolliforme*) from 400 to 25 m reported that some individuals survived at transplanted depths for over 2 years (Dayton et al. 1982). Differences in survival were said to be modulated by substrate availability, thus supporting the ability for deep-sea species to acclimatize to shallow water under otherwise suitable environmental conditions.

The submergence (shallow to deep) hypothesis has been supported mainly by fertilization trials with echinoderms and molluscs, along with survival of embryos and larvae during short-term compression (Tyler & Young 1998, Tyler & Dixon 2000, Villalobos et al. 2006). However, the present review noted a general decrease in tolerance to compression as development progressed (e.g. from early to late larvae; though at least one exception was compiled). We also found no evidence that complete development of shallow-water species from fertilization to juvenile is possible at elevated hydrostatic pressure and limited evidence (duration-wise) that adults of shallow-water species can tolerate deep-sea pressures. An important limitation is that compression studies seldom test the tolerance of larval and adult stages of the same species (e.g. Pechenik et al. 1984, Childress & Thuesen 1993, Tyler & Young 1998, Tyler & Dixon 2000, Villalobos et al. 2006, Ding et al. 2007, Aquino-Souza et al. 2008, Mestre et al. 2009, Vevers et al. 2010, Smith & Thatje 2012, Smith et al. 2013, Munro et al. 2015, Smith et al. 2015), which is important since pressure tolerances can vary ontogenetically (e.g. Munro et al. 2015, Brown et al. 2017) and all life stages and processes must be tolerant to variations in pressure to allow successful colonization. Further, experiments where shallow-water larvae survived pressures outside of their natural bathymetric ranges, and where successful metamorphosis or settlement was documented, are in contrast to the lack of adults of these species recorded at such depths in nature (Brown & Thatje 2014). While empirical evidence supporting the shallow-deep hypothesis appears weaker than that supporting the deep-shallow hypothesis at present, technological and logistical difficulties contribute to limiting the strength of compression studies on shallow-water taxa. For example, high-pressure tanks are few and it is generally difficult or impossible to feed animals for long-term holding within these pressure vessels (but see Shillito et al. 2020), let alone provide true mesocosms. Thus, the potential for shallow-water fauna to tolerate deep-sea pressure may be underestimated to the same (or greater) extent as the potential of deep-sea species to survive surface pressure discussed earlier. Furthermore, early studies found that exposure to non-lethal pressure (10–20 MPa) had a stimulating effect, i.e. caused an increase in the locomotor activity, ciliary action and heart rates of many intertidal marine species (Schlieper 1968). Similarly, increased feeding was noted in shallow-water echinoderms exposed to pressures of 5–6 MPa (Ammendolia et al. 2018). This initial metabolic stimulation may facilitate a slow stepwise descent of species towards greater depths, where they may have a chance to adapt.

Overall, the present synthesis found evidence for physiological capacity enabling transitions both from shallow water to deep sea and from deep sea to shallow water, with strongest evidence for the physiological capacity for bathyal taxa to transition to both shallow and abyssal depths.

Potential modulators of pressure tolerance

Ontogeny (trends across life stages)

The available empirical results that relate to the pressure tolerance of early (mostly larvae) versus late (mostly adult) life stages remain difficult to compare directly due to heterogeneous durations of exposure (inherently shorter for early, rapidly transitioning, life stages) and because few studies were conducted on embryos, larvae, juveniles and adults of the same species. After narrowing down to per cent survival obtained with early and late stages of the same species, this review found that decompression was tested ontogenetically in 20 deep-sea species and compression in a single shallow-water species. Most studies resulted in some degree of survival and no clear ontogenetic trends could be detected. Overall, larvae were not found to be more tolerant to decompression than adults, as might be predicted on the basis of early pelagic stages occupying broader bathymetric ranges than their benthic genitors. In the species-specific dataset, tolerance was the same or similar between life stages in half the species; in the other half, early life stages survived less than the adults (across six phyla) and the inverse was true in only one (annelid) species.

More broadly, reproduction/mating occurred, larvae developed and resulting juveniles survived for prolonged periods (years) at surface pressure in a diversity of deep-sea taxa collected from the Northwest Atlantic (Figure 7). Most of these events occurred in mesocosms where cold conditions (<10°C) were maintained by flowing seawater pumped directly from the ocean, which included natural planktonic particles; dark conditions were also generally implemented, thereby minimizing stress. Notably, adult pycnogonids *Nymphon hirtipes* collected at 700–1450 m depths successfully reproduced; egg masses were brooded by the males (Figure 7B) for 4 months until hatching and the young developed for another 5 months under the protection of the male, from walking leg-bearing stages until juvenile stages, before dispersing in the mesocosm (Mercier et al. 2015). Moreover, deep-sea annelids (*Ophryotrocha* sp.) collected between 500 and 1500 m reproduced at surface pressure after being maintained for a year (Figure 7C); juvenile stages had survival rates of 80%, with some individuals surviving to adult stages and themselves successfully reproducing, yielding a total of three generations at surface pressure (Mercier et al. 2014, Verkaik et al. 2017). Successful recruitment of species from non-chemosynthetic deep-sea environments is not restricted to taxa from the Northwest Atlantic. For example, deep-sea ascidians (Chordata) collected in the Northwest Pacific released larvae under surface pressure conditions that developed into juveniles and survived 7 months (Havenhand et al. 2006).

The compression of early life stages of shallow-water species was also assessed, showing that larvae of Chordata, Echinodermata and Mollusca are capable of surviving and developing under pressures that typically exceed the natural distribution of their adult stages (e.g. Young et al. 1997, Tyler & Young 1998, Tyler & Dixon 2000, Villalobos et al. 2006, Aquino-Souza et al. 2008, Mestre et al. 2009, Smith & Thatje 2012, Mestre et al. 2013, Brown & Thatje 2014, Sumida et al. 2015). High-pressure tolerance was often found to be greatest in early embryonic stages during cleavage, and to decrease with further development (Tyler & Dixon 2000, Pradillon & Gaill 2007, Mestre et al. 2013). Notably, fewer studies have investigated the effects of hydrostatic pressure on settlement processes and juvenile development, or even on adults in these shallow-water species (Young & Tyler 1993). In this review, compression studies across larval and adult stages were only found to exist for one arthropod species, resulting in survival for both.

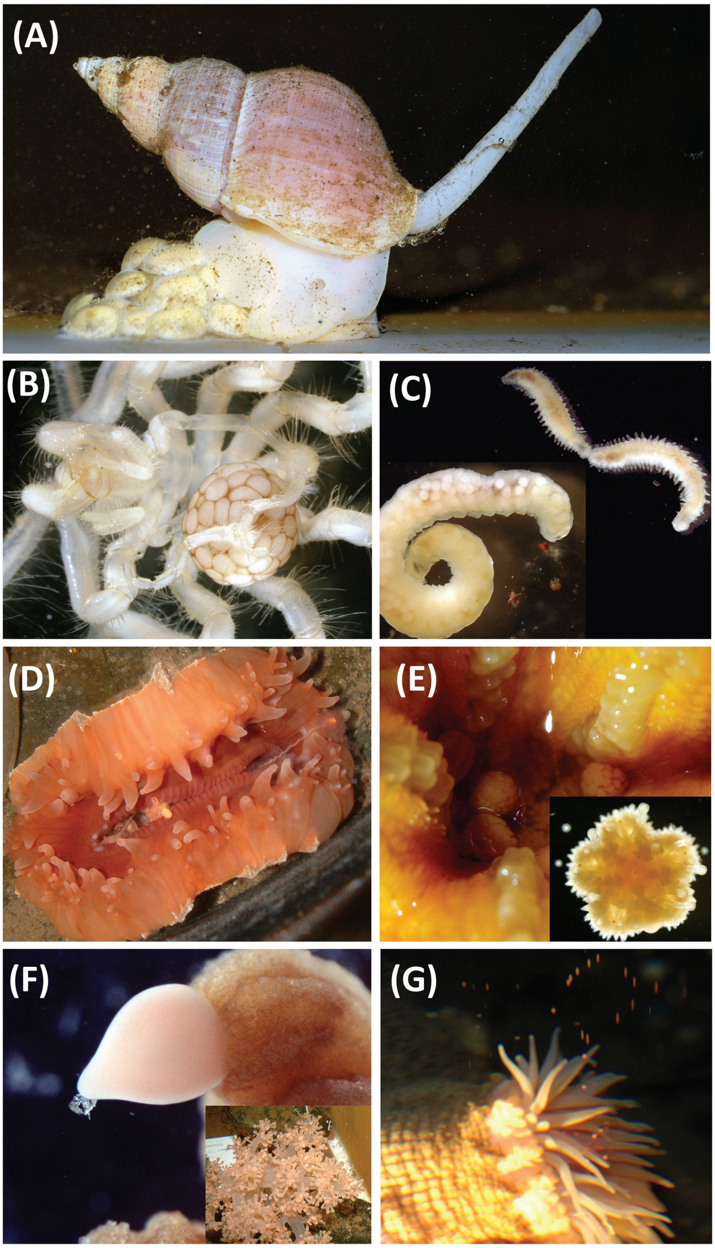

Figure 7 Examples of deep-sea benthic animals from the Northwest Atlantic, collected between 360 and 1500 m depth, held in mesocosms at atmospheric pressure and displaying reproductive behaviours. (A) The gastropod *Buccinum scalariforme* (~70 mm shell height) laying eggs (Montgomery et al. 2017). (B) A male pycnogonid *Nymphon hirtipes* (~55 mm leg span) brooding an egg mass (Mercier et al. 2015). (C) The polychaete worm *Ophryotrocha* sp. (~12 mm long) displaying mating behaviour, with insert showing mature oocytes (Mercier et al. 2014). (D) Female cup coral *Flabellum angulare* (~3.9 cm wide) releasing oocytes attached to threads (Mercier et al. 2011d). (E) Undersurface of a female sea star *Henricia lisa* (~4 cm in diameter) brooding embryos, with inset showing fully developed juvenile (1100 µm in diameter) (Mercier & Hamel 2008a). (F) Soft coral *Drifa* sp. releasing planula larvae (~300 µm in diameter), with inset showing an adult colony (~12 cm high) (Sun et al. 2009). (G) The sea anemone *Allantactis parasitica* (~4 cm in column diameter) broadcasting oocytes in the water column (Mercier & Hamel 2009a).

Taxonomy (trends across phyla)

The results of early pioneer experiments with intertidal species had proposed that taxonomic groups with the best resistance to high pressure were those with the greatest distributions in the deep sea: echinoderms, molluscs, amphipods, isopods and polychaetes (Schlieper 1968). It was also assumed that pressure resistance decreased as the level of organization increased, with protozoans being more resistant than metazoans, and the latter being decreasingly tolerant the higher their position in the taxonomic system (Cattell 1936, Schlieper 1968). However, taxonomic/phylogenetic trends were not evidenced in the present review, largely due to variability within phyla. For instance, survival in adults varied from 0% to 100% in Arthropoda and Annelida and from 60% to 100% in Cnidaria. Adult pressure tolerance had been proposed to differ among phyla in previous analyses based on more limited data (Brown & Thatje 2015). The present synthesis highlighted that generalization are difficult to make because sample sizes of species within phyla are often small, whereby repeated experiments (yielding separate records here) involve the same species. As an example, numerous studies have been conducted in the Azores on the life history, development and physiology of hydrothermal vent mussels (*Bathymodiolus azoricus*) collected from the Mid-Atlantic Ridge at ~850 m depth (Colaço et al. 2006, Kádár et al. 2006, Bettencourt et al. 2008, Kádár et al. 2008a, Bettencourt et al. 2010, Colaço et al. 2011, Martins et al. 2014, Barros et al. 2015, Bettencourt et al. 2017). Much of the Mollusca records therefore reflect the pressure tolerance of this species; investigators were able to maintain individuals for greater than 12 months under laboratory conditions at surface pressure. This mussel is protected by a hard shell and presumably sustains minimal physical damage from changes in pressure. Whether other types of molluscs would do equally well remains unclear.

The limited evidence we have suggests that the ability of a taxon to survive pressure shifts may relate to its complexity and level of protection (e.g. presence/absence of calcified exoskeleton). Mollusca, Echinodermata and Arthropoda tolerate compression and/or decompression better than invertebrates in the Chordata phylum (ascidians). These differences may reflect increasing difficulty in maintaining oxygen supply with greater organismal complexity, for example through ventilation and circulation, as suggested by Brown & Thatje (2015). Therefore, it is unlikely that vertical range extensions would involve mass movement/relocation of all taxa, but rather would be restricted to those that are more barotolerant under relatively isothermal conditions. For example, Ammendolia et al. (2018) tested the behavioural responses of three different echinoderms at pressures representing depths beyond their current bathymetric ranges. Increasingly severe responses to high pressures were demonstrated from Holothuroidea to Asteroidea and to Echinoidea (which are increasingly calcified). Establishing more definite conclusions regarding the contribution of body design complexity (morphology, calcification) and systems (circulatory and nervous) to barotolerance will require a study of the responses of multiple species from multiple classes under standardized conditions, following a comparative physiology approach (Garland et al. 2005). Physiological thresholds to pressure are also variable among highly mobile and wide-ranging vertebrate taxa. The present review did not examine barotolerance in fishes given their mobility and the additional layers of physiological complexity, which typically require studies to employ biochemical analyses (Yancey et al. 2014, Treberg & Speers-Roesch 2016). Through such work, it was generally found that fishes had more shallow physiological limits than non-chordate taxa, as demonstrated by groups such as Liparidae and Chondrichthyes limited by depths of 8500 and 4000 m, respectively (Yancey et al. 2014, Treberg & Speers-Roesch 2016).

While some phyla demonstrate greater pressure tolerance than others, taxon-specific modes of locomotion may affect potential for shifts in bathymetric distribution and range extension. Certain taxa may exhibit limited motility and be unable to successfully migrate, i.e. sessile adults of sponges and corals (anchored to a substrate). Instead, these taxa will depend entirely on dispersal of propagules for range shifts, and the capacity for broad vertical migration in some deep-sea larvae was already mentioned (Young et al. 2018). In contrast, adults of mobile taxa may have equal or greater capacity for movement within their lifespan than their brief larval stage. Consequently, more studies exploring pressure tolerances in all life-history stages of individual species are required. Further, whether taxa are able to exploit pressure tolerance and extend bathymetric range depends on ecological factors. For example, habitat availability (e.g. continental shelf and slope area for benthic species), suitability (e.g. primary productivity and food availability, seasonality) and accessibility (e.g. dispersal ability, current direction) will also limit the ability of species to migrate bathymetrically (see Barve et al. 2011 and references therein, Hamel et al. 2019). Similarly, light penetration may be particularly critical since adaptations in vision have been reported to shift with bathymetric changes in light parameters (Warrant & Locket 2004). Determining the most likely candidates for vertical range extension will therefore require further investigations to test the physiological, developmental and genomic barotolerance of multiple taxa.

Geographic location (latitudinal trends)

From the standpoint of geographic location of collection, the reviewed literature highlighted a possible difference in pressure tolerance between species occurring at lower versus higher latitudes rather than across specific regions. Bathymetric gradients in temperature are typically small at high latitudes and moderate at mid-latitudes, although there is seasonal variation at mid-latitudes as stratification builds between spring and autumn and dissipates during autumn (Gage & Tyler 1991). In contrast, bathymetric temperature gradients are typically large at low latitudes where permanent stratification occurs (Friedman & Sallan 2012). Consequently, deep-sea animals collected at high or mid-latitudes experience less severe temperature shocks during recovery from the deep sea than those collected in warmer/tropical waters (Tyler & Young 1998). Ravaux et al. (2009) highlighted the potential confounding effect of temperature stress by reporting that using insulated collection boxes on remotely operated vehicles markedly increased the survival of deep-sea species collected at abyssal depths at low latitudes. Similarly, the potential for bathymetric range extension in shallow-water taxa within tropical regions may be limited by thermotolerance. For instance, low temperatures cause physiological stress that increases mitochondrial oxygen demand in the subtropical shallow-water spider crab (*Maja squinado*), compounding challenges that high pressure presents to the maintenance of aerobic homeostasis (i.e. ventilation and circulation) (Frederich & Portner 2000, Brown & Thatje 2015). Consequently, bathymetric range extension in tropical areas may be restricted by thermal physiological bottlenecks that impose species-specific thresholds.

Perspectives

Current limitations in interpretation of findings

While the study of responses to hydrostatic pressure has progressed in leaps and bounds over the past 60 years, with major breakthroughs and the introduction of deep-water organisms to the experimental arena over the past 20 years, we are still comparing apples with oranges due to technical challenges. When it comes to the decompression of animals collected from the deep sea, some investigations have successfully maintained sufficiently adequate holding conditions to allow studies of complete development and even generational successions. For compression studies, only short-term exposure is yet possible, with very few exceptions. The situation was reversed in pioneer work up to the 2000s, whereby deep-sea animals could not be collected and held alive for more than a few hours. Hence, initial studies offered more convincing (if limited) demonstration of shallow-to-deep tolerance, whereas current studies offer more convincing (now fairly complete) demonstration of deep-to-shallow tolerance. For this reason, bi-directional movement is emerging as the most parsimonious explanation. Only further transplantation studies or technological advances allowing the maintenance of animals in compressed state for months to year will eventually confirm this.

Another short-term goal will be to refine our understanding of ontogenetic patterns, because comparing survival metrics does not paint an accurate enough picture. For example, full development of deep-sea progeny through embryonic and larval stages until the settlement of juveniles comes with natural mortality that may be unrelated to decompression (the number of surviving offspring may fundamentally decrease in a stage-wise manner) down to 50% or even 5%–10% survival. On the other hand, compression of a single chosen stage for a brief period may yield survival of 100% (e.g. a handful of pluteus or veliger larvae may all survive 24-hour exposure). Comparing these two examples will allude to better tolerance of the compressed than the decompressed larval species, when the inverse may be true since a single stage of the latter survives but only briefly, while the former successfully completes development outside its natural pressure range. Also of note is the fact that deep-sea larval stages were mostly obtained from the reproduction of decompressed genitors, rather than directly from the field.

Looking beyond lethal responses

Studies reporting sub-lethal responses to changes in hydrostatic pressure in shallow-water and/or deep-sea species are still relatively scarce. However, sub-lethal metabolic costs imposed by shifts in hydrostatic pressure may establish a narrower bathymetric range than suggested by the basic survival/mortality reviewed here. For example, the lithodid crab *Lithodes maja* (bathymetric range 4–790 m depth, approximately equivalent to 0.1–7.9 MPa hydrostatic pressure) has been reported to survive exposure to 20 MPa (Brown et al. 2017). However, heart rate decreased with increasing hydrostatic pressure, and was lower at ≥10 MPa than at 0.1 MPa. Oxygen consumption increased with increasing hydrostatic pressure to 12.5 MPa, before decreasing as hydrostatic pressure increased to 20 MPa: oxygen consumption was higher at intermediate levels of 7.5–17.5 MPa than at 0.1 MPa. Increases in expression of genes associated with neurotransmission, metabolism and stress were also observed between 7.5 and 12.5 MPa. Consequently, it has been suggested that hyperbaric tolerance in *L. maja* may be oxygen-limited by compression effects on heart rate and metabolic rate, but that its bathymetric range is limited by metabolic costs imposed by the effects of high hydrostatic pressure. Subsequently, it was proposed that hydrostatic pressure be included in a complex model of environmental tolerance, where energy-limitation constrains biogeographic range, and facilitating incorporating hydrostatic pressure into the broader metabolic framework for ecology and evolution (Brown et al. 2017).

Such an approach may be crucial for accurately projecting biogeographic responses to changing climate conditions, and for understanding the ecology and evolution of life at depth; it may also have implications for the present study. While individuals can survive exposure to hydrostatic pressure outside their normal range, individual fitness may be reduced by moderate stress imposed (Brown et al. 2017), as additional homeostatic energy costs lead to energetic trade-offs and result in reduced activity, scope for growth and/or reproductive output (Sokolova 2013). For example, increased allocation of energy to maintenance diminishes energy available for other functions such as buffering fluctuating food availability or provisioning offspring (Sokolova 2013). Consequently, analyses based on survival (even formal LD_{50} approaches) and short-duration pressure treatments may overestimate the capacity for range extension. Evidently, studies reporting persistence of a species through multiple generations at pressure outside that at which they normally live provide stronger support for potential range extension; as already discussed, they currently exist only for decompressed deep-water species.

Conclusions

Following a broad assessment of available studies, evidence suggesting that deep-sea benthic animals might have the physiological capacity to survive under surface pressure is at least as strong as evidence for shallow-water species tolerating high pressures, possibly stronger. Empirical data accumulated over the past seven decades also shed light on factors that may modulate pressure tolerance, providing insight into the potential for future vertical range extension in the ocean during changing environmental conditions. Overall, several conclusions may be drawn, and knowledge gaps identified from this review.

1. Empirical evidence supporting the deep-shallow hypothesis is extensive, with many deep-sea species thriving for months to years in shallow-water laboratory conditions, at least one through multiple generations. Empirical evidence supporting the shallow-deep hypothesis is more limited, with fewer shallow-water species shown to survive at deep-sea pressure for tens of days only. However, the latter body of evidence may be biased by as yet limited capacity to maintain optimal environmental conditions at experimental pressure (i.e. logistical constraints).
2. Species found in the bathyal zone (intermediate ocean depths) exhibit the greatest tolerance to decompression (and compression) in laboratory studies, suggesting physiological and developmental capacity to move both shallower and deeper than their known bathymetric ranges. It also evokes the possibility that range extensions/transitions by bathyal species have been important in establishing current biodiversity patterns. A formal assessment of eurybathic species with ranges that encompasses bathyal depths would be welcome. Future studies might collect individuals of these species from different depths and assess their tolerance to pressure shifts to determine if it is independent of depth of collection (whether it is expressed at the species or population level).
3. The tolerance to decompression shown by bathyal species, combined with the fact that empirical evidence exists to support both the shallow-deep and deep-shallow hypotheses, advocates formalization of a bi-directional hypothesis as the most parsimonious explanation for current biodiversity patterns. Such a hypothesis is consistent with inferences drawn from fossil and phylogenomic studies. However, ecological factors other than hydrostatic pressure must contribute to limiting bathymetric ranges, since the latter do not appear to strictly reflect the potential of a species to tolerate pressures shifts.
4. Differences between trial conditions when testing pressure tolerance in adults and larvae, and the very limited number of species for which pressure tolerance was assessed across life stages (nearly all under decompression scenarios), mean that ontogenetic comparisons remain tentative at best. No clear trend emerged from this review. Future compression and decompression studies should strive to combine the assessment of at least two life stages of a given species.
5. The pressure tolerance of species (chiefly in adult individuals) appears to vary widely both among and within the phylum they belong to, with more derived taxa (e.g. chordates) displaying slightly greater sensitivity to pressure shifts, possibly due to greater organismal complexity. The presence of protective features (e.g. calcification of exoskeleton) also appears to contribute to pressure tolerance. Additional research is required to assess which precise morphological, physiological and/or molecular aspects might drive variation in pressure tolerance among (and within) the various taxa.
6. Geographic location of occurrence impacts pressure tolerance, with some indication that species studied at mid- to high latitudes are more tolerant to changes in pressure than those studied at low (tropical) latitudes, likely due to the synergistic effect of thermotolerance. Indeed, the effect of temperature stress during collection and recovery from the deep sea at different latitudes, resulting from contrasting vertical temperature gradients, prevents unequivocal assertion of differences in the pressure tolerance of deep-sea taxa collected at different latitudes. Nonetheless, the potential for bathymetric range extensions appears greater in periods and regions associated with small vertical temperature gradients, such as are currently established at high latitudes.

7. Key knowledge gaps remain since high-pressure vessels for experimental studies are rare commodities and technological limitations constrain the duration of pressure exposures, restricting understanding of potential for shallow-deep, bathyal-abyssal and abyssal-bathyal transitions. Logistical constraints impeding the collection and maintenance of deep-sea animals also remain, which need to be overcome to further our understanding of potential for deep-shallow transitions.

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