The Macroecology of Biological, Life History and Ecological Traits of Invasive and Threatened Marine Invertebrates

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Abstract

Global environmental change is accelerating both species extinctions and species invasions, with extinction risk and invasion success thought to be mediated by biological, life-history and ecological traits. It is, therefore, important to understand how traits, phylogeny and environmental factors interact to characterise imperilment and invasiveness and to determine the vulnerability of species to climate change. In this thesis I aim to determine the key traits of invasive, native, and threatened marine invertebrates and to provide a framework for predicting native species likely to become invasive and for determining the life-history and environmental traits correlated with extinction risk and invasiveness. I compile trait datasets for 2,322 invertebrate species and use multivariate analysis to identify the discriminating traits between non-indigenous and native species and to propose a list of 'potentially invasive' native species. I further show that species from different risk categories display contrasting, although not opposite, life-history traits and that the risk status of marine molluscs is largely driven by phylogeny, with invasiveness and extinction risk not randomly distributed across families. I then combine species-trait data with environmental data to show that there is a strong phylogenetic signal in species' realised thermal niches. The relationship between the range of temperatures a species experiences (thermal tolerance breadth) and the maximum temperature to which it is exposed is stronger in shallow-water invasive species than other risk categories. Finally, I show that life-history variation across marine molluscs is largely consistent with Thorson's rule that in lower latitude environments species are typically small-bodied, early maturing and highly fecund, while the reverse is true in higher latitude environments. This thesis provides a foundation for future comparative macroecological studies investigating invasive and threatened species and makes a unique contribution to understanding the traits of marine invertebrates across multiple risk categories and their likely response to environmental change.

Declaration

The following people were involved in this research project:

Francesca G. Quell, Dr Tom J. Webb, Dr Michela Schratzberger, Dr Jorn Bruggeman and Dr Olivier Beauchard

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F.G.Q conceived the idea for the study;

F.G.Q performed the analyses and wrote the manuscript;

J.B ran Trait Explorer;

O.B provided the initial native species dataset;

T.J.W and M.S commented on drafts of the manuscript.

Chapter 3: A global comparative analysis of life history traits associated with imperilment and invasiveness in marine molluscs

F.G.Q conceived the idea for the study (with input from T.J.W);

J.B ran Trait Explorer;

F.G.Q performed the analysis and wrote the manuscript;

T.J.W and M.S commented on drafts of the manuscript.

Chapter 4: Global Analysis of thermal tolerance and latitude of invasive and threatened marine molluscs

F.G.Q and T.J.W conceived the idea for the study;

F.G.Q performed the analysis and wrote the manuscript;

T.J.W and M.S commented on drafts of the manuscript.

I, the author, confirm that this Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not been previously presented for an award at this, or any other, university.

“To people who allege that we

Incline to overrate the Sea

I answer, “We do not;

Apart from being coloured blue,

It has its uses not a few;

I cannot think what we should do

If ever ‘the deep did rot.”

-Sir Owen Seaman 1861-1936

1. General Introduction

1.1. Marine Macroecology

Macroecology first emerged around three decades ago due to the realisation that the abundance and distribution of species could not be explained solely by small-scale processes (Keith et al. 2012). The term 'macroecology' was first coined by James H. Brown and Brian A. Maurer in a 1989 paper in Science and has since stimulated broader scale thinking in the search for generalizable patterns in the distribution of biodiversity at large spatial and temporal scales (Brown & Maurer 1989). Macroecology is now a distinct field of research which is largely empirical in nature, involving the search for statistical patterns within and between key macroecological variables including species abundance, distribution, diversity, body size and range size (Brown & Maurer 1989; Brown 1995).

Initially macroecology was primarily a terrestrial endeavour (Raffaelli et al. 2005), with only two of the 21 chapters in Gaston and Blackburn's (2000) book 'Patterns and Processes in Macroecology', covering marine organisms. Although early treatments of macroecological relationships (e.g., Kritzer and Sale 2006), focused more on population dynamics, evolution and biogeography than on species richness, species diversity or species abundance, by the release of Whitman & Roy's 'Marine Macroecology' (2009) book, there was a clear trend towards quantifying macroecological patterns in the sea. The initial focus on terrestrial ecosystems likely stemmed from the fact that the marine environment presents several challenges (both logistical and financial) which makes collecting datasets comparable to those relied upon by terrestrial macroecologists difficult (Raffaelli et al. 2005). Despite the initial slow start in researching macroecological patterns in the marine environment, we now understand that these patterns are governed by many of the same broad trends as seen on land (Webb et al. 2012). For instance, most marine species are rare, whether you consider the number of individuals (species abundance distributions, SADs) (Grey et al. 2006) or the spatial distribution of species (species-range size distributions) (Gaston 2003). Furthermore, the relationship between local abundance and regional distributions (the abundance-occupancy relationship, AOR) is typically positive (Webb et al. 2011) and, in both marine and terrestrial systems, there is support for the species-area relationship (SAR) whereby larger areas contain more species and thus have a higher species richness (Neigel 2003; Drakare et al. 2006).

Likewise, species richness increases from polar regions towards the equator (Hillebrand 2004; Saeedi et al. 2019), reflecting a latitudinal gradient in species richness, while geographic range size tends to decrease from the polar region towards the equator, a pattern known as Rapoport's rule (Fortes & Absalão 2004). Finally, Bergmann's rule (Torres-Romero et al. 2016), which states that larger bodied species are found in colder regions while smaller bodied species are found in warmer regions, is an ecogeographical pattern which tends to be observed in both terrestrial and marine systems.

1.2. Biological Traits in Macroecology

Trait-based ecology aims to understand the drivers and processes of organismal trait diversity and their influence on ecosystem functioning (Mouillot et al. 2021). The ecosystem services we rely on are strongly dependent on the ecological processes occurring within the environment, which in turn are driven by the functional diversity of biological, life history and ecological traits possessed by constituent species (Marchini et al. 2008). This view that species can be categorised based on their traits has reshaped how ecologists determine ecosystem vulnerability, biological diversity and inter-species relationships (Cadotte et al. 2011). The growth of this approach has been facilitated by the realisation that species traits, more so than taxonomic nomenclature, influence how organisms respond to drivers of change (Tyler et al. 2012), and that taxonomically unrelated individuals can display similar trait attributes (Hewitt et al. 2014). This has enabled macroecologists to apply trait-based analysis to studies of community ecology (Naeem & Bunker 2009).

Traits are defined as measurable characteristics of organisms which influence their fitness and adaptability (Cadotte et al. 2011). Traits that determine how species affect ecosystem functioning, termed effect traits, may differ from those that mediate species response to environmental change, termed response traits (Díaz et al. 2013). Biological traits, when linked to ecosystem functioning, provide the opportunity to investigate the consequences of environmental pressures on species community assemblages (Queirós et al. 2015) and have the capacity indicate how changes in biodiversity affect ecological resilience and ecosystem service delivery (Tyler et al. 2012). Macroecology typically couples the ecological trait attributes of species (such as their thermal tolerance, latitudinal ranges and depth limits) with biological traits linked to life history (e.g. body size, longevity), reproduction (e.g. fecundity, maturity) and behaviour (e.g. dispersal activity) to predict the spatial-temporal distribution of marine biota over large scales (Tyler et al. 2012).

There has been a recent proliferation in trait-based research across numerous disciplines, from evolutionary science (Salguero-Gómez et al. 2018) to global patterns of biodiversity (Kort et al. 2021; Jackson 2022) and the relationship between ecosystem functions and species assemblages (Weiss & Ray 2019; Leuzinger & Rewald 2021). Despite the importance of trait-based approaches, their use is limited due to a heavy dependence on the availability and compatibility of trait data in addition to the level of taxonomic and regional coverage they provide (Schneider et al. 2019; Kuijk et al. 2021; Leitz 2022). Trait datasets remain further underexploited as they typically suffer from a lack of standardization and heterogeneity in data formats, meaning it can be difficult to combine trait information compiled by multiple data providers (Schneider et al. 2019).

Several global trait databases do exist, however, across both the terrestrial and marine realm. TRY, the plant trait database, for example provides information on 160,000 plant taxa spanning 2100 traits, including those associated with morphology, physiology and phenology (Kattge 2020) while Elton Traits is a species-level compilation of the diet and foraging attributes of the worlds extant bird and mammal species (Wilman et al. 2014). In the marine realm, Fishbase is a database of >33,000 fish species with information on their trophic ecology, life history and uses, as well as historical data reaching back 250 years (Froese & Pauly 2022), and DISPERSE is a trait database to assess the dispersal potential of European Aquatic Macroinvertebrates across 480 taxa including annelids, arthropods, molluscs and platyhelminths (Sarremejane et al. 2020). More specifically, Brun et al. (2017) developed a trait database for marine copepods looking across traits such as body size, egg size, fecundity and feeding mode while PolyTraits details approximately 60 biological traits of polychaetes (Faulwetter et al. 2014). Furthermore, the Biological Traits Information Catalogue (BIOTIC) considers over 40 biological trait categories for species present in benthic communities in NW European seas (MarLIN 2006).

1.3. Invasion Ecology

Human exploration and globalization have considerably changed the geographic patterns of invasion, increasing the rate at which species are able to colonise new areas

(Lockwood et al. 2013; Geburzi & McCarthy 2018). Rates of European plant, invertebrate and mammal invasions continued to increase throughout the 20th Century (Hulme 2009). This mass reshuffling of the Earth's biota has helped species to overcome several biogeographic barriers, and resulted in the redistribution of many organisms, creating novel ecosystems (Hobbs et al. 2009) and constituting a major feature of the Anthropocene (Lewis & Maslin 2015). An important avenue for research is the extent to which this species reshuffling breaks or modifies the macroecological patterns exhibited by native species (Blackburn 2019).

In contrast to terrestrial, and in some cases freshwater invasions, early texts give little attention to marine invasions (Hewitt et al. 2009). Over the last two decades however, a considerable volume of research has highlighted the scope and scale of marine invasions (Ruiz et al. 2000; Chan 2017), with almost every marine ecoregion on Earth subjected to the introduction of species (e.g., Leppakoski et al. 2002; Lewis et al. 2003; Castilla et al. 2005; Gollasch 2006). Ocean-going vessels now transport approximately 90% of all global trade via more than 50,000 commercial ships (Hulme 2009). It is unsurprising then, that one of the most comprehensive assessments of marine invasions to date (Molnar et al. 2008) found that over 80% of all known marine invaders were introduced through unintentional transport. In the Mediterranean Sea for example, a new invader was discovered every week for five years, from 2004 to 2009 (Rilov & Crooks 2009), with estimates now suggesting that roughly 7000 species are being transported in global ballast water at any moment in time, resulting in invasion rates which far exceed natural background levels (Rilov & Crooks 2009). Conspicuous examples of aquatic invasive species include the lionfish *Pterois volitans* in coral reef systems, the bivalve *Mytilus galloprovincialis* along temperate rocky shores, the reef-building polychaete *Ficopamatus enigmaticus* in estuaries and the zebra mussel *Dreissena polymorpha* in Great Lake communities (Preisler et al. 2009).

Most of our understanding of marine invasions comes from shallow coastal environments with very few studies having investigated how invasion rates compare between different marine habitats (Preisler et al. 2009). Introduced aquatic species have received more attention in north-western Europe recently following synopses from Britain and Ireland (Eno et al. 1997; Minchin and Eno 2002), Norway (Hopkins 2002), and the North Sea (Gollasch 1996; Reise et al. 1999), and from the compilation of inventories of invasive species for the German Coast (Nehring 2002; Nehring 2005), the Danish Coast (Jensen & Knudsen 2005) and the Dutch coast (Wolff 2005). A more recent global initiative for recording invasive species is the World Register of Introduced Marine Species (WRiMS), a database directly linked to the

World Register of Marine Species (WoRMS), which includes all introduced marine species and distinguishes between their native and introduced region (Rius et al. 2022).

It is important that we develop a clearer understanding of invasive species as they can be problematic at various ecological scales. At the genetic level for instance, invasives can hybridize with natives, producing often sterile offspring and altering the gene pool, causing a loss of genetic integrity. At the individual level, invasives can causes changes in the traits or fitness of natives, including morphological, behavioural, or demographic changes (Lockwood et al. 2013). At the population level, invasive species can influence native species abundance across its entire range, which, if persist for several years, could potentially drive native populations to extinction (Lockwood et al. 2013). Typically, invasives compete with natives for critical resources such as food, light or space, prey upon, or parasitise, native populations, or physically limit the growth or reproduction of natives, all resulting in changes to the native species' population structure, distribution, or abundance (Lockwood et al. 2013).

Finally, community and ecosystem level impacts can arise from invaders which bring novel diseases, use a wide variety of resources, or extract novel resources unobtainable by the native community (Schindler et al. 2001). Harris mud crabs, *Rhithropanopeus harrisii*, for instance, are carriers of white spot syndrome, a viral infection which causes a highly lethal contagious disease in commercially harvested and aquacultured penaeid ships (Katsanevakis et al. 2014). Furthermore, the presence of one non-native species can facilitate the establishment of several other non-natives. For instance, the bryozoan *Watersipora subtorquata* is tolerant of anti-fouling paints often applied to boat hulls to reduce encrusting non-native organisms, and so can establish colonies on these hulls (Floerl et al. 2004). *W. subtorquata* colonies have themselves been colonised by 22 non-native taxa found exclusively in association with this species (Floerl et al. 2004), some of these taxa being 248 times more abundant on *W. subtorquata* colonies than on non-bryozoan encrusted surfaces (Floerl et al. 2004).

The term "invasive species" has been widely adopted by many in the field to mean a non-indigenous species which has a demonstrable ecological, societal, or economic impact (Young & Larson 2011; Lockwood et al. 2013). Roughly a third of ecologists surveyed by Young & Larson (2011), however, felt that a species should be defined as invasive if its populations are self-sustaining and spreading in a new environment, regardless of impact (Richardson et al. 2000; Daehler 2001). While this removes the need for evidence of impact, which is often unavailable, it creates additional ambiguity with regards to what counts as ‘spreading’. For this reason, throughout this thesis, I use the former definition of an invasive species. Non-native species on the other hand are simply species which are living outside of their native distributional range and have been transported either intentionally or unintentionally by human mediated transport.

Although species dispersal, like species extinction, is a natural event, the current rate of human-mediated dispersal deposits species outside of their native range far quicker than that of natural dispersal (Vermeji 2005; Lockwood et al. 2013). Human-mediated dispersal differs from natural dispersal in that it: (i) deposits individuals into a novel environment multiple times and (ii) introduced individuals are from multiple source populations rather than just one (Lockwood et al. 2013). These two differences alter the genetic variation of colonizing populations, typically skewing them in favour of establishment success due to an ability of individuals selected to thrive in a broad range of habitats (Lockwood et al. 2013). Human-mediated dispersal also typically selected individuals which display generalized, opportunistic, weedy, or ruderal traits via selection pressures which are unlikely to come into play in natural dispersal scenarios (Lockwood et al. 2013; Qin et al. 2020). Therefore, the very process by which invasive species are transported tends to select for the most tolerant individuals (Lockwood et al. 2013) as the living conditions faced by individual organisms *en route* within the transport vector are harsh, and only those best able to tolerate changes in environmental conditions can survive and establish populations within the recipient region (Lockwood et al. 2013).

Stohlgren and Schnase (2006) state that, “Invasion is possible only when a vulnerable habitat meets with a species whose traits allow for establishment, growth and spread.” Many authors have thus attempted to characterize the trait profile of a successful invader (Williamson & Fitter 1996; Kolar & Lodge 2002; Devin & Beisel 2007; Grabowski et al. 2007; Statzner et al. 2008; Grabowska et al. 2015) to answer the critical question, “Do species traits determine the success of an invader?” And by extension, “Can species traits be used to predict and manage invasive species?”.

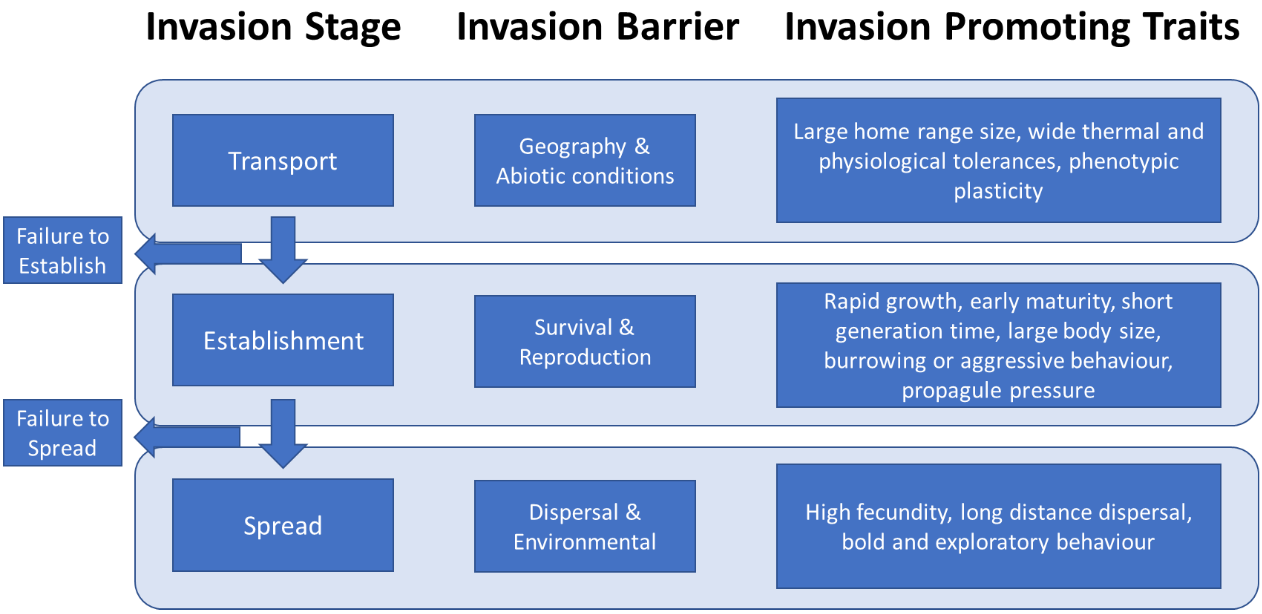

Figure 1: Unified framework for invasion ecology which combines the invasion stage, invasion barrier and invasion promoting traits.

A non-native species is faced with several complex challenges at each stage of the invasion process (Figure 1). How they respond to these challenges, be they biotic (predation, competition, mutualism) or abiotic (temperature, salinity, or pH fluctuations) depends largely on their life history (Kolar & Lodge 2001; Cassey et al. 2004). Several studies (e.g., Kolar & Lodge 2001; Cassey et al. 2004; Marchetti et al. 2004) have demonstrated that alternate suites of species-specific traits (trait syndromes) can be influential at different stages of the invasion processes (either positively or negatively), ultimately shaping the likelihood of establishment, spread and impact.

1.4. Biological Traits and Invasiveness

Life-history and biological traits commonly investigated in association with invasion success include maximum body size or body mass, propagule pressure, age of maturity, reproductive frequency, and annual fecundity, all of which are often considered to be key traits enabling success during the establishment stage (Kolar & Lodge 2001; Chen et al. 2021) whereby a population must overcome barriers associated with reproduction and survival i.e., those accompanying population density and biotic resistance (Lockwood et al. 2013). Dispersal ability is another oft cited trait associated with invasion success (Lockwood et al. 2013) and is considered to be important during the spreading stage of the invasion process whereby populations must overcome barriers associated with dispersal and environmental heterogeneity (Kolar & Lodge 2001).

Ecological characteristics of a species also come into play, with traits such as home range size, thermal tolerance, physiological tolerance, trophic level, and diet breath also playing a role (Lockwood et al. 2013; Fournier et al. 2019). Thermal tolerance breadth, specifically, is likely a key trait enabling success during the transportation stage whereby a population must overcome geographic barriers to survive the journey to the recipient environment (Lockwood et al. 2013). Additionally, phenotypic plasticity (the ability of an individual to alter its morphological, physiological, or behavioural traits in response to a change in the environment) and ecological competence (the ability to tolerate a wide range of environmental conditions) are also widely considered to be key traits of a successful invasive species (Davidson et al. 2011).

Kolar & Lodge (2002) were among the first to evaluate species traits across more than one invasion stage, focusing on non-native fishes in the North American Great Lakes. They found that traits could distinguish between both fast and slow spreading invaders with considerable accuracy (94%) and between high and low impact species (with 89% accuracy). Using these models, Kolar & Lodge (2002) created a list of 22 species which were predicted to pose a high risk of establishment in the Great Lakes. This work built on the previous findings of Rejmanek & Richardson (1996) that traits could distinguish between successful and failed invasions.

Differences in the traits of native and invasive species have further been proposed as a mechanism which may explain invasion success (Hulme and Bernard-Verdier 2017). If invasive species are functionally distinct from native species, they may face minimal competition and therefore more easily establish within communities by facilitating the exploration of unoccupied niches (Olden et al. 2006; Hulme and Bernard-Verdier 2017). This theory underpins both the biotic resistance hypothesis (that native species have the ability to compete with, and limit the spread of, invasive species) and Darwin's naturalization hypothesis (that colonization is less likely when the colonizing individuals are related to members of the invaded community) (Catford et al. 2008; Hulme and Bernard-Verdier 2017, Yannelli et al. 2017). On the other hand, the environmental filtering hypothesis (whereby the abiotic environment selects for species with only certain trait values) suggests that a higher trait similarity between invasive and native species may indicate the potential for competitive exclusion (Hulme and Bernard-Verdier 2017) as species with similar traits are likely to compete for occupation of the same niche, with invasive species typically prevailing if they possess space-occupying traits such as being larger bodied, faster growing or displaying earlier or prolonged reproduction and higher reproductive output. To date, there is support for both trait differences (Cleland et al. 2011; Statzner et al. 2008) and trait similarities (Leishman, Thomson & Cooke. 2009; Sol et al. 2022) between invasive and native species, but there is evidence that several life history traits do characterize successful invaders (Devin & Beisel 2007; Kolar & Lodge 2007; Grabowski et al. 2007; Statzner et al. 2008; Grabowska et al. 2015) and further, that traits can be used to discriminate between successful and failed invaders (Rejmanek & Richardson 1996; Miller 2000; Kolar and Lodge 2001; Prinzing et al. 2002; Miller et al. 2007; Miller 2009).

1.5. Threatened Species

In the Earth's history there have been five mass extinction events: the Ordovician-Silurian extinction 440 mya, the Devonian extinction 365 mya, the Permian-Triassic extinction 250 mya, the Triassic-Jurassic extinction 210 mya and the Cretaceous-Tertiary extinction 65 mya. Currently, we are faced with a sixth mass extinction event whereby species are becoming extinct at a rate 1000 to 10,000 times faster than background levels of extinction (Chirchorro et al. 2019). Unlike previous mass extinction events, however, the sixth mass extinction event is driven largely by anthropogenic factors.

Human activities have impacted 87-90% of global ocean surface (Halpern et al. 2015; Jones et al. 2018; Luypaert et al. 2019). Fishing, for instance, has caused marine fish abundances to decline by 38% compared to 1970 levels (Hutchings et al, 2010), while seagrasses and mangrove habitats have been depleted by over two-thirds (Lotze et al. 2006). Atmospheric carbon dioxide levels have increased by over 40% relative to pre-industrial levels due to anthropogenic activity (Caldeira & Wickett 2003) which has reduced ocean pH by 0.1 units in the past century, negatively impacting calcifying organisms (Orr et al. 2005). The cumulation of these impacts, alongside those witnessed on land, have resulted in a loss of global biodiversity comparable with previous mass extinction events (Barnosky et al. 2011; Ceballos et al. 2015; Luypaert et al. 2019).

Extinction risk is ultimately the measure of how likely a species is to undergo considerable population declines in the future (Chichorro et al. 2019). The International Union for the Conservation of Nature (IUCN), launched in 1964, has established the most authoritative and comprehensive system for quantifying extinction risk, compiling and regularly updating the global Red List of Threatened Species, which currently reports the conservation status of more than 147,500 species (IUCN 2022). Currently, 28% of assessed species (41,300) are threatened with extinction (IUCN categories Critically Endangered (CR), Endangered (EN) and Vulnerable (VU)). However, the RedList, is highly skewed towards the most well-known taxa, with 67% of vertebrates having already been assessed compared to just over 6% of marine animal species (Webb & Vanhoorne 2020). Current estimates suggest that it will take decades until a reasonable proportion of many less-well known taxa, such as marine invertebrates, are assessed (Cardoso et al. 2011; Chichorro et al. 2019).

Despite the increasing concern and attention attributed towards the effects of human activities on the marine environment, extinctions in the sea remain scarce (Webb & Mindel 2015). Of the >850 recoded extinctions, only 19-24 of these are marine, implying a 9-fold lower rate of marine extinction compared to non-marine (Webb & Mindel 2015). Despite the difficulties in detecting marine extinctions (Webb & Mindel, 2015) there are several notable examples of gastropod molluscs becoming extinct. The eelgrass limpet *Lottia alveus*, for instance, was once widespread around Long Island but went extinct due to disease decimating eelgrass populations (Carlton et al. 1991), while the horn snail *Cerithidea fuscata*, once restricted to San Diego Bay, went extinct following development of mudflats in the area (Carlton 1993).

The widely held, historical belief that marine species cannot be driven to extinction by exploitation has been disproven by the collapse of several fisheries worldwide (Mullon et al. 2005) and recent aquatic extinctions (Dulvy et al. 2014). Webb and Mindel (2015) compared extinction and extinction risk globally between marine and non-marine species and found that the lower rates of extinction in marine systems are at least partly explained by lower rates of conservation assessments: marine organisms represent less than 15% of all species assessed by the IUCN (IUCN 2021), and few of those are invertebrates (Collins et al. 2018; Webb & Vanhoorne 2020) but rates of extinction among those that have been assessed are frequently comparable to those in terrestrial taxa (Webb & Mindel 2015).

For instance, 33% of reef corals, 37% of sharks and rays and 28% of crustaceans are threatened with extinction (IUCN 2022). Rates are lower for gastropod (7.5%) and cephalopod (1.5%) molluscs (IUCN2021), but there have been substantial increases in the number of threatened molluscs recorded more generally over the course of the 21st Century (IUCN 2021). Given that much marine diversity remains to be discovered and described (Luypaert et al. 2019), methods for rapidly predicting the extinction risk of poorly known species are urgently needed (Chichorro et al. 2019).

1.6. Biological Traits and Extinction Risk

Traditionally, the vulnerability of species to extinction has been assessed using population dynamics, habitat suitability and genetics (Alvarez-Yepiz et al. 2019). More recently, however, investigations into the specific combinations of life-history, biological and ecological traits likely to lead to greater extinction risk have shown that extinction risk is non-random with regards to species life-histories (González-Suárez & Revilla 2013a, 2013b; Böhm et al. 2016; Verde Arregoitia 2016; Chichorro et al. 2019; Butt et al. 2022; Chen et al. 2022), with specific traits, or combinations of traits (termed trait syndromes), often conferring a higher risk of extinction than others (Van Allen et al. 2012).

Body size, for instance, is frequently cited as a trait positively correlated with extinction risk across multiple taxa (Seibold et al. 2015; Terzopoulou et al. 2015; Verde Arregoitia 2016). This is typically because larger species require more resources and are more easily targeted by exploitative fishing practices, or because body size is a proxy for other traits (species with a larger body size typically have slower life cycles in which they mature later in life, produce fewer offspring, and are live longer, meaning they have a slower response to change) (Chichorro et al. 2019). A small geographic range, narrow habitat breadth, specialist diet, poor dispersal ability, and lower reproductive output have also been linked to a greater extinction risk of species (Cardillo 2003; González-Suárez & Revilla 2013b; Böhm et al. 2016; Pinsky & Byler 2015; Chichorro et al. 2019).

The idea that high fecundity confers resilience to extinction has led to a perception that the threat of extinction in the sea is lower than that on land (Hutchings et al. 2012), because of the very high fecundity of many marine fish and invertebrates (Dulvy et al. 2003; Hutchings et al. 2012). However, for marine organisms which do possess a low annual fecundity they are likely at greater risk of extinction (Baker et al. 2009; Miranda et al. 2022) This is largely because low fecundity is associated with slower reproductive rates and reduced genetic diversity meaning that low-fecundity populations take longer to recover from population declines which could result in demographic collapse during periods of rapid environmental change (Bennet & Owens 1997; Purvis et al. 2000; Cardillo et al. 2003; Pincheira-Donoso et al. 2020).

A poor dispersal ability is another trait commonly linked to a high extinction risk (Chichorro et al. 2020). As climate change is causing habitats to become increasing fragmented, the ability to move to a more suitable habitat in the face of a changing environment is crucial to avoiding population declines (Chichorro et al. 2020). Species which are largely sedentary or have poor dispersal abilities are, therefore, likely to be unable to shift their distribution to keep pace with shifting areas of environmental suitability (Chichorro et al. 2020). Ecological traits have also been proposed to influence species vulnerability to extinction with characteristics such as ecological and habitat specialization, narrow thermal and diet breadth, and high susceptibility to harvesting (usually due to ease of capture from occurring in the upper ocean or on continental shelves) having been further linked to an increased risk of extinction (Powles et al. 2000). Additionally, Pearson et al. (2014) investigated the life history and spatial traits which predict extinction risk from climate change specifically and found that occupied range, population size and generation length were the most important in defining risk. It has been suggested that the loss of species threatened with extinction according to the IUCN will result in an increase in species' generalists and fewer species with unique trait combinations, potentially leading to morphological homogenization (Hughes et al. 2022).

It is vitally important to understand the causes of population decline and why some small populations go extinct (as with threatened species) while others can expand (as with recently introduced invasive species) (Kotiaho et al. 2005). As we become more aware of the key life history, biological and ecological traits which contribute to species vulnerability and species invasion success, we will become increasingly able to use trait profiles to identify both species at risk of extinction and species likely to become invasive (Chichorro et al. 2020). This would allow for a coherent framework to be created to help inform management of both species in need of protection and species likely to become successful invaders.

1.7. Thesis Structure

In this thesis I am going to determine the life-history and biological traits which characterize invasive, non-indigenous, native, threatened, non-threatened and data deficient marine invertebrate species. I will provide a framework for predicting native species likely to become invasive and for determining the life history and environmental traits highly correlated with extinction risk and invasiveness of marine molluscs. The remainder of this thesis is structured as follows:

Chapter 2: Biological trait profiles discriminate between native and non-indigenous marine invertebrates

The rate of marine biological invasions has increased to unprecedented levels in the latter half of the 20th century (Hulme 2009; Ojaveer et al. 2018). Central to the progress of understanding marine invasion biology is determining the trait attributes which underpin the ability of NIS to become invasive within new geographic regions (Gribbon et al. 2013). Therefore, in Chapter 2 I address two central questions in invasion biology: what allows an invader to be successful, and which species are likely to become invasive? I further propose a method based on trait profiles which can be used to predict non-indigenous species likely to cause the greatest impacts and native species with a tendency for invasion. Specifically, I use multivariate methods to determine:

- The main discriminating traits and typical trait profile of non-indigenous and native species.
- The accuracy with which traits can discriminate between native and non-indigenous marine invertebrates.
- The position of non-indigenous species and native species in the context of the POSE (Precocial-Opportunistic-Survivor-Episodic (Kindsvater et al. 2016) life history framework.
- The influence of non-indigenous marine invertebrates on the biological trait composition of marine communities.
- The accuracy with which potentially invasive native species can be predicted.

Chapter 3: A global comparative analysis of life-history traits associated with imperilment and invasiveness in marine molluscs

Growing evidence suggests that both extinction risk and invasion success are mediated by certain life history traits which influence intrinsic vulnerability, population dynamics and adaptive capacity to change (Olden et al. 2006; Chichorro et al. 2019). There is the assumption that globally abundant species, particularly invasives, share certain characteristics which are absent from the trait profile of threatened or extinction prone species (Jeschke & Strayer 2008). Therefore, in Chapter 3 I investigate the two-sides-of-the-same-coin hypothesis which suggests that the traits associated with invasiveness are the inverse of those associated with imperilment. Specifically, I apply a phylogenetic approach to test:

- Which traits correlate more strongly with, and are the most important drivers of, extinction risk and invasiveness.
- Whether invasive and threatened species lay at opposite ends of the POSE life history framework.

I discuss these findings in relation to taxonomic biases in the distribution of invasive-prone or extinction-prone species.

Chapter 4: Global analysis of the relationship between life-history traits and thermal tolerance, latitude and depth of invasive and threatened marine molluscs

Predicting how species and communities will respond to increasing temperatures is key to understanding the wider consequences of global climate change (Webb et al. 2020). A central tenet of macroecology is that physiological processes of organisms are linked to large scale geographic patterns in environmental conditions, such as those related to latitude, depth, and temperature (Sunday et al. 2011). Therefore, in Chapter 4 I undertake a global analysis to compare the response of invasive, native, threatened, non-threatened and data deficient species to thermal stress, to determine whether invasive species are less affected by temperature increases, as a product of climate change, compared to native and threatened species. Specifically, I use the species trait dataset from Chapter 3 coupled with occurrence records from the Ocean Biodiversity Information System (OBIS), an open access repository of occurrence records of marine species (OBIS 2022), and global sea temperature datasets from the Bio-ORACLE database, which provides marine layers for ecological modelling, (Assis et al. 2017; Tyberghein et al. 2012) to investigate according to different depth strata:

- The relationship between thermal tolerance breadth and absolute latitude.
- The relationship between thermal tolerance breadth and maximum thermal limit.
- The relationship between maximum temperature and life history traits.
- The relationship between latitude and life-history traits.

Chapter 5: General Discussion

In Chapter 5 I synthesise the results of Chapters 2-4, discussing the main findings and the contributions they make to marine invertebrate macroecology, invasion ecology and life-history theory. I highlight the applicability of these findings to the management of invasive species and the allocation of conservation resources for threatened species. I conclude by discussing avenues of future research which could expand upon the work presented in this thesis.

2. Biological trait profiles discriminate between native and non-indigenous marine invertebrates

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2.1. Abstract

The increasing rate of marine invasions to Western Europe in recent decades highlights the importance of addressing the central questions of invasion biology: what allows an invader to be successful, and which species are likely to become invasive? Consensus is currently lacking regarding the key traits that determine invasiveness in marine species and the extent to which invasive and indigenous species differ in their trait compositions. This limits the ability to predict invasive potential. Here I propose a method based on trait profiles which can be used to predict non-indigenous species likely to cause the greatest impact and native species with a tendency for invasion. I compiled a database of 12 key biological and life history traits of 85 non-indigenous and 302 native marine invertebrate species from Western Europe. Using multivariate methods, I demonstrate that biological traits were able to discriminate between native and non-indigenous species with an accuracy of 78%. The main discriminant traits included body size, lifespan, fecundity, offspring protection, burrowing depth and, to a lesser extent, pelagic stage duration. Analysis revealed that the typical non-indigenous marine invertebrate is a mid-sized, long-lived, highly fecund suspension feeder which either broods its offspring or has a pelagic stage duration of 1-30 days and is either attached-sessile or burrows to a depth of 5 cm. Biological traits were also able to predict native species classed as 'potentially invasive' with an accuracy of 78%. Targeted surveillance and proactive management of invasive species requires accurate predictions of which species are likely to become invasive in the future. My findings add to the growing evidence that non-indigenous species possess a greater affinity for certain traits. These traits are typically present in the profile of 'potentially invasive' native species.

2.2. Introduction

The rate of marine biological invasions has increased to unprecedented levels in the latter half of the 20th century (Hulme 2009; Ojaveer et al. 2018). The so-called 'great acceleration' of human activities (Steffen et al. 2015), including growing ease of trade, travel and transport, has facilitated the spread of invasive species beyond their traditional biotic range through various pathways of introduction, especially aquaculture, canal construction and shipping (Katsanevakis et al. 2014). This has resulted in new marine communities displaying novel combinations of biological traits which have unknown consequences on long-term ecosystem functioning and service provision (Guy-Haim et al. 2018). Upon arrival to recipient environments, non-indigenous species (NIS) face several reproductive, dispersal, biotic and environmental barriers (Theoharides and Dukes 2007). 'Invasive' species often constitute a subset of introduced NIS which have successfully overcome these barriers and established viable breeding populations. This establishment is often to the detriment of resident native species, with impacts to biodiversity, ecological processes, socio-economic values and ecosystem service delivery (Alpert 2006; Molnar et al. 2008: Olenin et al. 2010; Katsanevakis et al. 2014; Early et al. 2016; Hevia et al. 2017). Such invasive species are increasingly recognised as a major driver of biodiversity loss worldwide (IUCN 2018).

Central to the progress of understanding marine invasion biology is determining the trait attributes which underpin the ability of NIS to become invasive within new geographic regions (Gribben et al. 2013). Traits are measurable characteristics of organisms which influence their fitness and adaptability (Cadotte et al. 2011). Traits hypothesized to aid invasion include those related to reproduction, growth and dispersion, e.g. high fecundity, large body size, and long pelagic stage duration (Statzner et al. 2008; Cardeccia et al. 2018). From an adult life-history perspective, r-selected strategies or "opportunistic traits" e.g. short lifespan, small offspring size and lack of parental care are further expected to typify marine invasive species (McMahon 2002; Allen 2017; Jaspers et al. 2018). Furthermore, if NIS are functionally distinct from resident natives, then they may face minimal competition and thus more easily establish within communities, facilitating the exploration of unoccupied niches (Olden et al. 2006; Hulme and Bernard-Verdier 2017). This assumption underpins both the biotic resistance hypotheses (the ability of native species to compete with, and limit the spread of, invasive species) and Darwin's naturalisation hypotheses (that colonization is less likely when colonizing individuals are related to members of the invaded community) (Catford et al. 2009;

Hulme and Bernard-Verdier 2017; Yannelli et al. 2017). Alternatively, supporting the environmental filtering hypothesis (whereby the abiotic environment selects species with similar trait values) (Várbíró et al. 2020) is the theory that higher trait similarity between NIS and natives may indicate the potential for competitive exclusion (Hulme and Bernard-Verdier. 2017), with NIS typically prevailing if they possess space-occupying traits such as an earlier or prolonged reproductive period and higher reproductive output.

This combination of management relevance and theoretical interest has stimulated considerable research into whether the traits of NIS differ systematically from those of native species, but to date evidence remains mixed with some studies suggesting that invasive species are remarkably similar to resident natives (Cleland 2011) while others suggesting that invasives differ in key functional traits (Hodgins et al. 2018; Mathakutha et al. 2019). In addition, much of the work comparing the traits of native and NIS has focused on terrestrial plants (van Kleunen et al. 2010; Leffler et al. 2014; Hulme et al. 2017), while studies investigating aquatic species have largely focused on non-native freshwater fish (Alcaraz et al. 2005; García-Berthou 2007; Grabowska and Przybylski 2015), and freshwater invertebrates, specifically amphipods (Devin and Beisel 2007; Grabowski et al. 2007; Pöckl 2007). Identifying the key traits that determine invasiveness of marine organisms has, however, proved particularly difficult (van Kleunen et al. 2010; Verberk et al. 2013, Miller et al. 2018), with some arguing that because few traits have significant effects on invasiveness, and because of the potential rapid evolution of introduced species' 'invasive traits', biological traits may be poor predictors of invasive potential in marine species (Costello et al. 2015). Such inconsistencies, fuelled in part by the complex interactions between species invasive propensity (associated with propagule pressure and population growth rate) and recipient environmental characteristics (specifically biotic resistance and the availability of empty niches) (Miller et al. 2018), mean as yet, no consensus has been reached regarding how invasive and indigenous species differ in their trait compositions, and indeed whether these differences are universal across all taxonomic groups.

A more systematic approach to this question is particularly important given that, although the increase in terrestrial and freshwater European invasions has begun to level-off in recent years, marine and estuarine invasions continue to rise, with invertebrates at the forefront of this growth (Tricarico et al. 2016; EEA 2010, 2019). Since 1950, the number of non-indigenous invertebrates in European Seas has increased 94-fold (EEA 2019), with invertebrates now considered to be the most dominant, widespread and problematic of all marine invaders (Pettitt-Wade et al. 2017), making up ~63% of marine NIS in Europe (EEA

2019). Most research in Europe however has focused on the Mediterranean Sea (Kalogirou et al. 2012; Belmaker et al. 2013; Nawrot et al. 2015) which has been subject to increasing biological invasions from the Red Sea as a result of maritime traffic along the Suez Canal (Zenetos et al. 2017). Some attempts have been made to profile the traits of marine NIS in Western Europe (Cardeccia et al. 2018), and in other regions the trait overlap of native and tsunami-transported NIS has been used to identify subsets of native species which possess traits similar to invasives (Miller et al. 2018). However, to date there has been no comprehensive comparison of the biological traits of native and non-indigenous marine benthic invertebrate species throughout Western European seas, despite this region harbouring numerous invasive species (Leppäkoski and Olenin 2000).

Here I address the aforementioned taxonomic and geographical limitations of the current knowledge of the trait profiles of marine NIS by determining, at the scale of Western European seas, the influence of non-indigenous marine invertebrates on the biological trait composition of marine communities. I further propose a method based on trait profiles which can be used to identify native species possessing invasive characteristics, and predict those which may, therefore, have a tendency for invasion if they were to undergo the transportation stage. Although only a small proportion of introduced species are able to invade and thrive in non-native habitats, the most invasive of these species (those which are quick to colonize and reproduce) tend to alter the environment at the expense of native species, typically resulting in direct competition and native biodiversity loss (Molnar et al. 2008). In total, I characterized 387 species (85 non-indigenous and 302 native) using 12 biological and life history traits. These species include all known invasive invertebrates and a taxonomically matched set of common native European marine invertebrates. The specific objectives are: i) to ascertain the most common biological traits of non-indigenous invertebrates with the *a priori* expectation that traits indicative of successful invaders are related to opportunistic (*r*-selected) strategies e.g. short life expectancy and high fecundity (Sakai et al. 2001); ii) to test for differences in biological trait composition between native and non-indigenous species iii) to identify the characteristics of “key” ecosystem altering species, with the expectation being that NIS with severe impacts will be those which either differ markedly from native species in their trait compositions, (*sensu* “niche opportunists”, Olden et al. 2006), or those which have minor trait dissimilarities, thus influencing community composition via competitive exclusion (Hulme and Bernard-Verdier 2017); and iv) to identify indigenous species which have trait profiles similar to NIS to discover if traits can predict which native species could become invasive under the right conditions (Swart et al. 2018). The over-arching goal is to inform pro-active policies intended to limit the establishment of new NIS while also producing an updated inventory for both high-impact causing non-indigenous species and potentially invasive native species, i.e. those harbouring invasive-promoting, space-occupying, traits which mean they could be poised for invasion success were they to be transported beyond their native range (Keller et al. 2011). In doing this, I help address the difficulty in characterizing potent invasive species through life history and biological traits that promote invasion success (McKnight et al. 2017; Jaspers et al. 2018). This will be of use for meeting the Post-2020 Global Biodiversity Framework Target 5; that "By 2030, manage, and where possible control, pathways for the introduction of invasive alien species, achieving [50%] reduction in the rate of new introductions, and control or eradicate invasive alien species to eliminate or reduce their impact, including in at least [50%] of priority sites" (CBD 2020).

2.3. Materials and methods

2.3.1. Biological data

A list of 85 Western European non-indigenous invertebrate species (Table 1) was compiled using DAISIE (Delivering Alien Species Inventories for Europe; http://www.europe-aliens.org/aboutDAISIE.do), selecting for the areas encompassing Western Europe including the Eastern Atlantic Ocean, the North Sea, the English Channel, the Bristol Channel and the Irish Sea. Whilst my search incorporated all aquatic environments (marine, freshwater and oligohaline) only species recorded in WoRMS (World Register of Marine Species; WoRMS Editorial Board 2019) and OBIS (Ocean Biodiversity Information System; OBIS 2019) and listed as marine by EASIN (European Alien Species Information Network; https://easin.jrc.ec.europa.eu/easin) were included in the dataset. Information regarding the native region of NIS was collected from a variety of different sources including EASIN, JNCC (Joint Nature Conservation Committee; http://jncc.defra.gov.uk/), CABI's Invasive Species Compendium (Centre for Agriculture and Bioscience International; https://www.cabi.org/isc), BIOTIC (Biological Traits Information Catalogue; http://www.marlin.ac.uk/biotic/), NOBANIS (European Network on Invasive Alien Species; https://www.nobanis.org/), NEMESIS (National Exotic Marine and Estuarine Species Information System; https://invasions.si.edu/nemesis/) as well as journal articles and DAISIE (Supporting

Information, Table S4), while information relating to their introduction pathway and impact were collated primarily using EASIN databases. The list of NIS includes, alongside soft-bottom species, several conspicuous taxa such as biofouling, epifaunal, planktonic and parasitic species.

A complementary list of the most commonly recorded native marine invertebrate species of Western Europe was compiled using occurrence records from OBIS (OBIS 2019). The ten most commonly recorded native species from each of the 32 orders present in the NIS dataset were taken (less than ten when fewer such species occurred), to comprise a dataset of 302 native species that was taxonomically balanced with the NIS dataset. This native dataset builds upon a list of native species with documented qualitative life history traits (those listed in Table 2), collated by Beauchard et al. (submitted).

Table 1: The 85 non-indigenous species known to occur in the Eastern Atlantic Ocean, the English Channel, the Bristol Channel and the Irish Sea. *indicates species which have a high impact according to the EASIN, bold species are those which are also listed on DAISIE's 100 Worst List. Numbers (#) correspond to their position on the FCA plots and cluster dendrogram (Figure 2) and introduction refers to their primary introduction pathway with colours corresponding to introduction dates (red = pre-1900, dark orange = 1901-1949, light orange = 1950-1999, yellow = 2000-2018). Native refers to the native range whereby I = Indian, I-P = Indo-Pacific, M = Mediterranean, NE A = NE Atlantic, NE P = NE Pacific, NW A = NW Atlantic, NW P = NW Pacific, P-C = Ponto-Caspian, SE P = SE Pacific, SW A = SW Atlantic, SW P = SW Pacific, U = Unknown. POSE refers to their life-history strategies whereby P = precocial, O = opportunistic, S = survivor and E = episodic, corresponding to their groups within the cluster dendrogram (Figure 2a).

Taxonomic name	Introduction	Native	POSE	#
Annelida				
Boccardia polybranchia	Unknown	NE A	P	23
Clymenella torquate	Containment	NW A	P	18
Desdemona ornate	Stowaway	M	O	19
Ficopomatus enigmaticus	**Stowaway**	**I-P**	**O**	**20**
Goniadella gracilis	Stowaway	NW A	O	17
*Hydroides dianthus**	Stowaway	NW A	O	21
*Hydroides ezoensis**	Stowaway	NW P	O	22
Marenzelleria neglecta	**Stowaway**	**NW A**	**O**	**52**
Neodexiospira brasiliensis	Stowaway	SW A	O	26
*Pileolaria berkeleyana**	Stowaway	NW P	O	27
Polydora ciliate	Unknown	I-P	P	24
Streblospio benedicti	Stowaway	NW A	P	25
Terebella lapidaria	Containment	M	O	28
Arthropoda				
*Acartia tonsa**	Stowaway	I-P	O	62
Acartia (Acartiura) omorii	Stowaway	I-P	O	46
Ammothea hilgendorfi	Stowaway	NW P	O	29
Amphibalanus amphitrite	Unknown	I-P	O	72
Amphibalanus eburneus	Stowaway	NW A	O	73
Amphibalanus improvisus	**Stowaway**	**NW A**	**O**	**74**
*Austrominius modestus**	Stowaway	SW P	O	81
Fistulobalanus albicostatus	Stowaway	NW P	O	79
Bythocaris cosmetops	Unknown	U	O	60
*Callinectes sapidus**	Stowaway	NW A	O	6
*Caprella mutica**	Stowaway	NW P	P	43
*Eriocheir sinensis**	Stowaway	NW P	O	8
Eurytemora pacifica	Stowaway	NE P	O	56
Eusarsiella zostericola	Containment	NW A	P	13
Grandidierella japonica	Stowaway	NW P	P	59
*Hemigrapsus takanoi**	Stowaway	NW P	O	63
*Homarus americanus**	Escape	NW A	O	47
Macromedaeus voeltzkowi	Stowaway	I-P	O	53
Megabalanus tulipiformis	Unknown	NE A	O	5
*Monocorophium sextonae**	Stowaway	SW P	P	44
*Mytilicola intestinalis**	Containment	M	O	15
*Mytilicola orientalis**	Containment	NW P	O	16
*Palaemon macrodactylus**	Stowaway	NW P	O	51
*Penaeus japonicus**	Escape	SW P	O	54
Pseudomyicola spinosus	Containment	NW A	O	14
*Rhithropanopeus harrisii**	Containment	NW A	O	7
Synidotea laticauda	Stowaway	NE P	O	61
Bryozoa				
Tricellaria inopinata	**Containment**	**NW A**	**O**	**9**
*Victorella pavida**	Stowaway	P-C	P	10
Chordata				
*Botrylloides violaceus**	Stowaway	NW P	P	45
Corella eumyota	Stowaway	I	O	50
*Molgula manhattensis**	Stowaway	NW A	O	3
Perophora japonica	Stowaway	I-P	O	2
Styela clava	**Stowaway**	**NW P**	**O**	**4**
Cnidaria				
Diadumene cincta	Containment	NW P	E	1
Diadumene lineata	Containment	NW P	E	64
*Gonionemus vertens**	Stowaway	NW P	O	12
Maeotias marginata	Corridor	P-C	O	58
Nemopsis bachei	Stowaway	NW A	P	11
Mollusca				
Anomia chinensis	Containment	NW P	O	57
Aulacomya atra	Stowaway	SE P	E	77
Bankia fimbriatula	Stowaway	U	O	39
Brachidontes exustus	Unknown	NW A	E	65
Calyptraea chinensis	Containment	M	O	30
Corambe obscura	Containment	NW A	O	32
Crassostrea rhizophorae	Unknown	NW A	O	70
*Crassostrea virginica**	Escape	NW A	E	38
Crepidula fornicata	**Stowaway**	**NW A**	**O**	**31**
*Dendostrea frons**	Corridor	NW A	E	71
Ensis leei	**Stowaway**	**NW A**	**O**	**84**
Gibbula albida	Containment	M	P	41
Haliotis tuberculata	Escape	M	E	33
Hexaplex trunculus	Containment	M	P	34
Magallana angulata	Unknown	NW P	E	85
Magallana gigas	**Escape**	**NW P**	**E**	**82**
Magallana rivularis	Release	NW P	E	83
*Mercenaria mercenaria**	Escape	NW A	E	42
*Mya arenaria**	Stowaway	NW A	E	37
Mytilopsis leucophaeata	Stowaway	NW A	O	48
*Mytilus platensis**	Release	SE P	E	78
Ocinebrellus inornatus	Containment	NW P	P	80
Ostrea angasi	Escape	SW P	E	66
Ostrea chilensis	Escape	SE P	E	67
Ostrea denselamellosa	Escape	NW P	E	68
Ostrea puelchana	Escape	NW P	E	69
Ostrea stentina	Escape	NW A	E	76
*Petricolaria pholadiformis**	Stowaway	NW A	O	49
Rapana venosa	**Escape**	**NW P**	**O**	**35**
*Ruditapes philippinarum**	Containment	NW P	E	55
Teredo navalis	**Stowaway**	**I-P**	**O**	**40**
*Urosalpinx cinerea **	Containment	NW A	P	36
Platyhelminthes				
Koinostylochus ostreophagus	Containment	NW P	O	75

2.3.2. Selection of traits for analysis

Currently, no accepted method exists for selecting the most appropriate traits to include in macroecological analyses (Marchini et al. 2008; Bolam et al. 2017), with selection partially guided by data availability (Bolam et al. 2017). For my purposes, I selected a suite of 12 biological and life history traits (Table 2) based on those expected to affect invasive ability and survival potential in non-native habitat (Bolam et al. 2017; Cardeccia et al. 2018). Traits included those related to growth (body size, longevity), reproduction (age at maturity, fecundity), resilience to physical disturbance (offspring protection, burrowing depth) and dispersal (mobility, pelagic stage duration). The 12 traits were subdivided into a total of 56 modalities to comprise the range of possible attributes of the species included. Modalities represent possible values that a trait can take (e.g. the modalities for body length are <1cm, 1-3cm, 3-10cm, 10-20cm and >20cm). There were between two and nine modalities for each trait, with ordinal categories for some traits (e.g. body length) and qualitative categories for others (e.g. mobility) (Paganelli et al. 2012). Biological trait information for NIS and native species was collected from a variety of published sources including trait databases such as BIOTIC, SeaLifeBase, Polytraits and from a large range of dispersed expert knowledge within both published and unpublished literature (Table S5, S6 and S7), with DAISIE also being used specifically for NIS. The full list of references used to construct the trait databases for native and NIS are provided in the Supplementary material (Appendix S1 and S2).

Species life-history traits can be broadly categorised into four strategies: Precocial, Opportunistic, Survivor and Episodic (POSE) (Kindsvater et al. 2016; Dulvy 2017). Short lifespans, quick maturity, small body size and the production of copious small non-protected offspring are the defining traits of opportunistic species, with precocial differing only in terms of their reproductive strategy, instead producing few large offspring. Survivor and episodic species are large bodied, long-lived, late maturing species with the former producing few large offspring and the latter producing many small offspring. This framework, which builds upon the work of Winemiller (2005), splits traits along two dimensions; the first being between fast (precocial and opportunistic) and slow (survivor and episodic) life-histories and the second being between high (opportunistic and episodic) and low (precocial and survivor) juvenile mortality rates (Kindsvater et al. 2016; Dulvy 2017). Superimposed on this framework are *r* and K-selected strategies; the former being synonymous with opportunistic species and the latter with survivor species, which will henceforth be referred to in terms of this POSE framework (Figure S3). Each NIS was broadly categorised into one of these four life history strategies based on the trait modalities previously assigned. The trait modalities associated with each of the four life history strategies are detailed in Figure S3.

Table 2: Biological and life history traits considered, and the modalities included for each. 1 = the maximum reported length in cm. 2 = the movement of species, which influences foraging mode, dispersal and predator escape. 3 = the common diet of an organism and how that organism acquires energy via food. 4 = the maximum lifespan in years. 5 = the age at which species are able to reproduce. 6 = the regularity of reproductive events. 7 = an organism's reproductive capacity (the number of offspring produced per year). 8 = the form of offspring released from the female body, and the stage at which offspring are fully capable of feeding themselves. 9 = the diameter of eggs spawned by an organism in µm. 10 = a parental trait which enhances offspring fitness once it is released from the female body. 11 = the length of time offspring spends in the water column before settling. 12 = the ability of species to dig beneath substrate, linked to environmental position. POSE refers to life-history traits associated with precocial-opportunistic-survivor-episodic strategies.

No.	Biological Trait	Trait Modalities	Trait Code	P	O	S	E
1	**Body length**	< 1cm	B1	+	+		
		1-3cm	B2	+	+		
		3-10cm	B3				
		10-20cm	B4			+	+
		>20cm	B5			+	+
2	**Mobility**	Crawler	M1				
		Crawler-Swimmer	M2				
		Swimmer	M3				
		Drifter	M4				
		Tubicolous	M5				
		Attached-Sessile	M6				
		Planktonic	M7				
		Burrower	M8				
3	**Feeding method**	Deposit feeding	F1				
		Suspension feeding	F2				
		Deposit-suspension	F3				
		Carnivore	F4				
		Omnivore	F5				
		Parasite	F6				
		Scavenger	F7				
		Wood-boring	F8				
		Herbivore	F9				
4	**Longevity**	<1year	L1	+	+		
		1-3 years	L2	+	+		
		3-10 years	L3			+	+
		>10 years	L4			+	+
5	**Age of maturity**	<1 year	Am1	+	+		
		1-3 years	Am2				
		>3 years	Am3			+	+
6	**Reproductive frequency**	Continuous	Rf1				
		Seasonal	Rf2				
7	**Annual fecundity**	<100	Af1	+		+	
		100-1000	Af2	+		+	
		1000-10,000	Af3				
		10,000-100,000	Af4		+		+
		>100,000	Af5		+		+
8	**Offspring type**[a]	Egg	O1				
		Juvenile	O2				
		Larva	O3				
9	**Offspring size**	<100	Os1		+		+
		100-500	Os2		+		+
		500-1500	Os3	+		+	
		>1500	Os4	+		+	
10	**Offspring protection**	Brooding	Op1				
		Gel	Op2				
		Capsule	Op3				
		None	Op4				
11	**Pelagic stage duration**	1-15 days	P1				
		15-30 days	P2				
		1-2 months	P3				
		>2 months	P4				
		Benthic	P5				
12	**Burrowing depth**	0-5cm	Bd1				
		5-15cm	Bd2				
		>15cm	Bd3				
		None	Bd4				

[a] Eggs for instance would result from oviparous individuals in which the development of offspring occurs outside the mother's body, while juvenile/larvae (with juveniles referring to a post-larval stage in which the individual is not yet sexually mature) occur from viviparous individuals in which fertilization and development occurs within the female body with the embryo receiving direct nourishment from the female and being released as live young (Smiseth, et al. 2012; Faulwetter et al. 2014).

2.3.3. Traits data, encoding and interpolation

The values of a given trait can vary within species with age, biotic interactions and environmental conditions (Bolam et al. 2017). As such, it becomes difficult to assign some species to a single modality within a trait. Therefore, a fuzzy coding approach (Chevenet et al. 1994) was adopted which allows for species to have an affinity to multiple modalities by assigning a score of between 0-3 for each category within a trait. A score of 0 indicates no affinity, 1-2 indicates partial affinity and 3 indicates a high affinity (Bolam et al. 2017). Following Bremner (2005) and Cardeccia et al. (2018), the total of the affinity score for each trait was limited to 3. This allowed for qualitative information to be transformed into quantitative values appropriate for multivariate analysis (Table S5, S6 and S7). For consistent application of the fuzzy coding approach i) the modality representative of the adult life stage always received the highest affinity compared to the larval stage as this is typically the life stage in which an individual spends most of its time and is more likely to influence native species and ecosystem functioning and ii) expert judgement, based on taxonomically similar species, was used to assign values for which the literature provided contradictory information, typically choosing the trait value which was most recently published (Cardeccia et al. 2018).

Similar to other studies of biological traits (Tyler et al. 2012), I lacked complete trait data. For NIS trait information was missing for between 2.4% (body size) and 58.8% (burrowing depth) of species, while for native species trait information was missing for between 3% (each for feeding method, mobility and offspring type) and 24.8% (pelagic stage duration) of species. Trait Explorer (http://www.marine-ecosystems.org.uk/Trait_Explorer) was used to fill in these gaps by applying “automated expert judgement” to estimate the missing trait values based on their taxonomic relationships and patterns of covariation between traits (see Bruggeman et al. 2009 for detailed methods).

While NIS trait data was recorded both in qualitative and fuzzy coded format, the native species dataset was only available as a qualitative table. Therefore, for combined analysis to enable comparisons between the two datasets, both were subsequently converted into a complete disjunctive binary table whereby a value of 1 was ascribed to the dominant modality shown per trait, with 0 elsewhere (Beauchard et al. 2017). Any analysis performed only on NIS used the fuzzy coded dataset. NIS displaying crawling and swimming modalities at different life stages and hence fuzzy coded as crawling (2) and swimming (1) for instance, would translate as crawling (1) in the binary table as opposed to crawler-swimmer. However, the modality crawler-swimmer is still possible in the binary table if species are fuzzy coded as either having an affinity of 3 or 2 to this modality.

2.3.4. Data analysis

2.3.4.1. Dominant traits of NIS in the context of the POSE framework

Fuzzy Correspondence Analysis (FCA) was used to ordinate species based on their Euclidean distances in fuzzy coded trait space (Chevenet et al. 1994; Paganelli et al. 2012; Cardeccia et al. 2018). Fuzzy coded affinity scores for each trait modality were used to summarise the distribution of traits by taxa. FCA produced two-dimensional ordination plots for the NIS dataset as a whole and for each trait individually, summarising the fuzzy coded data across multiple variables into two principal components. A hierarchical *k*-means cluster analysis was performed on the matrix of species x trait modalities, using the silhouette method which revealed the optimal number of clusters to be 5 for the NIS dataset and 8 for the native and NIS dataset. This identified functional groups present within the data as well as clusters of species with similar or identical trait characteristics (termed ‘ecological equivalents’) (Cardeccia et al. 2018).

To investigate whether traits indicative of successful invaders are related to opportunistic life history strategies, the number of NIS displaying opportunistic traits according to the POSE framework (Table 2, Figure S3) were filtered from the dataset and investigated according to their level of impact and taxonomic group. Species with attributes indicative of precocial, survivor, and episodic life-history traits were also extracted from the dataset as a means of further characterizing the functional groups identified earlier.

2.3.4.2. Differences between native and NIS

To test for differences in biological traits between native and NIS, the complete disjunctive table of native trait data was combined with the existing NIS trait dataset. I calculated and plotted the percentage of native and NIS expressing each modality, to determine their dominant biological trait characteristics.

2.3.4.3. Predicting invasiveness

Regularized Discriminant Analysis (RDA) was used to determine if I could reliably identify invasiveness on the basis of traits alone. RDA is robust to the presence of multicollinearity, and so is particularly suitable for large multivariate datasets with potentially correlated predictor variables (Friedman 1989). RDA used a random subset of 20% of the combined native and NIS dataset (77 species, 17 non-indigenous and 50 native) to test how well traits could be used to categorise species as either native or non-indigenous. To determine whether NIS (Table 1) differ markedly from natives in terms of their trait compositions, i) high-impact, ii) worst-list, and iii) key species were compared to the wider dataset of both NIS and native species. High impact species are those present on the 'high impact' species lists of GISD, NOBANIS, CABI, and SEBI-2010 according to EASIN 2019; worst-list species are those present on DAISIE's '100 of the Worst' list; and key species are those known to influence community structure and diversity and which are thus considered 'key species' according to Cardeccia et al. (2018), specifically the crabs *Callinectes sapidus* (Rathbun, 1896), *Eriocheir sinensis* (Edwards, 1853), and *Rhithropanopeus harrisii* (Gould, 1841), the oyster *Magallana gigas* (Thunberg, 1793), and the tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923). Cluster analysis was again used to identify functionally similar native and NIS, allowing for the creation of a list of potentially invasive native species (those possessing invasive-promoting traits which make them successful colonizers of space) which was then assessed in terms of their general trait assemblages and taxonomic composition.

All data manipulation and analysis were performed in R 3.5.1 (R Core Team 2018), using the packages 'ade4' (Bougeard and Dray 2018) and 'mda' (Hastie, Tibshirani and Friedman 2009).

2.4. Results

2.4.1. Dominant traits of NIS in the context of the POSE framework

2.4.1.1. *Biological trait modality ordination and functional groups*

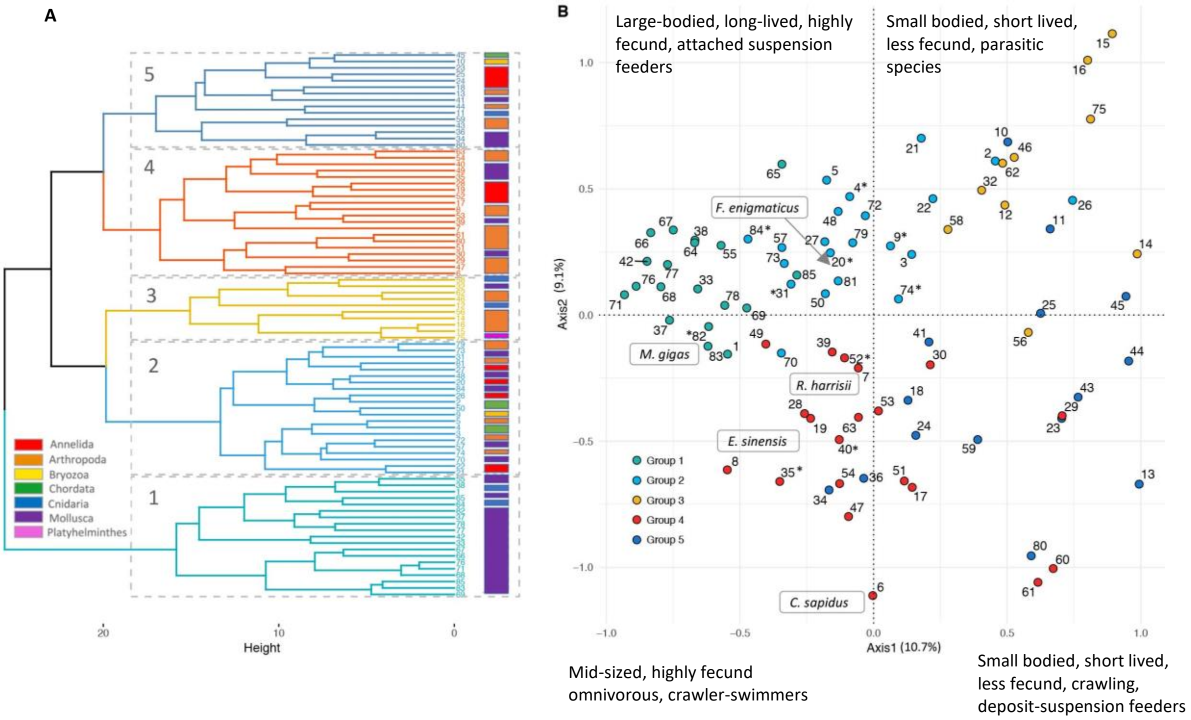


Figure 2: A) Cluster dendrogram of non-indigenous species split into functional groups using the optimal number of clusters indicated by the silhouette method, with a bar showing their taxonomic group. Numbers correspond to the species names listed in Table 1. B) The position of individual non-indigenous invertebrate species within a Fuzzy Correspondence Analysis, coloured according to their functional groups defined in cluster analysis. Variables close to the centre of the plot are less important to explain the first components. Key invasive species are labelled, and asterisks correspond to 'worst list' species.

A hierarchical *k*-means cluster dendrogram revealed five key clusters - or functional groups - in the trait profiles of NIS (Figure 2a). Based on the fuzzy coded data, no NIS are ecological equivalents (i.e. none display the exact same biological profile), hence all NIS considered in the study are biologically unique with respect to their trait affinities. However, when considering the qualitative trait data several groups of individuals have the same trait profile (Table S5). The key biological and life history characteristics of each functional group are visualised in Figure 2b. Broadly speaking, the 19 NIS in Group 1 are episodic in terms of their life history characteristics, being larger bodied, longer-lived and later maturing than any other group, and producing many, reasonably small, offspring. The 21 NIS in Group 2 are more difficult to place within the life history framework on account of them being commonly small bodied, long-lived, quick maturing species which display a range of fecundities. The same is also true of Group 3, comprised of 10 species from four phyla (platyhelmines, arthropods, cnidaria and molluscs) which are typically small bodied, short-lived, quick maturing species which produce few small offspring. The 20 species in Group 4, however, display traits typically of an opportunistic life history on account of them being small bodied, short lived, quick maturing species which produce many small offspring. Finally, the 15 species in functional Group 5 display traits typical of a precocial life history, i.e. they are small bodied, short-lived, quick maturing species which produce few offspring. Group 4 has the greatest proportion of high impact species (55%) and three of the five key species (*Callinectes sapidus* Rathbun, 1896, *Rhithropanopeus harrisii* Gould, 1841, *Eriocheir sinensis* Edwards, 1853), while Group 2 has six of the ten species listed on DAISIE’s worst list, shown in Figure 2b.

Across the 12 biological traits investigated for NIS, the first FCA axis explains 10.7% of total variation in trait composition and is strongly correlated with body size, longevity and fecundity and the second axis explains 9.1% of total variation and is moderately correlated with offspring protection, pelagic stage duration and burrowing depth (Figure 2b, Figure S1). As shown in Figure 2b the first axis (dimension 1) distinguishes small bodied, short lived, parasitic, egg releasing species with a low annual fecundity (mainly upper right quadrant corresponding to Group 3 species, with some extreme parasitic positioning at points 15 (*Mytilicola intestinalis*) and 16 (*Mytilicola orientalis*)) from mid-sized, omnivorous, crawler-swimmers with high annual fecundities (lower left quadrant of the plot corresponding mainly to Group 4). The second axis (dimension 2) extricates large-bodied, long-lived, highly fecund, attached suspension feeders (upper left quadrant corresponding to Groups 1 and 2) from small bodied, short lived, less fecund, crawling deposit-suspension feeders (lower right quadrant corresponding mainly to Group 5. The trait modalities driving the greatest variation along the axes of this plot, with correlation ratios higher than 0.4 are L1 (lifespan of <1 year), B1 (body size of <1cm), O1 (production of eggs), Af1 (<100 offspring) and Af2 (100-1000 offspring) for axis 1 and Am2 (maturing at 1-3 years), F5 (omnivory feeding method) and M2 (crawler-swimmer) for axis 2 (Table S2). Modalities associated with longevity are highly correlated with both axes (Table S2). Conversely, no modalities from the traits ‘reproductive frequency’ exhibit any strong correlation (positive or negative) with the axes, revealing that this trait accounts for low variability within the NIS dataset. Patterns of feeding method and mobility modalities are better encompassed within axis three (Figure S2) which is correlated with the following trait modalities; B5 (a body length >20cm), F6 (a parasitic feeding method), M2 (crawling-swimming mobility), Af2 (a low fecundity of 100-1000) and Bd2 (a burrowing depth of 5-15cm).

Due to the nature of fuzzy coded data, NIS were able to show affinity to multiple modalities within a trait. Within the category ‘reproductive frequency’ only 11% of species showed an affinity to both Rf1 and Rf2, while for ‘offspring type’ 75% of species displayed an affinity to multiple modalities, mostly represented by species with an affinity to both O1 (eggs) and O2 (juveniles). Few species (12) had an affinity to multiple feeding methods, with the most dominant combination being an affinity for omnivory and one other feeding method. The few behaviours of ‘offspring protection’ for which only 8% of species show an affinity to multiple modalities, are mainly represented by species expressing an affinity to both brooding and no protection. Conversely, the numerous behaviours of ‘longevity’ include several combinations of trait categories including an affinity to a lifespan of <1 year and a lifespan of 1-3 years, and a lifespan of 3-10 years and one other modality.

The trait ‘pelagic stage duration’ includes unique trait modality groupings whereby only one species (*Mytilus platensis* d’Orbigny, 1842) displays an affinity to both a pelagic stage duration of >2 months and 1-2 months, signifying a low level of affinity for this trait in NIS. In terms of the proportion of all possible modality combinations, 70% are observed for ‘offspring type’ (7 out of 10 possible combinations) and 65% for both ‘longevity’ and ‘burrowing depth’ (13 out of 20 possible combinations). Fewer ‘occupied’ modality combinations were found for ‘feeding method’ (only 18%), ‘mobility’ (only 32%) and ‘body size’ (only 37%).

2.4.1.2. POSE Framework

Across the dataset four NIS display all trait modalities considered typical of opportunistic species (shown in Table 2), three belonging to functional Group 2 (*Hydroides ezoensis* Okuda, 1934, *Amphibalanus amphitrite* Darwin, 1854, *Amphibalanus improvisus* Darwin, 1854) and one belonging to functional Group 4 (*Hemigrapsus takanoi* Asakura & Watanabe, 2005*)*. With the inclusion of species lacking offspring protection (a trait commonly considered typical of *r*-selected species but currently not integrated into the opportunistic section the POSE framework) and the exclusion of any body size limits (typically not mentioned in r-selected characterization), seven such NIS were found. Two of these occur on the worst list: *Styela clava* (Herdman, 1881) and *Marenzelleria neglecta* (Sikorski & Bick, 2004), with all but one (*Megabalanus tulipiformis* Ellis, 1758) also considered to be high impact according to EASIN. No species included in the dataset presents all biological attributes considered typical of a survivor life-history strategy. Three species were identified as possessing all the traits indicative of a precocial life history strategy: *Monocorophium sextonae* (Crawford, 1937), *Botrylloides violaceus* (Oka, 1927) and *Bythocaris cosmetops* (Holthuism 1951). The first two clustered within functional Group 5 (dominated by species displaying broadly precocial life histories) and the last within Group 4 (dominated by species displaying broadly opportunistic traits). With regards to episodic species, these typically display bet-hedging life histories (as displayed in Table 2). Two such species (*Mya arenaria* Linnaeus, 1758 and *Ostrea angasi* Sowerby, 1871), both of which are within functional Group 1, are present within the dataset and display all traits indicative of an episodic life history. Ten species are considered both worst-list and high-impact species, of these, nine are considered opportunistic in terms of their life-history traits, with only *Magallana gigas* (Thunberg, 1793) considered episodic.

2.4.2. Differences between native and NIS

The combined faunal list (including both NIS and natives) comprised seven phyla: Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria, Mollusca and Platyhelminthes, each present in both datasets in similar percentages (Table S1). Molluscs (101 native and 32 NIS), Arthropods (80 native and 27 NIS) and Annelids (50 native and 13 NIS) were the three largest phyla, making up 34.4%, 27.7% and 16.3% of the combined NIS and native species dataset respectively.

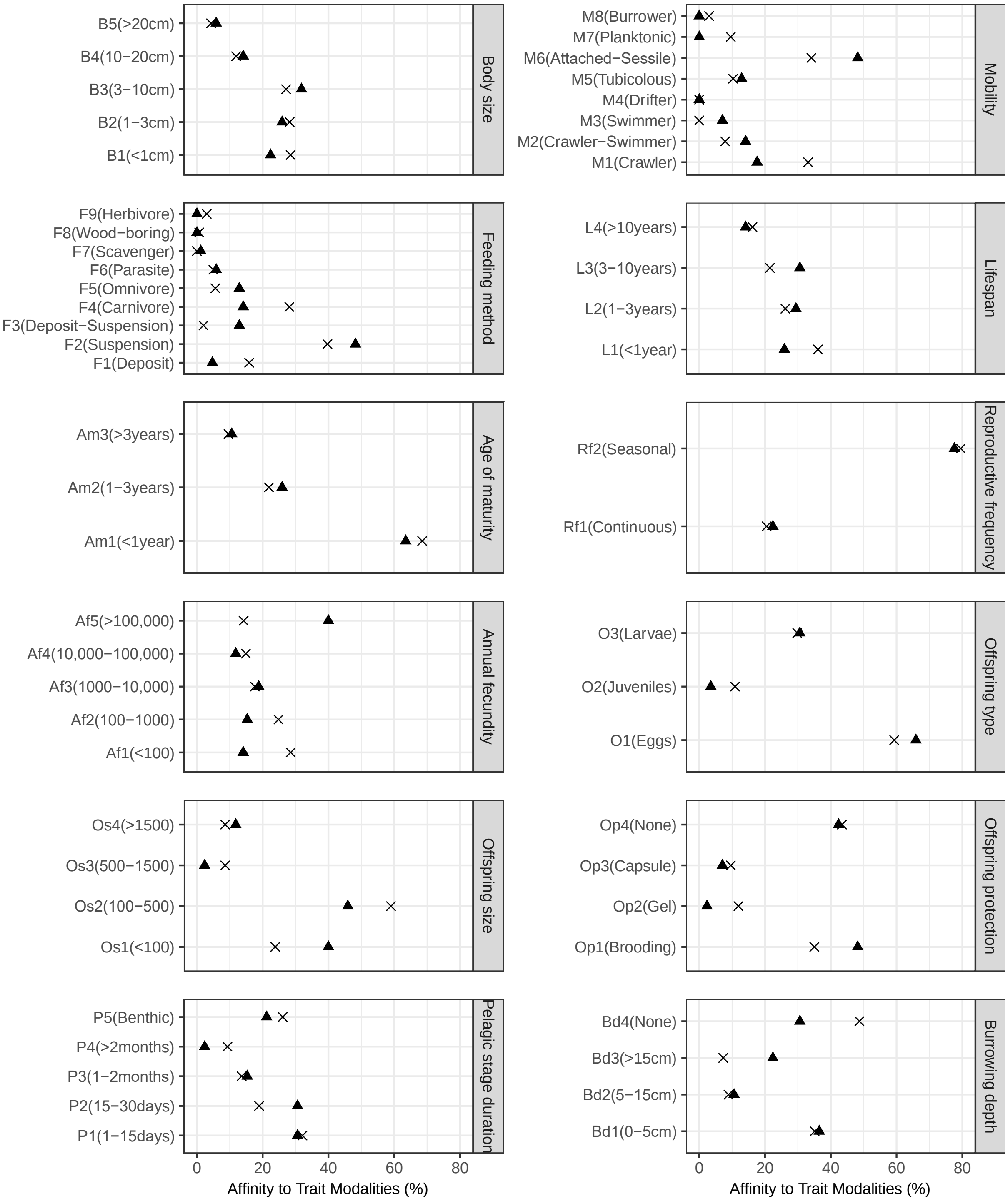


Figure 3: Affinity (in %) of 302 native and 85 non-indigenous invertebrate species to the 56 modalities of 12 biological traits. Offspring size is measured in micrometres. Native species are indicated by a cross and non-indigenous species by a black triangle.

The differences in the affinity of non-indigenous and native species to trait modalities varied depending on the trait considered (Figure 3). Five key traits discriminated between natives and NIS: body size, lifespan, fecundity, offspring protection, burrowing depth and, to a lesser extent, pelagic stage duration. NIS most commonly display some combination of the following trait modalities: body size of 3-10cm (31.8%), lifespan of 3-10 years (30.6%), high fecundity (40% have an annual fecundity of >100,000), offspring protected via brooding (48.2%), pelagic stage duration of either 1-15 or 15-30 days (both 30.6%), and a burrowing depth of 0-5cm (36.5%). Native species, in contrast, are more frequently smaller bodied (28.5% are <1cm), short lived (36.1% live <1 year), less fecund (28.5% produce fewer than 100 offspring), offering no offspring protection (43.4%), with a short pelagic duration of 1-15 days (32.1%) and no burrowing behaviour (48.7%). Both native and NIS exhibited similar patterns in terms of their mobility (both typically attached-sessile, 34.1 % and 48.2% respectively, with their secondary mobility being crawling), feeding method (both commonly suspension feeders, 39.7% and 48.2% respectively) age of maturity (both typically maturing at < 1 year, 68.5% and 63.5%, respectively) and reproductive frequency (both typically reproducing seasonally, 77.6% and 79.5%, respectively). Similarly, with regards to offspring type natives and NIS typically produce eggs (59.3% and 65.9%, respectively) 100-500 µm in size (59% and 45.9% respectively).

Regularized discriminant analysis (RDA) accurately discriminated species being either native or non-indigenous with an accuracy of 77.9% based on biological traits alone. Notwithstanding, RDA also falsely classified eight natives as NIS: *Corbula gibba* (Olivi, 1972), *Polycarpa scuba* (Monniot, 1970), *Ostrea edulis* (Linnaeus, 1758), *Littorina littorina* (Linnaeus, 1758), *Upogebia deltaura* (Leach, 1816), *Anomia ephippium* (Linnaeus, 1758), *Solen marginatus* (Pulteney, 1799) and *Propeamussium lucidum* (Jeffreys, 1879).

2.4.3. Predicting invasiveness

2.4.3.1. None-indigenous and native clusters

A hierarchical cluster dendrogram of all native and NIS, delimited via the silhouette method, revealed eight groups (or clusters) of species, the life history and biological traits of which are described in Table 3. Group 1 contains two opportunistic species, both of which are native molluscs (*Nototeredo norvagica* Spengler, 1792, and *Psiloteredo megotara* (Hanley in Forbes & Hanley, 1848) while Group 2 contains 76 primarily mollusc species (55 native and 21 NIS) which are broadly episodic in terms of their life-history. Group 3 has the highest number of NIS (26, with 37 natives) most of which are annelids, which, on account of their mid-range lifespan, body size and fecundity do not clearly fit into a life history strategy. Nine native mollusc and arthropod species make up Group 4 which, despite being small bodied, are broadly survivor species. Precocial life histories dominate in Groups 5 (46 mostly mollusc species, 5 NIS, 41 native), 6 (35 mostly arthropod species, 8 NIS, 27 native) and 7 (111 species, 22 NIS, 89 native) on account of these species producing few large offspring (particularly Group 6), and being small-bodied, short lived and quick maturing. Finally, Group 8 (35 mostly arthropod species, 3 NIS, 32 natives), much like Group 3, does not fit clearly into a life-history strategy on account of producing few, small offspring.

Table 3: Dominant trait modalities of the groups identified in cluster analysis of both native and non-indigenous species.

Group	Body size	Mobility	Feeding method	Lifespan	Age of maturity	Annual fecundity	Offspring size	Offspring protection	Pelagic stage
1	1-3cm	Burrowers	Wood-borer	1-3 years	<1 year	>100,000	<100µm	None	15-30 days
2	3-10cm	Attached	Suspension	>10 years	1-3 years	>100,000	<100µm	None	15-30 days
3	3-10cm	Tubicolous	Deposit	1-3 years	<1 year	100-1000	100-500µm	None	1-15 days
4	<1cm	Crawling	Herbivore	>10 years	>3 years	<100	100-500µm	Gel	1-15 days
5	1-3cm	Crawling	Carnivores	<1 year	<1 year	100-1000	100-500µm	Capsule	Benthic or 1-15days
6	<1cm	Crawler-swimmer	Deposit	<1 year	<1 year	<100	>1500µm	Brooding	Benthic
7	<1cm	Attached	Suspension	<1 year	<1 year	<100	100-500µm	None	1-15 days
8	<1cm	Planktonic	Parasitic	<1 year	<1 year	<100	<100µm	Brooding	1-15 days

2.4.3.2. Potentially invasive native species

Potentially invasive native species are considered to be those which possess invasive-promoting, space-occupying, life history or biological traits e.g. larger body size, higher fecundity, greater dispersal etc, which mean they could be poised for invasion success were they to be transported beyond their native range (Keller et al. 2011). In this study I define potentially-invasive native species as those closely clustered to NIS, i.e. sharing at least half of their trait profile with a known NIS, or those predicted to be non-indigenous according to RDA (Table S3). Three species were found to meet both of these criteria: *Corbula gibba* (Olivi, 1792) *Ostrea edulis* (Linnaeus, 1758), and *Littorina littorea* (Linnaeus, 1758), which are all molluscs. These species express traits generally indicative of the wider NIS trait profile in that they are larger bodied (typically medium sized, 3-10 cm), longer lived (3-10 years), highly fecund (10,000-100,000 or >100,000 offspring) species, which have a long pelagic stage duration (either 15-30 days or >2 months).

Fifty-nine native species (39% molluscs, 20% arthropods and 19% annelids) were identified more widely as potentially invasive to varying degrees, 54 identified through cluster analysis and a further five through RDA. Generally speaking, these fifty-nine potentially invasive native species also display traits which more widely reflect the characteristics of NIS i.e. they are typically 3-10cm and live for 1-3 years rather than the typical <1cm body size and <1-year lifespan of native species. These potentially invasive species also produce >100,000 offspring, compared to natives more generally which tend to produce <100. Of the 54 species identified through cluster analysis, 37 share between 6-9 traits with a known NIS, 14 share 10-11 traits and three have an identical trait profile to a known NIS (the chordate *Polycarpa pomaria* Savigny, 1816, and the molluscs *Euspira catena* da Costa, 1778, and *Atrina pectinata*) (Table S3).

P. pomaria displays the same trait profile as the non-indigenous *Megabalanus tulipiformis* (Ellis, 1758). Despite the former being chordate and the latter being an arthropod both species are mid-sized (3-10cm), attached-sessile, suspension feeders which live 1-3 years, mature at <1 year and release 10,000-100,000 offspring annually which receive no protection and are pelagic for 1-15 days. *E.catena* is biologically similar to the invasive *Urosalpinx cinerea* (Say, 1822), both of which are carnivorous bivalves which grow to 3-10 cm, live for 3-10 years and produce 10,000-100,000 eggs annually which are protected via capsules while *A. pectinata,* is biologically identical to the highly invasive *Magallana gigas* (Thunberg, 1793). Both are large bodied (>20 cm), long lived (>10 years), highly fecund species (>100,000 offspring annually) which produce small offspring (<100 µm) which receive no protection and are pelagic 15-30 days. 18 (33%) of these potentially invasive native species identified through cluster analysis are from Group 7, followed by 13 (24%) from Group 2, 12 (22%) from Group 3, 6 (11%) from Group 5 and 5 (9%) from Group 4. Species classed as ‘potentially invasive native species’ could be predicted from the wider native dataset with a 78% accuracy (misclassification rate of 13.58% (apparent) and 19.50% (cross-validated)).

2.5. Discussion

I proposed a method based on trait profiles to predict native species with a propensity for invasiveness and NIS likely to cause the greatest impact. I attempted to discriminate between likely and unlikely future invasive species based on natives with similar biological profiles to known highly invasive species. This was done in response to two of the most central questions in invasion biology: which species are likely to become invasive and what are their likely impacts? (Fournier et al. 2019). Presently, increased pressure exists to accurately predict species likely to become invasive in order to provide targeted surveillance and proactive management against the growing threat of biological invasions (Vilà et al. 2010; Capinha et al. 2013; Seebens et al. 2015; Anton et al. 2019; Fournier et al. 2019). Knowledge of the biological traits that confer invasiveness would therefore be invaluable to create effective screening of potential invaders and allow for a rapid response to invasions based upon early detection (Devin and Beisel 2007; Kaiser et al. 2010). Trait-based risk assessments are increasingly used to profile species which may have invasive potential and are becoming a valuable tool to control species introductions (Liu et al. 2017), yet this investigation goes beyond traditional biological trait analysis by using such attributes to estimate species invasiveness applied to a dataset of non-invasive species, complimentary to the work of Fournier et al. (2019).

The previous use of invasive profiling within the terrestrial environment indicates that this framework is applicable to other taxa for which there is known information regarding the traits of current NIS. Fournier et al. (2019) for instance, applied a similar approach using ecological characteristics to predict ant species likely to invade and those with the most detrimental impacts. Based on the profiles of 1,002 ant species they identified 13 native ants with ecological profiles matching those of known invasive species and suggested that these species are poised to become the next global invaders (Fournier et al. 2019). While this investigation is limited in terms of coverage (and hence may only be applicable to Western European marine species), the pool of non-indigenous invertebrate species was large due to the imputation method of Trait Explorer which allowed us to estimate values for which trait information was lacking. This has the advantage of meaning less well-known species were not removed, which could have resulted in biased parameter estimates and improper predictions of native species with invasive propensity.

Post hoc analyses of the fifty-nine potentially invasive native species identified throughout my investigation found that 13 of these species are currently known to be invasive outside of their native Western European range. *Corbula gibba*, *Ostrea edulis* and *Littorina littorea*, all identified through RDA and cluster analysis to be potentially invasive, were among the species found to be invasive elsewhere. *Corbula gibba*, for instance, invaded Port Philip Bay, Australia as early as 1987 and has since become widespread and abundant due to its fast growth rate which provides it with a competitive advantage over native endemic species of commercial importance, such as the scallop *Pecten fumatus*. *Ostrea edulis* has itself been introduced to numerous regions around the world for cultivation purposes, and has since established wild populations in some of these regions, North America in particular (ISSG, 2021). While in Atlantic waters, *Ostrea edulis* became infected with a parasitic disease known as bonamiasi (*Bonamia ostreae*), which upon translocation of North American invasive populations back to Europe has been responsible for widespread mortality among the native European populations (ISSG 2021). Also invasive to North America is *L. littorea,* typically transported through aquaculture. It has been reported that *L. littorea* competes with other native littorines and drastically alters intertidal communities as it aids the slower growing *Chondrus crispus* in overtaking the faster growing green algal species (Global Invasive Species Database 2021).

2.5.1. Dominant traits of NIS and differences between native and NIS

This is the first research of its kind to successfully discriminate between native and NIS based upon their biological traits with an accuracy of 77.9%, with body size, lifespan, fecundity, offspring protection, burrowing depth and, to a lesser extent, pelagic stage duration identified as the most important distinguishing traits. Western European non-indigenous benthic invertebrates are typically medium-sized, fast maturing, attached suspension feeders which reproduce seasonally, producing >100,000 small eggs protected via brooding or which are pelagic for 1-30 days and have a typical burrowing depth of 0-5cm. This suggests that non-indigenous species do indeed display a greater affinity for certain ‘invasive promoting’ traits than their native counterparts. Overall, I found that NIS are typically 3-10 cm while natives are <1cm, supporting the underlying assumption that NIS are typically larger-bodied and thus display enhanced performance, in terms of resource and space acquisition, over native species in their introduced regions (Roy et al. 2002; Grosholz and Ruiz 2003; Darling et al. 2011; Hänfling et al. 2011; Parker et al. 2013; Liu et al. 2017). Despite the evidence for this assumption, however, there is a growing body of literature suggesting that the perceived tendency for invasives to be larger-bodied is strongly context dependent and should not be generalized (Parker et al. 2013; Junior et al. 2015). For example, Miller et al. (2002) found no relationship between invasion success and body size in marine bivalves, while Junior et al. (2015), examined fish species on neotropical floodplains and found no colonization advantage for larger species. When looking within the specific taxonomic groups of my investigation, it is clear that the assumption that NIS are larger bodied does not always hold true. With regards to molluscs, both NIS and native molluscs were both commonly found to be 3-10 cm, while native annelids were in fact larger bodied (3-10 cm), than NIS annelids (typically 1-3 cm). It is clear therefore, that NIS must also remain competitively advantageous via other traits.

The widely-held theory that invasive species have short lifespans in which they rapidly reproduce (Sol et al. 2012) was not supported by this investigation. Instead, I found NIS to commonly live for 3-10 years while natives lived <1 year. Despite this difference in lifespan, both NIS and native species commonly became sexually mature at <1 year of age. This may indicate that non-indigenous benthic invertebrates are able to make both current and future reproduction a high priority, initially investing in rapidly producing large broods, thereby allowing the population to grow quickly (population growth hypothesis) and also reproducing throughout their longer lifespan, providing time for the introduced individuals to adapt to the new environment, without initially delaying reproduction.

Fecundity is a key trait distinguishing between native and non-indigenous invertebrates, with the former more commonly producing fewer than 100 offspring and the latter typically producing in excess of 100,000 offspring. Several studies (Torchin et al. 2001; Lockwood et al. 2005; Keller et al. 2007; Lockwood et al. 2009) also highlight propagule pressure as a key trait explaining invasive success of marine and freshwater non-indigenous species, encompassing both the number of reproductive events and number of offspring released (Brandner et al. 2018). Despite the well-documented correlation between body size and fecundity (Gribben et al. 2013) this association does not appear to be the driving force of the high prolificacy of NIS within this investigation given the low number of large bodied NIS (6%) within my dataset. While thirty-four NIS produce in excess of 100,000 offspring annually, only four of these species are large bodied (>20cm) with species sized between 3-10cm being more frequently highly fecund (15 in total). This instead indicates that high fecundity is an inherent trait of successful invaders and that these attributes favour a tendency to spread from native regions to colonize new areas, possibly aided by early maturity and small offspring size (Alonso and Castro-Diaz 2008: Brandner et al. 2018), also observed to be dominant traits of non-indigenous benthic invertebrates within my investigation.

NIS further possessed a greater affinity towards brooding than any other form of offspring protection, alongside a higher affinity to producing a large number (>100,000) of offspring. Several studies have shown that invasive molluscs display brooding parental care and a high reproductive output, as in the case of *Crepidula fornicata* (Richard et al. 2006; Le Cam et al. 2009). This is also supported by Marchetti (2004) who investigated fish invasions throughout California and found that NIS display a high reproductive capacity and exhibit parental care, the latter being favourable to invasiveness via increasing offspring survival rates and reducing dispersal into unfavourable environments. Marchetti (2004) also observed that a wide physiological tolerance (to temperature, salinity, oxygen and turbidity), and prior invasion success are important distinguishable characteristics which promote invasion success. My investigation, however, did not consider physiological tolerance nor other traits (e.g. metabolic and growth rate (Le Cam et al. 2009; Lagos et al. 2017)) reported to be important to invasive success, nor was it within the scope of this paper to investigate phenotypic plasticity, primarily due to a lack of species-specific data (Weis 2010). It is likely, however, that invasion success stems from an affinity to multiple biological trait modalities (Hänfling et al. 2011), many of which were captured within this investigation.

Non-indigenous species acting as “ecosystem engineers” via bioturbating activities such as burrowing represents a major impact of invasive species on aquatic systems. Many species choose to burrow for refuge, defence or reproductive purposes (Harvey et al. 2019) and while burrowing may bring ecosystem benefits via contributing to nutrient cycling, it also changes the landscape many native species are adapted to, potentially resulting in these species being outcompeted (Harvey et al. 2019). In the case of my investigation, burrowing depth was identified as a key trait distinguishing between native and NIS, with natives being more likely to display no burrowing behaviour and NIS more often burrowing to 0-5cm. In crustaceans, certain behaviours associated with burrowing have been shown to contribute to their success over native species (Weis et al. 2010). Predator avoidance and habitat alteration are two such examples, whereby NIS are more successful at avoiding predators than natives due to their burrowing behaviour which subsequently also alters the environment in a way that may displace natives (Weis et al. 2010). Once these burrows are created there is also evidence that invasive species are more likely to occupy these shelters, often directly displacing native species and thus increasing their risk of predation (McDonald et al. 2001; Gilbey et al. 2008). In my investigation, while almost a quarter of NIS are able to burrow to >15 cm, conversely this is the case for only 7% of natives. Comparing within taxonomic groups and the same trend is observed for molluscs, arthropods and annelids, with NIS universally displaying enhanced burrowing behaviour. Although I did not consider aggression directly, this may represent an important behavioural trait which is instrumental in allowing invasives to dominate over natives for both habitat and food (Weis et al. 2010).

The final trait which, to a lesser extent, distinguishes between native and NIS is pelagic stage duration. In NIS which are not brooders, a pelagic stage duration of either 1-15 days or 15-30 days was common, longer than that of natives which was typically only 1-15 days. Organisms which have a longer planktonic or pelagic stage are particularly prone to ‘spill over’ from their culture areas into the surrounding environment (Geburzi et al. 2018). In the case of NIS this allows for long-distance dispersal beyond the point of introduction, and as such, is a key invasive-promoting trait which ultimately enhances dispersal potential to new environments.

Although I did not directly quantify the potential for NIS to exploit human transportation systems, I observed that NIS possess a higher affinity towards being attached-sessile, likely to be favourable for vessel hull fouling, and were more commonly small, rather than large bodied, enabling easier concealment and infiltration within cargo and ballast water. This coincides with Alonso and Castro-Diez (2008) who reported that a high dispersal ability via natural mechanisms (i.e., a long pelagic stage duration), is favourable to invasives, alongside high plasticity that allows for the colonization of new environments, and aggressiveness/ territoriality (particularly among crustaceans) (Hänfling and Kollmann 2002). I found, however, that NIS which were not brooders displayed the lowest affinity towards a long pelagic stage of >2 months and hence are unlikely to be primarily dispersed in this way. Furthermore, although both native and NIS commonly produce similar sized eggs (between 100-500μm), non-brooding NIS possessed a higher affinity than natives towards small offspring sizes (<100μm). These smaller eggs allow for easy dispersal as they can enter ballast water tanks undetected and require less energy investment possibly allowing for a greater overall egg production (McAlister et al. 2012).

2.5.2. High impacts species

The impact of invasive species is not necessarily related to their invasiveness (Ricciardi and Cohen 2007), suggesting that different sets of traits may be associated with impact than invasiveness. I addressed this by considering the traits of the highest impact NIS, (i.e. those present in the 'high impact' or 'worst invasive' species lists of DAISIE, GISD, NOBANIS, CABI, and SEBI-2010 according to EASIN 2019). Five of the NIS I consider are known to influence community structure and diversity and are considered 'key species' according to Cardeccia et al. (2018); crabs *Callinectes sapidus, Eriocheir sinensis,* and *Rhithropanopeus harrisii,* the oyster *Magallana gigas,* and the tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923). Ten are also present on DAISIE's '100 of the Worst' list including the limpet *Crepidula fornicata,* the clam *Ensis leei,* the whelk *Rapana venosa* (Valenciennes, 1846) and the sea squirt *Styela clava* with a further thirty-eight classified by EASIN as having a 'high' impact. With regards to *Mallagana gigas* for instance, several expressed traits appear to contrast with those suggested by Ricciardi (2015) to characterize invasiveness e.g. displaying episodic life-history strategies such as being long-lived and late-maturing, yet this high-impact invasive bivalve is known to cause national concern within the UK where it is known to displace *Sabellaria spinulosa* (Leuckart, 1849; Dubios et al. 2006) reefs, compete with natives such as the European Oyster *Ostrea edulis* (Zwershke et al. 2018), for food and space during the creation of large oyster beds, and hybridize with local oyster species promoting the transferal of disease and parasites to native populations (Padilla 2010; Herbert et al. 2012; Goedknegt et al. 2019).

I found that high impact species (including key and worst-list species) generally have traits reflecting the wider non-indigenous dataset, although there were some noteworthy differences regarding discrepancies in body size, feeding method and age of maturity. For instance, key NIS tend to be either large bodied (>20cm) or small bodied (1-3cm) rather than the typical mid-size (3-10cm) to which the greatest affinity is given across the whole dataset, and are more commonly omnivorous crawlers with a later maturity at 1-3 years. Moreover, deposit-suspension feeders are more commonly represented in worst list species than in the full NIS list, with high impact NIS more likely to have a higher reproductive output (42% produce >100,000 offspring annually), than low-impact NIS (36%) or natives (12%), a trend that is commonly noted in other studies (Kolar and Lodge 2001; 2002; Kulhanek et al. 2011). However, it is not universally the case that high-impact NIS possess these traits (Sol et al. 2012). For instance, in my dataset while *Eriocheir sinensis,* a key Arthropoda species influencing community structure and diversity, produces in excess of >100,000 eggs annually (Czerniejewski 2013), the 'high impact' Arthropoda *Caprella mutica* produces <100 propagules annually.

The invasive crab *Rhithropanopeus harrisii*, a key and high-impact species, was found to be biologically unique within my dataset. *Rhithropanopeus harrisii* carries white spot syndrome and affects ecological functioning and ecosystem service delivery by competing with native crabs and altering food webs (Jormalainen et al. 2016). My result thus appears to give weight to the hypothesis that non-indigenous invertebrates capable of causing the greatest ecological impacts are those which are functionally distinct from native taxonomically-similar species, indicating that the similarity (or lack thereof) of traits between native and non-native species influences invader impact (Ricciardi and Atkinson 2004; Ricciardi and Mottiar 2006; McKnight et al. 2017).

While some NIS rapidly spread and have negative ecological impacts on their recipient communities, other introduced species may have minimal or positive impacts beyond their native geographical range (Rodriguez 2006; Bates et al. 2013). These positive impacts could stem from introduced species sharing similar ecological roles to natives and thus providing functional redundancy, helping to retain ecosystem functioning in the event of species loss (Stavert et al. 2017). *Ficopomatus enigmaticus,* for instance, is a small polychaete key high-impact species known to positively affect other benthic species via improving water quality and both oxygen and nutrient conditions (Keene 1980; Davies et al. 1989). This filter-feeding species also has a beneficial effect on native communities as it removes material from suspension (particularly advantageous within enclosed waterbodies) (Thomas and Thorp 1994) and is a well-documented ecosystem engineer capable of creating new habitats for epibenthic species amongst the reef tubes it builds (Thomas and Thorp 1994). This successful non-native species is characterized by traits previously hypothesized to be favourable for invasives, including low age of maturity and the production of small, non-protected eggs. Despite its benefits, *F. enigmaticus* is still considered high impact largely due to both its socio-economic impacts, including fouling aquaculture ponds and blocking thermal effluents and its high probability of being introduced to new regions, particularly estuaries and harbours (CABI 2021).

2.5.3. Outlook

Coordinated research through databases such as WoRMS and OBIS likely offer a promising avenue for furthering our knowledge of the key traits of invasive and non-indigenous marine species (Swart et al. 2018). It is likely that as biological trait information becomes more widely available for marine species there will be a greater ability to detect differences between native and NIS in order to provide a clearer delineation of an invader profile (Verberk et al. 2013; Miller et al. 2018). Once additional information is collated present lines of enquiry should be readdressed, with species listed as potentially invasive being investigated further to enable predictions to be made regarding both the regions they are likely to invade (via plausible introduction pathways (Roy et al. 2018)) and their likely impact upon arrival (Devin and Beisel 2007) based on similar invasive species. Prior invasion history has been identified as a potential predictor of future invasion success (Kulhanek et al. 2011; Fournier et al. 2019) and coupled with biological traits was used here to strengthen my list of potentially invasive native species. Although beyond the scope of the current investigation, which considers only mean trait values at the species level, the role of intraspecific trait variability may also influence invasive success and should be considered in future studies.

Once established in a suitable location, non-indigenous benthic invertebrates are near impossible to eradicate due to the difficulty in dealing with species within the marine environment (which is an open and continuous habitat allowing easy dispersal of marine species). Considering, therefore, the growing number of NIS introduced to Western Europe in recent decades, reliable estimates of the potential impacts and dominant biological traits of invasive species would greatly help to prioritize limited management resources towards highly disruptive and potential invaders (Ricciardi 2003; Kulhanek et al. 2011). Predictive tools, like the one presented here, which can forecast native species likely to become invasive would greatly benefit detection programs world-wide and provide an insight into invasion dynamics via the monitoring of potential invaders (Hui and Richardson 2017). This framework provides the opportunity to implement targeted and timely management to marine biological invasions. I recommend applying this methodology to assess and predict the invasive potential of other taxa for which biological and life-history trait information exists (Fournier et al. 2019).

2.6. Supporting material

Table S1: The proportion of each phyla included in the native and non-indigenous species dataset. The total number is given, with the percentages in parenthesis.

Table S2: The most important positive and negative loadings of trait modalities on dimension 1 and dimension 2 of the bidimensional plot encompassing the whole non-indigenous species dataset (Table 1, Figure 2b).

Table S3: List of fifty-nine potentially invasive native species. * signifies those identified through RDA, ** indicates those which share 6-9 traits with a known NIS, *** represents those share 10-11 traits with a known NIS, and bold indicates those with identical trait profiles to a known NIS. Invasive refers to whether these native European species are themselves invasive elsewhere.

Table S4: References for the native ranges of non-indigenous species used in the study.

Table S5: Qualitative biological traits information for non-indigenous species. Red are the traits filled in using Trait Explorer.

Table S6: Raw data: Disjunctive table of trait modalities for NIS and native species. Trait codes correspond to the modalities listed in Table 2. The species number is its AphiaID in the World Register of Marine Species.

Table S7: Raw data: fuzzy coded data for non-indigenous species. Trait codes correspond to the modalities listed in Table 2. The species number is its AphiaID in the World Register of Marine Species.

Appendix S1: Reference list for the trait data of non-indigenous species used in Chapter 2.

Appendix S2: Reference list for the trait data of native species used in Chapter 2.

Figure S1: Fuzzy Correspondence Analysis bidimensional plots representing the 12 biological traits investigated. Each plot represents the distribution of trait modalities across the first two axes, with points (dots) corresponding to non-indigenous species listed in Table 1. Eigenvalue bars informs on the dimensionality of the cloud of species, i.e., how much variance is explained by each axes or dimension, with each bar representing an axis from 1 to 10 (left to right).

Figure S2: Fuzzy Correspondence Analysis bidimensional plot representing the 12 biological traits investigated. Each plot represents the distribution of trait modalities across axes 1 and 3, with points (dots) corresponding the non-indigenous species listed in Table 1.

Figure S3: Adapted from Kindsvater et al (2016). Life history traits typical for each category of the POSE framework (Precocial-Opportunist-Survivor-Episodic) as dictated by differences in adult and juvenile mortality, shown on the left. Trait modalities considered in this investigation are also placed within this framework, shown on the right.

3. A global comparative analysis of life history traits associated with imperilment and invasiveness in marine molluscs

3.1. Abstract

Global environmental change is accelerating both species extinctions and invasions, contributing to the mass reshuffling and potential taxonomic and functional homogenization of species assemblages. Evidence indicates that both extinction risk and invasion success are mediated by life-history traits. Here, I aim to determine on a global scale whether invasive and imperilled (IUCN Red List) marine molluscs lay at opposite ends of the life-history continuum and attempt to correlate species life-history traits with the likelihood of being either imperilled or invasive. I collated life history trait data (including body size, longevity, maturity, fecundity, pelagic stage duration and egg size) for 1935 gastropod and bivalve molluscs, which were also classified according to risk status (Invasive, Native, Non-threatened, Threatened and Data Deficient). Using principal component analysis (PCA) and phylogenetic generalised least squares (PGLS) models I identified that while phylogeny may be used to predict risk status in marine molluscs, the inclusion of trait data adds very little to the predictive power of the models. Extinction risk and invasiveness were not randomly distributed across families, with some families containing larger proportions of threatened (*Provannidae* and *Pinnidae*) or invasive-prone (*Teredinidae* and *Chamidae*) species than others. I observed a disparity between life-history-driven sensitivity to extinction and invasion whereby different risk categories occupied differing positions within trait space. Considering where a species' life history falls on the POSE spectrum can help to diagnose vulnerability to human exploitation and can also show which species may be poised for invasion success.

3.2. Introduction

Global environmental change is accelerating both species extinctions and invasions, contributing to the mass reshuffling and potential taxonomic and functional homogenization of species assemblages (Jeschke & Strayer 2008; Ceballos et al. 2015; Liu et al. 2017). Conservationists and invasion ecologists are equally interested in understanding the causes of extinction risk at low population sizes (van Kluenen & Richardson 2007; Blackburn & Jeschke 2009). The former approach the issue with the aim of preventing extinctions in threatened and imperilled populations by discovering which traits allow small populations to persist through time (Blackburn & Jeschke 2009). The latter focus more on understanding how founder populations of exotic species can overcome the barriers faced by small population sizes, and subsequently spread (Blackburn & Jeschke 2009). The processes of extinction and invasion are worth studying in tandem as this allows the key question to be addressed of whether certain traits mediate extinction probability at low population sizes, and if so, how these trait ranges then vary between invasive and extinction prone species (Blackburn & Jeschke 2009).

Growing evidence suggests that both extinction risk and invasion success are mediated by certain life history traits which influence intrinsic vulnerability, population dynamics and adaptive capacity to change (Olden et al. 2006; Bradshaw et al. 2008; Larson & Olden 2010; Chichorro et al. 2019). Links between life history and either invasion success or extinction risk have been documented predominantly in vertebrates, including mammals (Isaac 2009; Capellini et al. 2015), birds (Sol et al. 2012; Wang et al. 2017), reptiles (Allen et al. 2017; Tingley et al. 2013), amphibians (Salice 2009; Allen et al. 2017) and fish (Vila-Gispert et al. 2005; Olden et al. 2006; Reynolds et al. 2005; Liu et al. 2017). Most studies of invertebrates have focused on terrestrial or freshwater arthropods (Larson & Olden 2010; Krushelnycky et al. 2010; Engelkes & Mills 2011), although recent analysis has revealed life history correlates of invasiveness in marine invertebrates too (Quell et al. 2021). Suggested life-history correlates of increased extinction risk include K-selected strategies (or ‘slow’ life histories) such as a large body size (Gaston & Blackburn 1995; Fisher & Owens 2004; Chichorro 2019), long lifespan, late maturation (Reynolds et al. 2005) and low fecundity, all of which increase a species’ vulnerability to human exploitation and reduce their ability to compensate for losses (Webb 2002; Fisher & Owens 2004; Olden et al. 2007). Life history correlates of invasiveness, meanwhile, include r-selected strategies (or ‘fast’ life histories) such as a small body size, short lifespan, quick maturation and high fecundity (Statzner et al. 2008; Cardeccia et al. 2018).

These traits, along with a widely dispersive larval phase, provide invasives with a high recovery potential and allow for quick reproduction and spread in their recipient environment.

Building upon the ideas of the r/K selection theory is the POSE framework (Kindsvater et al. 2016; Dulvy & Kindsvater 2017). This conceptual framework allows species life-history traits to be broadly categorised into four strategies: Precocial, Opportunistic, Survivor and Episodic. Short lifespans, quick maturity, small body size and the production of copious small non-protected offspring are the defining traits of opportunistic species, with precocial species differing only in terms of their reproductive strategy, instead producing few large offspring. Survivor and episodic species are large bodied, long-lived, late maturing species with the former producing few large offspring and the latter producing many small offspring. This framework, which builds upon the work of Winemiller (2005), splits traits along two dimensions; the first being between fast (precocial and opportunistic) and slow (survivor and episodic) life-histories and the second being between high (opportunistic and episodic) and low (precocial and survivor) juvenile mortality rates (Kindsvater et al. 2016; Dulvy & Kindsvater 2017).

Much of this research has fuelled the two-sides-of-the-same-coin hypothesis which suggests that the traits associated with invasiveness are the inverse of those associated with imperilment (Lockwood 1999; Jeschke & Strayer 2008; Bradshaw et al. 2008: Blackburn & Jeschke 2009; Liu et al. 2017). This debate reflects the assumption that globally abundant species, in particular invasives, share certain characteristics which are absent from the trait profile of threatened or extinction prone species (Jeschke & Strayer 2008). Evidence to date is inconclusive, either supporting or contradicting the two-sides-of-the-same-coin hypothesis with several existing studies differing in terms of taxonomic resolution and spatial extent. For instance, Larson and Olden (2010) found evidence supporting the hypothesis and reported that invasive crayfish from south-eastern USA were typically highly fecund, large bodied, habitat generalists, while threatened crayfish were less fecund, small bodied, habitat specialists. Previous studies (Davies et al. 2004; Munday 2004; Moyle and Marchetti 2006; Bates et al. 2013) have also supported the theory that habitat and diet generalists are less extinction-prone and more likely to become invasive, than specialists. It is also widely assumed that species with larger geographic ranges are less likely to face extinction and more likely to be introduced to new environments, while the inverse is true for species with small geographic ranges (Reynolds et al. 2005; Jeschke & Strayer 2009).

Other studies, however, have raised doubts as to the validity of this theory and its applicability across different taxonomic groups. Jeschke & Strayer (2008) and Blackburn and Jeschke (2009), for instance, found that the attributes of invasive birds and freshwater fish from Europe and North America were not opposite in sign to those of threatened species. In birds, both extinction risk and invasion success increased with body mass, while for fish, egg size increased with the growing risk of both extinction and invasion (Jeschke & Strayer 2008). As such, the validity of the two-sides-of-the-same-coin hypothesis is very much still in question (Liu et al. 2017). Despite this uncertainty, however, trait-based risk assessments have been applied to species profiling in an attempt to predict and prevent future invasions and extinctions (Liu et al. 2017). Given the pressing need to manage both species in decline and species on the move, comparative studies are increasingly used to understand which life history and biological traits are critical for determining whether a species is likely to become imperilled or invasive (Murray et al. 2002; Gabrielova et al. 2013).

Molluscs, the second largest animal phylum after Arthropods, make up 23% of all named extant marine organisms (Joseph 2017; MolluscaBase 2020). Despite sixty percent of described mollusc species being marine, and thus representing the single largest marine phylum, non-marine molluscs tend to dominate the literature with regards to studies of extinction risk and global decline (Cuttelod et al. 2011; Lydeard et al. 2014; Seddon et al. 2014). Not only do molluscs stand out as a group most severely impacted by extinction (around 40% of recorded extinctions over the past five centuries are molluscs, primarily gastropods, Lydeard et al. 2004; Cowie et al. 2017), but invertebrates in general are typically poorly assessed (fewer than 10% have been assessed or are planned to be assessed by 2030; Cazalis et al. 2022). In addition to having the highest number of recorded extinctions, molluscs are also the world’s most ecologically and economically damaging invasives (Tang & Aldridge 2019). However, no global review has been undertaken to determine the life history traits indicative of imperilled and invasive marine molluscs.

The principal aims of this investigation are, therefore,

(a) to determine on a global scale whether invasive and imperilled (IUCN Red List categories VU, EN, and CR) molluscs lie at opposite ends of the life-history continuum and

(b) to correlate species life-history traits with the probability of being either imperilled or invasive.

To achieve this, two objectives must be met:

(1) to determine which trait combinations are the most important drivers of extinction risk and invasiveness and to evaluate the relative importance of these life-history traits in predisposing species to an elevated extinction or invasion risk. This will involve testing the hypothesis that (H1) age of maturity and fecundity are likely to be key drivers of elevated extinction or invasion risk.

(2) to determine how the life-history traits of invasive, native, threatened, non-threatened and data deficient molluscs differ. This will be achieved by testing three hypotheses: (H2) invasive species are more likely to display fast or ‘r-selected/opportunistic’ traits (i.e., are faster-lived, quick maturing and more highly fecund) compared to imperilled species, (H3) invasive species display greater trait variability than imperilled species (assuming that different traits are likely to be selected for at different stages of the invasion processes whereas more specific trait combinations predispose species to a higher risk of extinction (Liu et al. 2017)), and (H4) threatened species (those categorised as Critically Endangered, Endangered or Vulnerable) will be larger bodied species which display slower life histories (i.e., are longer lived, later maturing and less fecund) compared to non-threatened species (those categorised as Near Threatened or of Least Concern).

This comparative analysis will provide the first global-scale assessment of the association between life history traits and invasion success or extinction risk for marine bivalve and gastropod molluscs and will determine the feasibility of developing effective risk assessment protocols aimed at proactively identifying species which are likely to become imperilled or invasive in the future.

3.3. Materials and methods

3.3.1. Biological data

Six life history traits were investigated across a total of 1935 species of marine gastropod and bivalve molluscs (see Appendix S3 and S4). These species fall into one of three categories according to their distributional status at a global scale. Invasive alien species (n =

250) are those which have been introduced, either accidentally or deliberately, outside of their native range, typically with negative consequences for their recipient environment. The invasive dataset was downloaded from the World Register of Introduced Marine Species on the 1st September 2020. The search was completed at the species level selecting for any global origin and any measure of invasiveness. On the same date, the Red List dataset (n = 689) was downloaded from the IUCN Red List of Threatened Species using the advanced search option to select for gastropod and bivalve molluscs from all marine regions. Red List species are further split into three sub-categories; Threatened species (n = 65) which are those listed as Critically Endangered (CR, n = 8), Endangered (EN, n = 24), or Vulnerable (VU, n = 33), Non-threatened species (n = 519) which are those considered to be either Near Threatened (NT, n= 20) or Least Concern (LC, n = 499), and Data Deficient species (DD, n = 105) which are those with insufficient information for an adequate assessment of conservation status.

I define a third category that I term ‘Native species’ (n = 996), including species which are not invasive and have not been Red List assessed. As gastropods comprised 85% of the invasive and imperilled dataset combined, an equivalent ratio was decided when collecting the native species dataset which was compiled on the 13th October 2020 by downloading species with the greatest number of occurrence records from the Ocean Biodiversity Information System (OBIS 2022). OBIS, an open access global repository, is the largest holder of marine bioregional datasets with >59M occurrence records of >120,000 marine species. I selected species with a large number of occurrence records because more trait data is available for species with a greater number of OBIS occurrence records (Tyler et al. 2012). Additionally, this method of selecting native species minimises the chance of including species that would be classified as threatened if formally IUCN assessed, as species with many distribution records are more likely to be non-threatened than threatened (albeit this trend is rather weak; Webb & Vanhoorne 2020). For the native group, selected a similar number of gastropods and bivalves as present in the combined invasive and Red List datasets, including only marine species, and excluding any species already present in these other two datasets. The final database contained 1652 gastropods (149 invasive, 650 Red List and 853 native) and 283 bivalves (101 invasive, 39 Red List and 143 native) from 39 orders and 238 families. Although the categories of Red List, invasive and native species are not always mutually exclusive in nature, in this case no species were included which were both invasive and threatened. Nevertheless, given that the goal of this study is to identify broad relationships and signals of status, this investigation should be robust to a few outlying cases of species groups overlapping.

3.3.2. Taxonomic bias in assessments of invasiveness and threat status

IUCN assessments have not been conducted on a phylogenetically random subset of molluscs and the very process of assessing extinction risk is taxonomically biased. For example, certain taxa have been targeted for IUCN assessment (e.g., the >600 species in the genus *Conus;* Peters et al. 2013), whereas species with narrow distributions, smaller body sizes and lower dispersal abilities have often been excluded (Cardoso et al. 2011). As of 2010, only 4% of all mollusc species had been evaluated (IUCN 2010; Cardoso et al. 2011), and, given the taxonomic biases in these evaluated species, it follows that many species which may be considered threatened have currently not been assessed. Although phylogenetic clustering has been found to be much weaker in studies of invasiveness (Lambdon 2007; Pigot et al. 2017), it is still the case that assessments of invasive species are highly taxonomically biased and not phylogenetically random (Jelbert et al. 2019). For instance, Pysek et al. (2008) found that between 1980 and 2006, although 892 invasive species were the subject of at least one detailed study, certain species were more intensively researched than others, with the Zebra mussel *Dreissena polymorpha* for instance, being the subject of 64 separate studies. This non-randomness in species sampling is commonplace in phylogenetic studies of both invasiveness and extinction risk (Hau & Lanfear 2018), mine being no exception. Estimates of phylogenetic signal in either invasiveness or IUCN assessment status are, therefore, likely to overstate the true signal across all molluscs.

3.3.3. Trait data

Traits included were maximum body size (in cm, defined as the maximum linear dimension), lifespan (defined as the maximum number of years an organism lives), age at maturation (the time taken for an organism to become sexually mature, in years), annual fecundity (defined as the total number of eggs or offspring produced in one year), egg size (defined as the mean diameter of mature ovarian oocytes in micrometres), and pelagic stage duration (the length of time offspring spend in the water column before settling, in days). Life history trait data was collected from a variety of online published sources. For invasive species this included trait databases such as BIOTIC (Biological Traits Information Catalogue) (MarLin 2006), NEMESIS (National Exotic Marine and Estuarine Species Information) (Fofonoff et al. 2018), CABI (Invasive Species Compendium) (CABI 2022) and SeaLifeBase (Palomares & Pauly 2022). For Red List species the IUCN Red List of Threatened Species (IUCN 2022) and The Conus Biodiversity Website (https://biology.burke.washington.edu) proved useful, while for native species GBIF (the Global Biodiversity Information Facility) (https://www.gbif.org), BIOTIC, The Natural History Museum of Wales (https://naturalhistory.museumwales.ac.uk) and the Animal Diversity Web (Myers et al. 2022)) were frequently consulted. In addition, data from a large range of dispersed expert knowledge within both published and unpublished literature proved useful in filling all three datasets.

Table 4: Summary of data availability for the six life history traits investigated according to each species status before using Trait Explorer (https://www.marine-ecosystems.org.uk/Trait_Explorer). Both total number and percentages (in parentheses) are shown.

Trait	Invasive	Native	Red List	Total
Body size	247 (98.8%)	994 (99.8%)	668 (96.8%)	1909 (98.5%)
Lifespan	82 (32.8%)	272 (27.4%)	31 (4.5%)	385 (19.9%)
Age at maturity	82 (32.8%)	139 (14.0%)	14 (2.0%)	235 (12.1%)
Annual fecundity	87 (34.8%)	189 (19.1%)	46 (6.7%)	322 (16.6%)
Offspring size	86 (34.4%)	259 (26.1%)	83 (12.0%)	428 (22.1%)
Pelagic stage duration	93 (37.2%)	216 (21.8%)	119 (17.3%)	429 (22.1%)

Similar to other studies using biological and life-history traits (Tyler et al. 2012; Liu et al. 2016), I initially lacked a complete trait dataset. The mean proportion of missing trait data varied across the databases from 54.9% for invasive species, to 68.4% for Red List species and 65.3% for native species (Table 4). Overall body size had the most trait data available, missing only 1.5% in total, while age of maturity was missing for 87.9% of species across the three datasets. In order to complete the datasets Trait Explorer (http://www.marine-ecosystems.org.uk/Trait_Explorer) was used to fill in these gaps by applying "automated expert judgement" to estimate the missing trait values based on their taxonomic relationships and patterns of covariation between traits (see Bruggeman et al. 2009 for a full explanation of the methods). Following this extrapolation additional ground-truthing was performed ensuring for example that age of maturity is always less than lifespan. The datasets used in this study are fully documented in the University of Sheffield's Online Research Data repository (Appendix S3 and S4).

3.3.4. Mollusc phylogeny

I relied on phylogeny from the Open Tree of Life using the ‘rotl’ package (Michonneau et al. 2016) which produces branched and rooted phylogenetic trees built by combining taxonomic information with published phylogenies. For the purpose of analysis, separate phylogenetic trees were created for gastropods and bivalves. The names of species in the phylogenetic trees were matched to those in the bivalve and gastropod datasets ensuring taxonomic name consistency throughout. After dropping unmatched taxa 275 species were plotted within the bivalve phylogenetic tree and 1458 species within the gastropod phylogenetic tree. For these species branch lengths were computed using the Grafen method (see Grafen 1989 for more details). Phylogenetic trees of the bivalves and gastropods are shown in Figure 4. Although these are not definite phylogenies, they provide a useful framework, and the comparative analysis I conducted is robust to small inaccuracies in phylogeny (Symonds & Blomberg 2014). The trees were made using ggtree version 3.6.2 (Yu 2022).

3.3.5. Data analysis

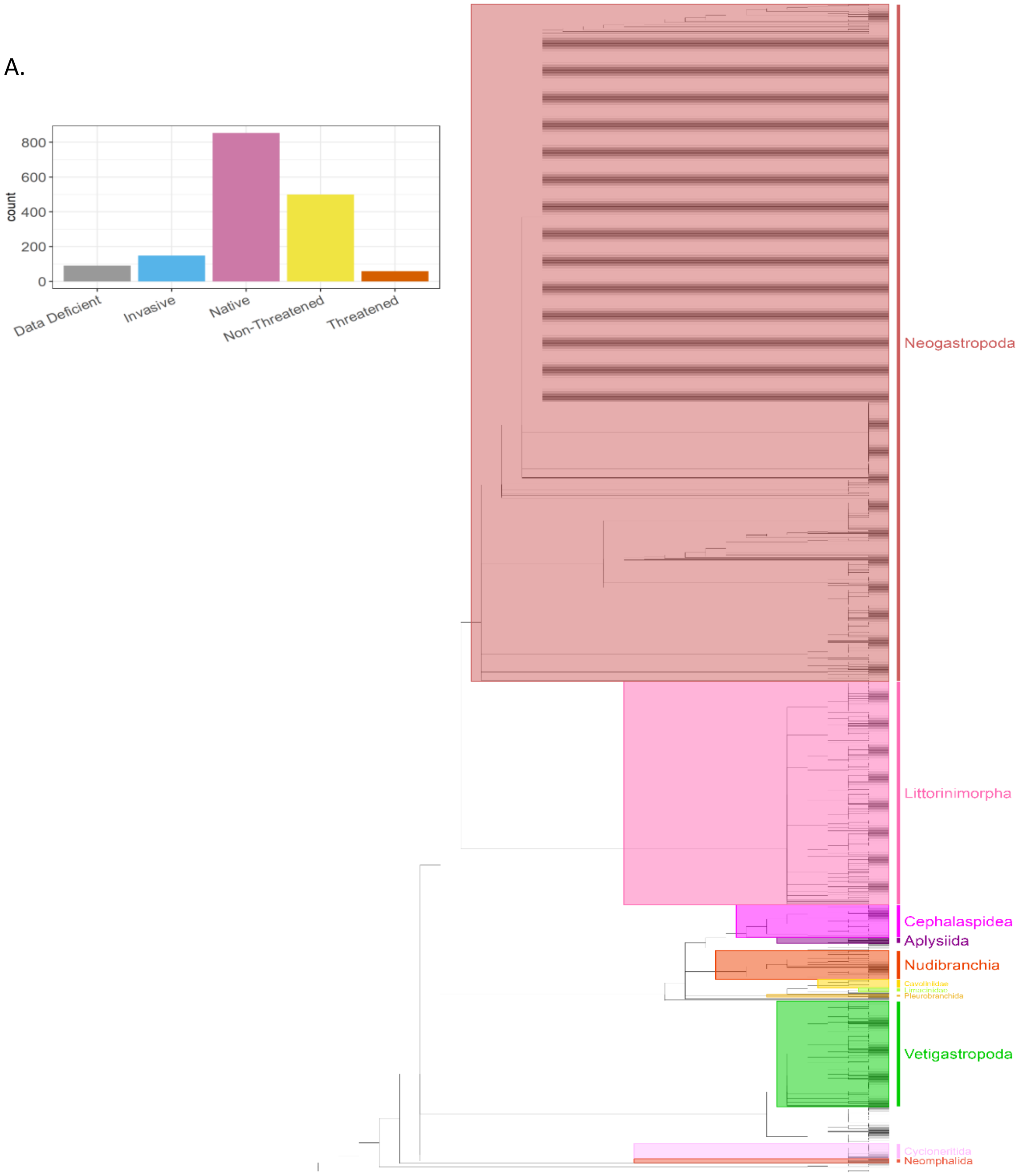
Statistical analysis was carried out in R version 4.2.1. (R Core Team 2021). Principal Component Analysis (PCA) was performed on the bivalve and gastropod datasets separately, using the “prcomp” function within the ‘factoextra’ package v1.0.7 (Kassambara & Mundt 2020), to reduce the dimensionality of the dataset. To address H1 that age of maturity and fecundity are likely to be key drivers of elevated extinction or invasion risk I recorded the proportion of variation explained by principal components one and two, along with the trait loadings for both PC1 and PC2. The principal component analyses plotted were colour coded for each risk category (Data Deficient, Invasive, Native, Non-Threatened and Threatened), helping to test H2 that invasive species are more likely to display fast or ‘r-selected/opportunistic’ traits compared to threatened (imperilled) species, H3 that invasive species display greater trait variability than threatened species and H4 that threatened species will be larger bodied and display slower life histories compared to non-threatened species. All life-history predictor variables are continuous and log-transformed for analysis.

To further investigate H1, gastropods and bivalves were then plotted independently within the POSE framework whereby individual species were categorized according to their age at maturation and fecundity (Dulvy & Kindsvater 2017). Age of maturation is inversely related to adult morality rates, as delayed maturation indicates a low natural mortality (Kindsvater et al. 2016) while fecundity is related to juvenile survival as species with lower fecundities tend to have greater survival. Again, the species were colour coded within the POSE framework to highlight their level of risk (Data Deficient, Invasive, Native, Non-Threatened and Threatened), helping to address H2 and H4.

As species are not independent data points for analysis due to a shared evolutionary history, phylogenetic generalized least squares models (PGLS) were used to determine which traits are the most important drivers of extinction risk and invasiveness in marine molluscs while accounting for nonindependence of data due to shared ancestry (Pagel 1999; Freckleton et al. 2002). PGLS fits a linear regression to investigate the impact of one or more predictor variables on a single response variable while controlling for potential phylogenetic signal in the response. I followed Revell (2010), Böhm et al. (2017) and Wang et al. (2017) and optimized Pagels λ, a branch length transformation indicating the strength of the phylogenetic signal, in each PGLS model using the maximum likelihood method (lambda = 'ML'). Models were run without an intercept to determine the coefficient for each risk level. In order to address H1 two groups of PGLS models were run. I began the analysis by examining the significance of the relationship between risk category and PC1 and PC2 (identified during principal component analyses) for both bivalves and gastropods. I then tested the importance of the relationship between risk category and age of maturation and annual fecundity for both bivalves and gastropods. The function "pgls" was used within the package 'caper' to run the models (Orme et al. 2013). This function has been found to outperform other comparative methods when the response variable is ordinal and the phylogenetic tree includes a large number (>100) taxa (Graber 2013; Caviedes-Solis et al. 2020).

3.4. Results

3.4.1. Trait differences between invasive, native, threatened, non-threatened and data deficient molluscs



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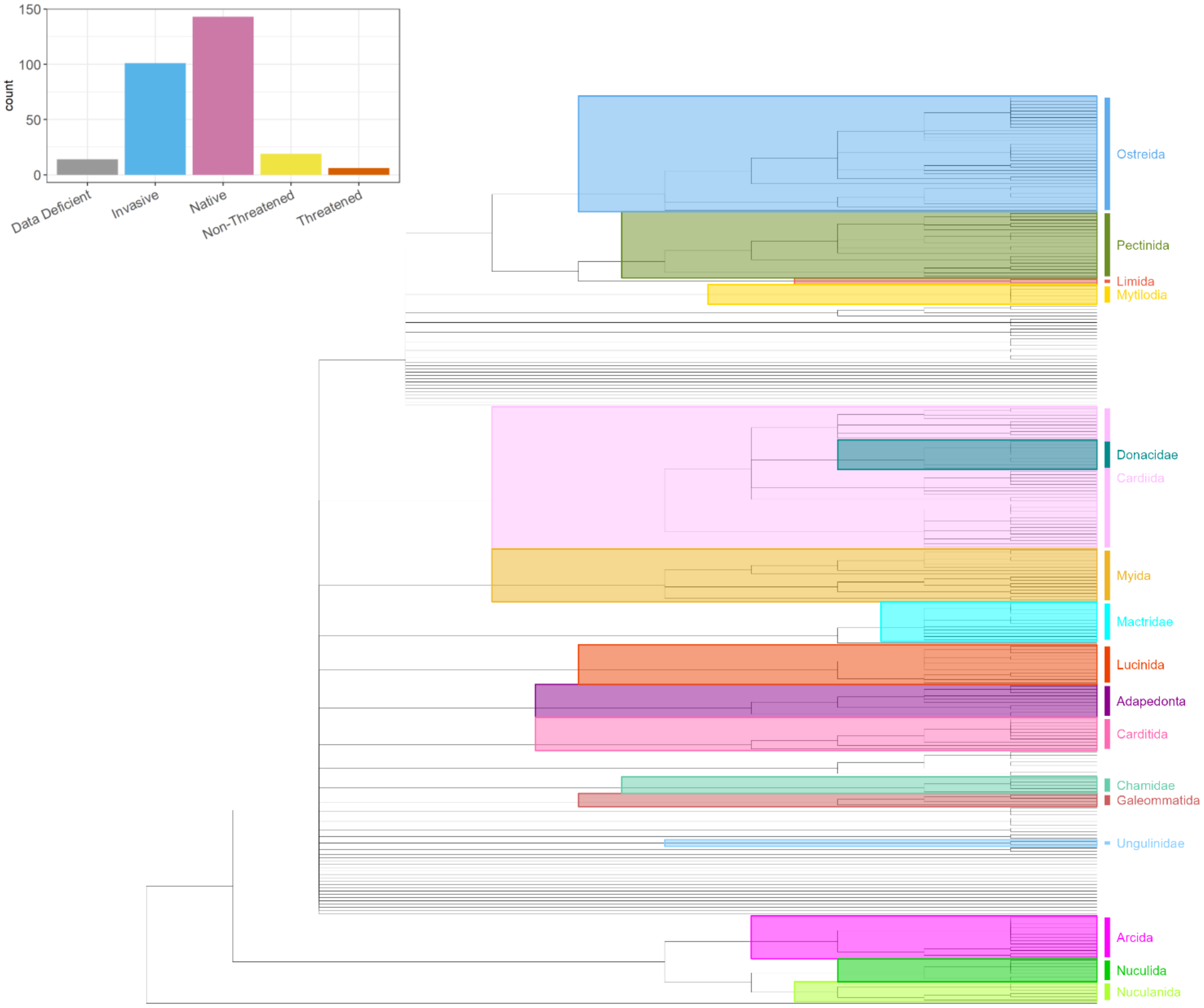


Figure 4: Phylogenetic trees of (A) 1458 marine gastropod species and (B) 275 marine bivalve species, coloured according to key clades Inserts show the number of species belonging to each risk category (Data Deficient, Invasive, Native, Non-threatened and Threatened).

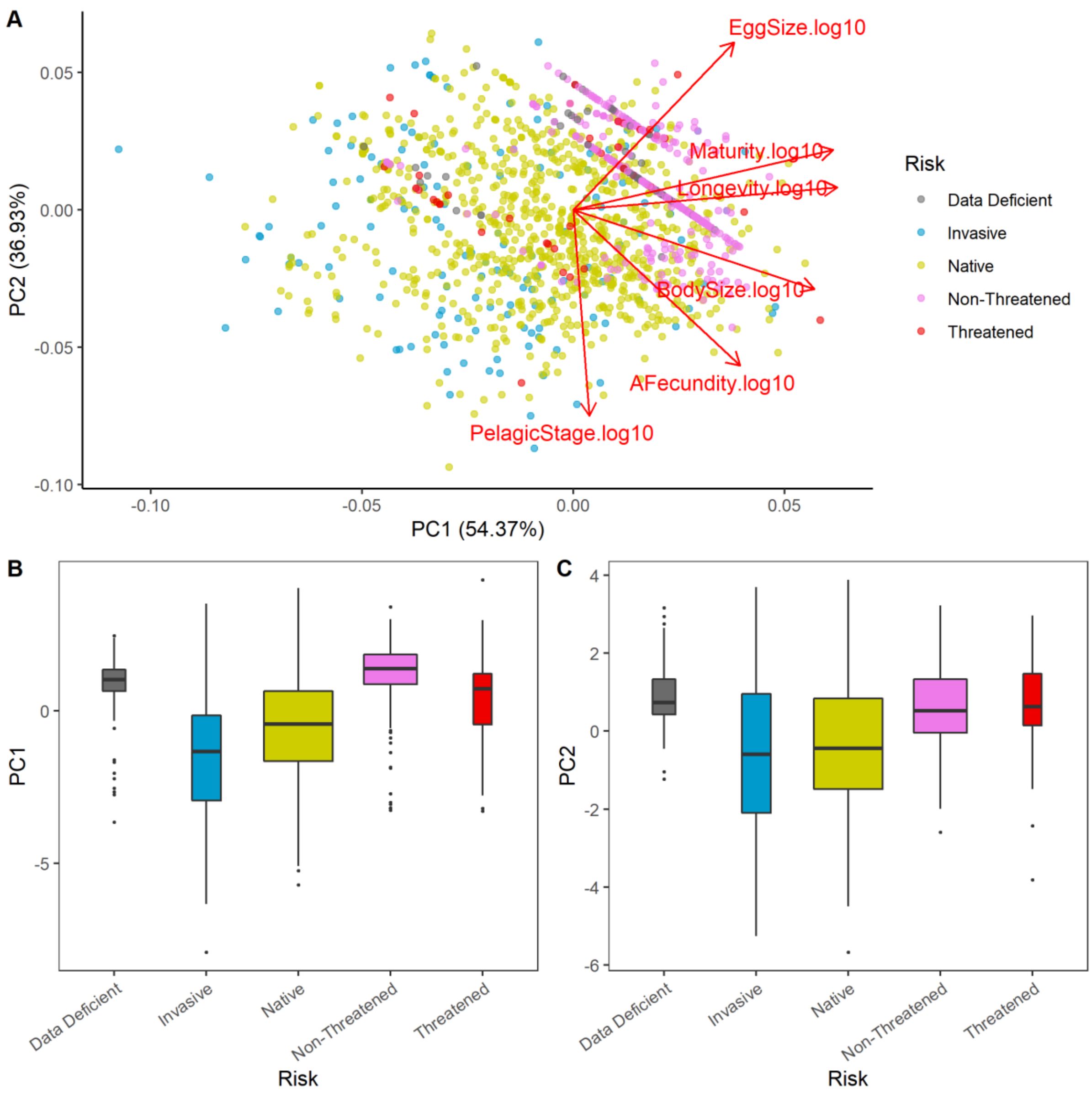


Figure 5: A) Principal Component Analysis (PCA) of 1652 gastropod species split by five risk categories (Data Deficient (n= 91), Invasive (n=149), Native (n=853), Non-threatened (n =500) and Threatened (n=59)) defined by the first two principal components (PC1 and PC2). PCA is a form of multivariate data analysis which is used to reduce the dimensionality of the data in order to provide a set of summary indices. Arrows indicate mean loadings (direction and weighting) of each life history trait in the PCA. Each point represents the position of a species within two-dimensional space. B) Boxplot of each risk category against PC1 C) Boxplot of each risk category against PC2. Width of the boxplots are scaled to the number of observations.

In gastropods, 91.3% of variation in life history traits is explained by the first two principal components (PC1 = 54.37% and PC2 = 36.93%) (Figure 5a). Axis 1 of the PCA was effective in separating species with large and small body sizes, long and short lifespans and early and delayed maturation while axis 2 of the PCA was effective in separating species according to annual fecundity, egg size and pelagic stage duration (Figure 5a, Table 5). Longevity, maturity, and body size were all strongly positively correlated with PC1 (0.96, 0.94 and 0.98, respectively), while pelagic stage duration, egg size, and fecundity were all strongly negatively correlated with PC2 (-0.95, -0.77 and -0.72 respectively).

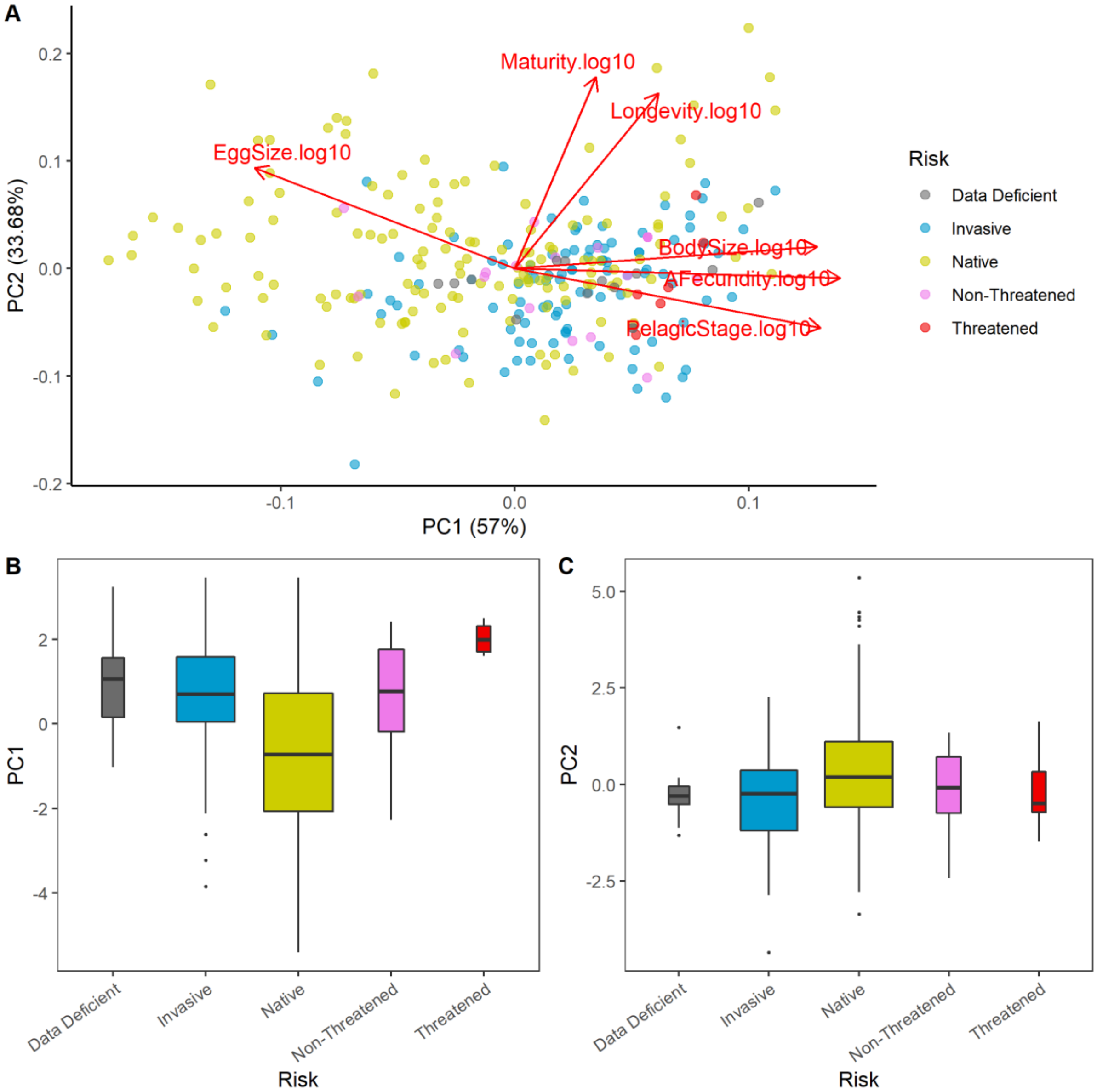


Figure 6: A) Principal Component Analysis (PCA) of 283 bivalve species split by five risk categories (Data Deficient (n= 14), Invasive (n=101), Native (n=143), Non-threatened (n =19) and Threatened (n=6)) defined by the first two principal components (PC1 and PC2). PCA is a form of multivariate data analysis which is used to reduce the dimensionality of the data in order to provide a set of summary indices. Arrows indicate mean loadings (direction and weighting) of each life history trait in the PCA. Each point represents the position of a species within two-dimensional space. B) Boxplot of each risk category against PC1 C) Boxplot of each risk category against PC2. Width of the boxplots are scaled to the number of observations.

In bivalves, 90.7% of variation in life history traits was explained by the first two principal components (PC1 = 57% and PC2 = 33.68%) (Figure 6a). Axis 1 of the PCA was effective in separating species according to large and small body sizes, number of offspring produced (annual fecundity) and pelagic stage duration, while axis 2 of the PCA was effective in separating species according to long and short lifespans and early and delayed maturation (Figure 6a, Table 5). Fecundity, pelagic stage duration and body size were all strongly positively correlated with PC1 (0.97, 0.91 and 0.90, respectively), while egg size was negatively correlated with PC1 (-0.78). Age at maturity and longevity were strongly positively correlated (0.95 and 0.87) with PC2.

Table 5: Summary of Principal Component Analysis (PCA) of trait data for gastropod (n = 1652) and bivalve species (n = 283) split according to risk (Invasive, Native, Data Deficient, Non-threatened and Threatened).

	Gastropods		**Bivalves**	
	PC1	**PC2**	**PC1**	**PC2**
Variation explained (%)	54.4	36.9	57.0	33.7
Trait loadings (%)				
Body Size	23.4	6.0	23.7	0.6
Longevity	27.9	0.5	5.3	37.7
Age at maturity	27.1	3.4	1.7	44.9
Annual Fecundity	11.2	23.1	27.5	0.1
Pelagic Stage Duration	0.1	40.4	24.3	4.3
Egg Size	10.4	26.7	17.6	12.4

Table 6: Results of the Phylogenetic Least Squares Models showing the relationship between Risk and PC1 and Risk and PC2 for both gastropod and bivalve species. Models are fitted with lambda = 'ML' (Maximum likelihood) and without an intercept.

Gastropods

	Risk	Coefficient Estimate	S.E	t-value	Pr(>|t|)	p-value	Model adjusted R^2	Lambda [ML]	Lambda 95% CI (lower, upper)
PC1						0.054	0.004	0.811	0.773, 0.845
	Data Deficient	-0.763	0.662	-1.151	0.250				
	Invasive	-0.734	0.642	-1.143	0.253				
	Native	-0.582	0.637	-0.913	0.361				
	Non-Threatened	-0.493	0.654	-0.754	0.451				
	Threatened	-0.802	0.663	-1.210	0.227				
PC2						0.012	0.006	0.802	0.755, 0.840
	Data Deficient	-0.313	0.696	-0.450	0.653				
	Invasive	-0.736	0.673	-1.093	0.274				
	Native	-0.847	0.668	-1.269	0.205				
	Non-Threatened	-0.598	0.687	-0.871	0.384				
	Threatened	-0.168	0.670	-0.241	0.810				

Bivalves

	Risk	Coefficient Estimate	S.E	t-value	Pr(>|t|)	p-value	Model adjusted R^2	Lambda [ML]	Lambda 95% CI (lower, upper)
PC1						0.011	0.034	0.626	0.407, 0.802
	Data Deficient	-0.532	0.736	-0.723	0.470				
	Invasive	0.188	0.549	0.343	0.732				
	Native	-0.442	0.545	-0.811	0.418				
	Non-Threatened	0.121	0.658	0.185	0.854				
	Threatened	1.435	1.029	1.39	0.164				
PC2						0.138	0.011	0.621	0.356, 0.842
	Data Deficient	-0.092	0.626	-0.147	0.883				
	Invasive	-0.100	0.466	-0.215	0.830				
	Native	0.319	0.463	0.689	0.492				
	Non-Threatened	-0.144	0.559	-0.258	0.800				
	Threatened	0.921	0.876	1.051	0.294				

PGLS analysis showed that in gastropods there is a strong phylogenetic signal in both PC1 and PC2 (λ = 0.811 and 0.802, respectively; Table 6). Accounting for this phylogenetic structure, both PC1 (which distinguishes between species with long and short lifespans and early and delayed maturation) and PC2 (which separates species according to egg size and pelagic stage duration) were significantly associated with risk status (p = 0.05 and 0.01, respectively), although in both cases the models have very low explanatory power (adjusted R^2

= 0.004 and 0.006, respectively; Table 6). The largest differences in PC1 values were between threatened and non-threatened species, while native and threatened gastropods differ the most with respect to PC2, although none of the coefficients individually differed significantly from 0 (Table 6). For both PC1 and PC2, however, invasive and native species differed very little.

PGLS analysis further showed there to also be a moderate phylogenetic signal in both PC1 and PC2 for bivalves (λ = 0.626 and 0.621, respectively; Table 6), although slightly less so than for gastropods. Accounting for this phylogenetic structure, only PC1 (which separates species according to large and small body size, number of offspring produced and pelagic stage duration) was significantly correlated with risk status ($p = 0.01$), while this was not the case for PC2 ($p = 0.14$). In both cases, however, the models have low explanatory power (adjusted $R^2 = 0.034$ and 0.011; Table 6). Although PC1 values differed the most between data deficient and threatened species, large differences were also observed between both threatened and non-threatened species and invasive and native species (Table 6). With regards to PC2, non-threatened and threatened species differed the most, although again, none of the coefficients individually differed significantly from 0 (Table 6). Large differences were also observed between invasive and native bivalves with regards to PC2 (Table 6).

3.4.2. Importance of age at maturity and annual fecundity in driving extinction and invasion risk

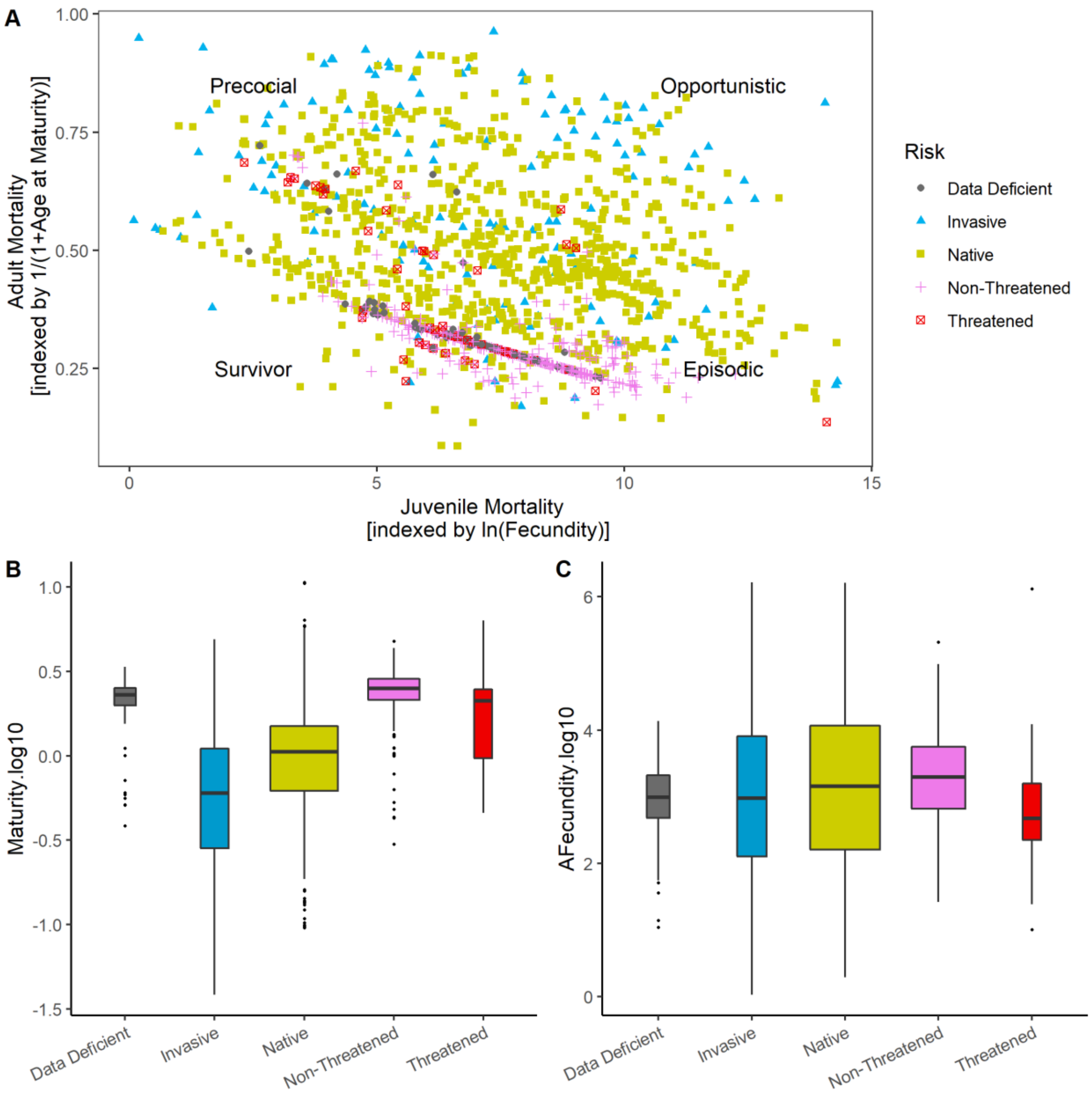


Figure 7: A) The relationship between life history and Precocial, Opportunistic, Survivor and Episodic (POSE) category for 182 families of gastropods representing 1652 species. The natural log of fecundity (x-axis) is assumed to correlate with juvenile mortality. The inverse of age at maturity, standardized between 0 and 1, reflects adult mortality risk, as increased adult mortality leads to earlier maturation (Dulvy & Kindsvater 2017). Each point represents a species, and the colour corresponds to risk category split by Data Deficient, Invasive, Native, Non-threatened (IUCN categories of Least Concern or Near Threatened) and Threatened (IUCN categories of Vulnerable, Endangered and Critically Endangered). B) Boxplots showing the relationship between risk status and age at maturity. C) Boxplots showing the relationship between risk status and annual fecundity. Width of the boxplots are scaled to the number of observations.

Age of maturity contributes considerably, and is highly correlated, to PC1 for gastropods and PC2 for bivalves, and annual fecundity contributes considerably, and is highly correlated, to PC2 for gastropods and PC1 for bivalves (Figures 5 and 6, Table 5), supporting H1. I investigate this further within the POSE framework which explicitly considers both maturity (the inverse of which reflects adult mortality) and fecundity (the natural log of which is assumed to correlate with juvenile mortality). Figure 7a and 8a highlight the disparity between life-history-driven sensitivity to extinction and risk category. Almost all non-threatened gastropods are positioned between survivor and episodic life history strategies and are therefore characterized by being larger bodied, long-lived species which mature later in life, relative to other gastropods (Figure 7a, b). Comparatively, threatened gastropods, in relation to other species in my dataset, are mainly positioned near the centre of the plot, with several falling close to the categories of Precocial and Survivor, but none near Opportunistic. This indicates that threatened gastropods are typically characterised by the production of few, large offspring (as shown in Figure 7c where they have the lowest fecundity of any risk category), highlighting an extreme parental investment in their offspring, again supporting H2 for gastropods. Native gastropods occupy all life history strategies available while many, but not all, invasive gastropods are positioned around and between Precocial and Opportunistic life history strategies (Figure 7a), confirming H2 for gastropods.

In bivalves (Figure 8a), threatened species, when scaled to the range of my data, are exclusively positioned between the opportunistic and episodic life history strategies, suggesting the production of many, small offspring (as supported by Figure 8c in which threatened bivalves have the highest annual fecundity relative to other risk categories). Of the two life history strategies, threatened bivalves which fall into the episodic category typically have the lower compensatory capacity due to their slower growth rate and later maturation. Figure 8b confirms that due to threatened bivalves typically maturing later in life than other risk categories, it is likely they fall more within the episodic than opportunistic life history strategy, supporting H2 for bivalves. Similarly, non-threatened bivalves, although closest to the opportunistic life history strategy, typically lie in the centre of the plot relative to other bivalves. Considering invasive bivalves, Figure 8a shows that, like threatened bivalves, these tend to cluster between episodic and opportunistic life history strategies relative to other bivalves, with a few positioned near the precocial life history strategy but none considered to express a survivor life history. Figure 8b confirms that invasives mature earlier in life than any other risk category (apart from data deficient) and as shown in Figure 8a, are therefore, more commonly associated with an opportunistic life history strategy, confirming H2 for bivalves. As was the case with native gastropods, native bivalves also tend to broadly occupy all life history strategies,

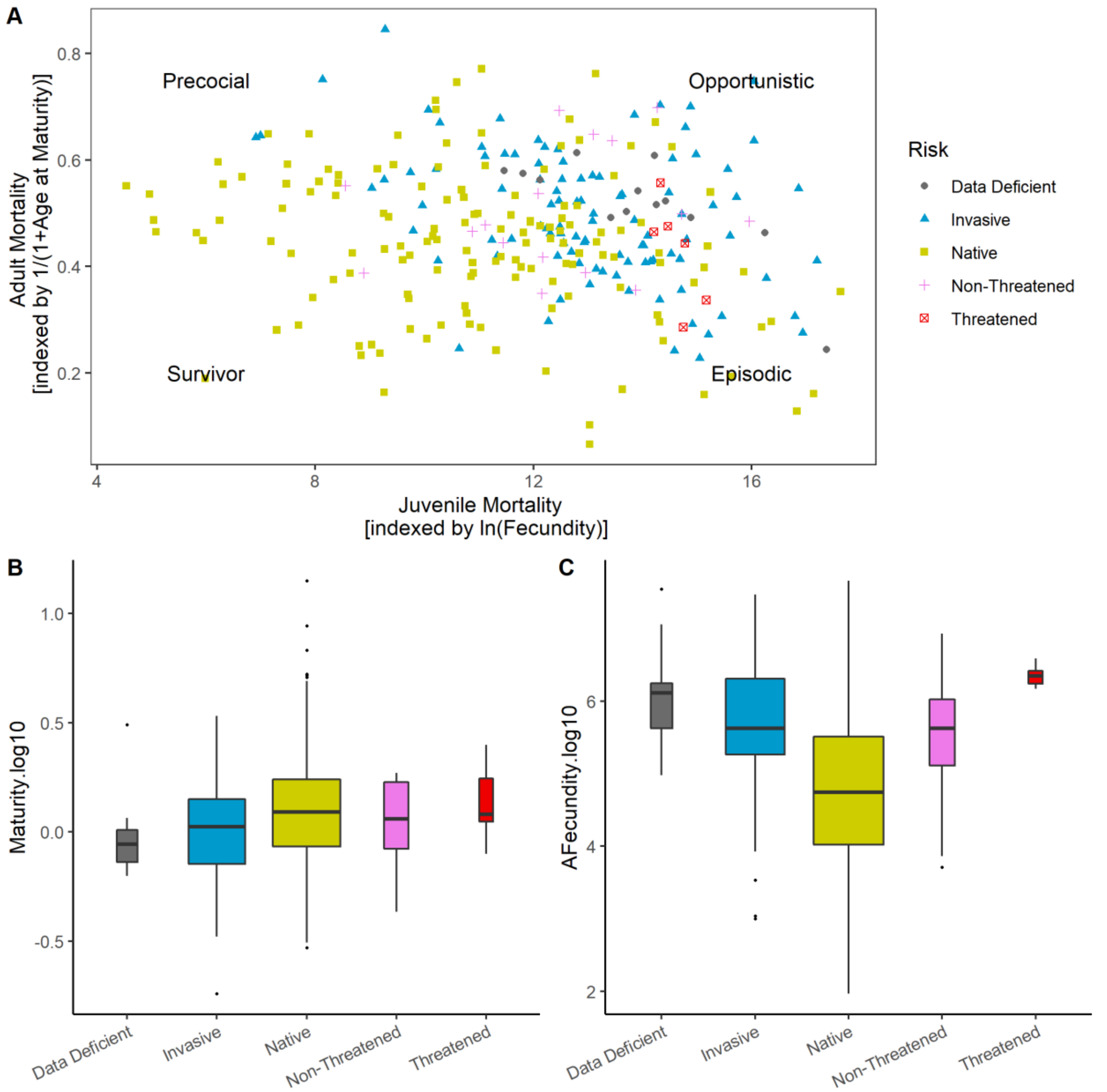


Figure 8: A) The relationship between life history and Precocial, Opportunistic, Survivor and Episodic (POSE) category for 56 families of bivalves representing 283 species. The natural log of fecundity (x-axis) is assumed to correlate with juvenile mortality. The inverse of the age at maturity, standardized between 0 and 1, reflects the adult mortality risk, as increased adult mortality leads to earlier maturation (Dulvy & Kindsvater 2017). Each point represents a species and the colour corresponds to risk category split by Data Deficient, Invasive, Native, Non-threatened (IUCN categories of Least Concern or Near Threatened) and Threatened (IUCN categories of Vulnerable, Endangered and Critically Endangered). B) Boxplots showing the relationship between risk status and age at maturity. C) Boxplots showing the relationship between risk status and annual fecundity. Width of the boxplots are scaled to the number of observations.

Table 7: Results of the Phylogenetic Least Squares Models showing the relationship between Risk and Age at Maturity and Risk and Annual Fecundity for both gastropods and bivalve species. Models are fitted with lambda = 'ML' (Maximum likelihood) and without an intercept.

Gastropods									
	Risk	Coefficient Estimate	S.E	t-value	Pr(>|t|)	p-value	Model adjusted R^2	Lambda [ML]	Lambda 95% CI (lower, upper)
Age at Maturity						0.019	0.006	0.769	0.723, 0.809
	Data Deficient	-0.038	0.091	-0.417	0.677				
	Invasive	-0.086	0.088	-0.970	0.332				
	Native	-0.045	0.087	-0.519	0.604				
	Non-Threatened	-0.009	0.090	-0.104	0.917				
	Threatened	-0.035	0.092	-0.384	0.701				
Annual Fecundity						0.008	0.007	0.824	0.786, 0.857
	Data Deficient	3.023	0.502	6.020	<0.001				
	Invasive	3.223	0.487	6.615	<0.001				
	Native	3.301	0.484	6.820	<0.001				
	Non-Threatened	3.245	0.496	6.539	<0.001				
	Threatened	2.897	0.502	5.766	<0.001				
Bivalves									
	Risk	Coefficient Estimate	S.E	t-value	Pr(>|t|)	p-value	Model adjusted R^2	Lambda [ML]	Lambda 95% CI (lower, upper)
Age at Maturity						0.192	0.008	0.479	0.185, 0.763
	Data Deficient	0.002	0.111	0.019	0.985				
	Invasive	0.057	0.074	0.766	0.445				
	Native	0.120	0.074	1.634	0.104				
	Non-Threatened	0.050	0.095	0.524	0.601				
	Threatened	0.272	0.151	1.804	0.072				
Annual Fecundity						0.033	0.025	0.696	0.489, 0.844
	Data Deficient	4.856	0.453	10.719	<0.001				
	Invasive	5.308	0.355	14.958	<0.001				
	Native	4.957	0.354	13.996	<0.001				
	Non-Threatened	5.203	0.413	12.587	<0.001				
	Threatened	5.730	0.640	8.948	<0.001				

PGLS analysis showed that in gastropods there is a strong phylogenetic signal in both age at maturity and annual fecundity (0.769 and 0.824, respectively; Table 7). Accounting for this phylogenetic structure, both age at maturity and annual fecundity were significantly associated with risk status (p = 0.019 and 0.001 respectively), supporting H1 for gastropods, although in both cases the models have very low explanatory power (adjusted R^2 = 0.006 and 0.007, respectively; Table 7). Although the largest differences in age at maturity values were between invasive and non-threatened species, both threatened and non-threatened species and invasive and native species also showed large differences in coefficient estimates (-0.035 and -0.009, -0.086 and -0.045, respectively). With regards to annual fecundity native and threatened gastropods differed the most, with large differences also being seen between threatened and non-threatened species, although none of the coefficients individually differed significantly from 0 (Table 7). With regards to annual fecundity, invasive and native gastropods differed very little with coefficient estimates of 3.2 and 3.3, respectively (Table 7).

PGLS analysis further showed that in bivalves there is also a moderate phylogenetic signal with regards to both age at maturity and annual fecundity, particularly the latter (0.479 and 0.696, respectively; Table 7), though both are lower than in gastropods. Accounting for this phylogenetic structure, only annual fecundity was significantly correlated with risk status ($p = 0.03$), partially supporting H1 for bivalves, although for both age at maturity and annual fecundity the models have very low explanatory power (adjusted R^2 = 0.008 and 0.025, respectively; Table 7). The largest differences in both age at maturity values and annual fecundity values were between threatened and data deficient bivalves. Not including data deficient, however, threatened and non-threatened species bivalves differ the most with regards to age at maturity, with large differences also being observed between invasive and native species (Table 7). With regards to annual fecundity moderate differences are apparent between the coefficient estimates of threatened and non-threatened species (Table 7).

Table 8: The most and least threatened and most invasive taxonomic families of gastropods and bivalves of those so far IUCN assessed.

Most Threatened Gastropod Families 1. Deep water sea snails (Provannidae 88%) 2. Deep sea snails/limpets (Peltospiridae (80%) 3. Sea snails (Skeneidae 50%) 4. Nutmeg snails (Cancellariidae 50%)	**Most Threatened Bivalve Families** 1. Pen shells (Pinnidae 100%) 2. Mussels (Mytilidae 14%)
Least Threatened Gastropod Families 1. Aquatic snails (Stenothyridae 80%) 2. Cone snails (Conidae 80%) 3. Nerites (Neritidae 32%) 4. Palmleaf snails (Assimineidae 25%)	**Least Threatened Bivalve Families** 1. Bean clams (Donacidae 80%) 2. True oysters (Ostreidae 17%)
Most Invasive Gastropod Families 1. Dorid nudibranchs (Polyceridae 83%) 2. Sea hares (Aplysiidae 83%) 3. Pyramid shells (Pyramidellidae 43%) 4. Ceriths (Cerithiidae 28%) 5. Predatory sea snails (Muricidae 18%)	**Most Invasive Bivalve Families** 1. Shipworms (Teredinidae 100%) 2. Jewel box clams (Chamidae 100%) 3. Ark clams (Arcidae 56%) 4. Venus clams (Veneridae 48%) 5. Mussels (Mytillidae 44%) 6. True oysters (Ostreidae 40%)

3.5. Discussion

My study is the first to investigate in tandem the drivers of extinction and invasion risk in marine molluscs to determine if they occupy opposite ends of the life-history continuum and whether traits can be used to predict risk status. I observed that while traits themselves were unable to distinguish between different risk categories, there was a considerable phylogenetic component to risk. As such, I found risk status in both bivalves and gastropods to be more driven by phylogeny than by traits, and that while phylogeny may be used to predict risk status in marine molluscs, the inclusion of trait data adds very little to the predictive power of the models. Furthermore, extinction risk and invasiveness of marine molluscs in this study was not randomly distributed across families, but rather certain families contained a larger proportion of threatened and invasive-prone species than others, as has been observed in other studies (Bennet & Owens 1997; Purvis et al. 2000; Wang et al. 2017). For instance, I found that pen shells (*Pinnidae*) are the most threatened bivalve family (Table 8), largely as a result of illegal fishing activities, pollution, habitat loss and their relatively large body size, while the most threatened gastropod families are predominantly deep-water dwelling snails and limpets from the families *Provannidae* and *Peltospiridae*. Least threatened families, in my study, are comprised of clams and oysters for bivalves and venomous predatory cone snails for gastropods (Table 8), owing largely to their wide distribution and abundance, while nudibranchs and sea hares are particularly dominant invasive gastropods (Table 8), likely due to their fast growth and often larger body sizes compared to natives, and shipworms and box clams are the most invasive bivalves, the former likely related to its wood-boring ability.

Considerable evidence now exists to suggest that extinction risk clusters according to phylogeny, more so than simply by chance (Bennet & Owens 1997; Purvis et al. 2000). One of the main explanations for this observation of phylogenetic non-randomness is that members of the same evolutionary lineage share specific endangerment promoting life-histories predisposing them to extinction (Bennet & Owens 1997; Purvis et al. 2000; Wang et al. 2017). Extinction events tends to remove large bodied, long-lived species with slow life histories and small geographic ranges. As many of these extinction-promoting traits demonstrate phylogenetic conservatism (Fritz & Purvis 2010) (whereby they are clustered phylogenetically), it follows that extinction risk also clusters according to phylogeny (Yessoufou & Davies 2016). Phylogenetic selectivity in extinction risk may also arise from geographical patterns of extinction whereby closely related species tend to occur in close geographical proximity and share similar niches and habitats, meaning they will be exposed to similar drivers of decline (Yessoufou & Davies 2016). Furthermore, as IUCN assessments have not been conducted on a phylogenetically random subset of molluscs, the very process of assessing extinction risk is taxonomically biased with regards to well-studied species e.g., those in the genus *Conus* (Peters et al. 2013).

A common approach to determining generalized predictors of risk status is to correlate species' ecological and life history traits with the probability of becoming either extinct or invasive (Carmona et al. 2021). Despite life history traits in my study overall not being very discriminatory between these different risk categories, I did detect, after accounting for shared ancestry, some significant correlations between life history principal components and risk. In gastropods, for instance, PC1 distinguished between species with large and small body sizes, long and short lifespans and early and delayed maturation while PC2 separated species according to egg size and pelagic stage duration. In bivalves, I found that PC1 distinguished between species with varying body sizes, annual fecundities and pelagic stage durations while PC2 was found not to be statistically significant with respect to life history traits. The models, however, showed a low explanatory power (small adjusted R^2 values of less than 0.03 for both gastropods and bivalves) and a moderate-strong phylogenetic signal (lambda values greater than 0.6 for bivalves and 0.8 for gastropods). Previous studies have also found there to be weak correlations between life history traits and extinction risk and invasiveness. Jeschke & Strayer (2006) for instance, found that body size and most life history variables (such as fecundity, offspring size and age at reproduction) were poor predictors of invasion success in vertebrates while Sodhi et al. (2008) found that, despite accounting for phylogeny, only a small degree of the variation in extinction probability in angiosperms could be explained by life history traits.

Despite the caveats of low explanatory power and high phylogenetic signal, I found there to be statistically significant differences between risk status and the traits associated with PC1 and PC2 in gastropods and between risk status and the traits associated with PC1 in bivalves. The first principal component in both gastropods and bivalves splits species according to their body sizes. A larger body size has repeatedly been linked to an elevated extinction risk across multiple taxa (Chichorro et al. 2019; Carmona et al. 2021), including marine fish (Olden et al. 2007), marine invertebrates (Payne et al. 2016), beetles (Seibold et al. 2015), lizards (Tingley et al. 2013), birds (Wang et al. 2017), and mammals (Cardillo et al. 2005). This relationship is likely due to either direct effects (whereby larger species require more resources), as a proxy for other traits (e.g., larger species tend to have slower lifecycles and as such respond more slowly to change) (Carmona et al. 2021) or simply because larger species tend to be hunted more often (Chichorro et al. 2019). Conversely, short generation times and small body sizes are traits commonly linked to increased invasion risk across multiple taxa including reptiles (Tingley et al. 2013), amphibians (Allen et al. 2017), and fish (Grabowska et al. 2015). I observed that in the case of gastropods, invasive species were on average 5% larger than threatened species, whereas for bivalves threatened species were on average 30% larger than invasives.

I further found that both age at maturity and annual fecundity were significantly associated with risk status in gastropods, while only annual fecundity was significantly associated with risk status in bivalves. However, as with the correlation between risk status and principal components, I observed a strong phylogenetic signal and for both traits the models had a very low explanatory power (with adjusted R^2 values of <0.007). Nevertheless, fecundity is another trait often reported to be strongly associated with both extinction and invasion risk (Torchin et al. 2001; Lockwood et al. 2005; Liu et al. 2016; Chichorro et al. 2019; Jelbert et al. 2019). In my study, I observed that invasive and non-threatened gastropods displayed higher average fecundities than did threatened gastropods, while annual fecundity of bivalves was similar for both invasive and threatened species. These results partially mirror those of other studies which suggest that threat status is positively related to reduced fecundity (Böhm et al. 2016; Chichorro et al. 2019) (in the case of gastropods in my study) and longer generation lengths and lifespans (Anderson et al. 2011; Hanna & Cardillo 2013; Chichorro et al. 2019) (as is the case with both threatened gastropods and bivalves in my study). Low fecundity and long lifespans are considered traits which reduce the capability of species to compensate for high mortality rates (Purvis et al. 2000). In the case of invasiveness, previous studies have correlated fast life histories (specifically being short lived and quick maturing) with promoting invasion success in amphibians and reptiles (Allen et al. 2017) by allowing for rapid increases in population size and limiting vulnerability to stochastic events. A successful reproductive strategy is crucial to the success of the establishment stage during the invasion processes (Grabowska et al. 2015) and many studies have identified reproductive traits as predictors of success or failure during this stage (Garcia-Berthou 2007). As was observed in my investigation, however, the relationships between fecundity and intrinsic sensitivity to extinction is weak (this has also been observed in Dulvy et al. 2003 and Dulvy & Kindsvater 2017). This is often reported to be because populations of highly fecund species are more likely to have strong density-independent juvenile mortality (see Kinsdvater et al. 2016., for more information).

An inability to predict invasion or extinction risk using biological and life history traits may indicate that my choice of variables failed to include the main traits driving risk. However, given that the traits I included in the analysis were selected based on those which previous studies have found to be important in independently driving invasion success or extinction risk, this seems unlikely. Alternatively, an important aspect of extinction risk or invasion success is the physical process of threat (e.g., overfishing, water pollution, climate change) or transportation (e.g., an increase in oceangoing vessels covering greater distances, thus connecting multiple environments), and so it could be that these processes are greater drivers of risk irrespective of traits. A third explanation, which supports my results, is that phylogeny is a more dominant driver of extinction risk and invasion success in molluscs than previously thought. While this is likely the case, analysing the environmental context and ecological affinities of threatened and invasive species would also be worthwhile.

The analyses presented here support the previous findings of Jeschke & Strayer (2008), Blackburn & Jeschke (2009), Tingley et al. (2013) and Colautti et al. (2017), that invasive and threatened species are not simply ‘two sides of the same coin’ and the assumption that they lie on opposite ends of a continuum appears to be an oversimplification. I observed for instance, that with regards to the POSE framework (which explicitly considers the traits of annual fecundity and age at maturation; the former of which was found to differ significantly with risk status in both gastropods and bivalves, and the latter of which differed significantly with risk status in gastropods), that both threatened and invasive bivalves were commonly positioned near opportunistic and episodic life histories while both threatened and invasive gastropods were typically positioned near to the precocial life history strategy, relative to other gastropods. The limited support for the ‘two sides of the same coin hypotheses’ contradicts the cross-continental study of Liu et al. (2017), which investigated freshwater fishes and found mean trait differences between invasive and threatened species, and the US based study of Larson & Olden (2010) which investigated latent extinction and invasion risk of crayfish populations. Discrepancies in evidence for this hypothesis may arise from differences in taxonomic composition (the previous studies considering freshwater fishes and crayfish while my study investigates marine gastropod and bivalve molluscs), the geographical area of the study (global vs regional scales), the statistical approaches taken to compare species (e.g. multivariate methods vs machine learning algorithms) or the varying definitions of invasive species (e.g. any introduced species or specifically those causing negative impacts).

Although I did not find strong support for the hypothesis that individual traits predispose species to becoming threatened or invasive, or that invasive and threatened species lay at opposite sides of the life-history continuum, I did find that species belonging to different risk categories display contrasting life histories with regards to certain traits and are thus at varying, although not opposite, positions within the POSE framework. For instance, threatened gastropods commonly displayed either precocial or survivor life history strategies relative to other gastropods, and as such typically produced few, large offspring, in addition to having the lowest fecundity of any risk category. These traits may contribute to their higher extinction risk due to an inability to compensate for species loss due to either human driven population declines or environmental change. Conversely, non-threatened gastropods were typically positioned between survivor and episodic life history strategies, therefore being characterised by along lifespan and late maturity. Non-threatened gastropods also displayed the highest fecundity of any risk category, likely contributing to their lower extinction risk. Invasive gastropods and bivalves in my study are relatively opportunistic meaning that a key characteristic is their early maturity and high fecundity. Typically, species which mature earlier in life can capitalize on sudden favourable environmental conditions, which aid the establishment of invasives. Threatened bivalves on the other hand, were typically episodic and matured later in life than any other risk category. As such threatened bivalves are characterized by high juvenile mortality and low adult mortality and likely display bet-hedging life histories. This reproductive strategy can be quickly overwhelmed by density independent processes such as unfavourable climate and is thus driven largely by environmental variability (Dulvy & Kinsdvater 2017). As demonstrated, the POSE framework provides insights complementary to, and beyond what is gained, from the principal component analysis of life history traits, and allows for connections to be made between life histories and sensitivity to risk even when little is known about a species population biology. Conversely, both non-threatened and native bivalves typically lie at the centre of the plot with the former typically being closer to opportunistic and thus differing from threatened bivalves in terms of their growth rate, body size, maturity, and lifespan. The POSE framework explicitly considers the relationship between species life history traits and the strength of density-dependent regulation of populations (Kindsvater et al. 2016) and explores factors relating to species resilience and compensatory capacity, which is crucial for effective management and conservation.

Considering where a species' life history falls on the POSE spectrum can help to diagnose vulnerability to human exploitation or other drivers of decline and can also show which species may be poised for invasion success. This can be useful particularly for data deficient species. Although the IUCN is the most authoritative organization in classifying species according to a particular extinction risk category, they do not have the time or resources to undertake in depth analyses of all species, meaning inferences have to be made based on phylogeny and life histories. As such, I want to emphasize that conservation and management of marine molluscs should be informed by these life histories and, therefore, call for more studies to investigate extinction risk and invasiveness in tandem to determine to what extent certain life histories mediate extinction probability at low population sizes, or in the case of invasives, what allows these species to overcome the challenges faced by small populations. Future work should incorporate human affiliation and the specific threats faced by species in addition to investigating differences in adaptive plasticity (which has been suggested to help facilitate the spread of invasive species within novel environments (Colautti et al. 2017)).

From a life history perspective, I suggest that management for long-lived marine molluscs should focus on protecting the age classes with the greatest reproductive potential and those most likely to contribute to population fitness (MacArthur 1960). Typically, this means females recently starting to reproduce or juvenile stages with a high per capita survival (Kindsvater et al. 2017). Focus should also be placed on protecting habitats associated with key life stages. With regards to invasive species, I encourage more attention to be given to the dispersal ability of potential invaders when transporting species for use as bait or in the aquarium trade. When it comes to control efforts, I suggest that prioritizing the removal of highly dispersive or highly fecund life stages would be most beneficial (Elofsson & Gren 2014). Future studies should also aim to explore the role of habitat characteristics and biotic resistance which is likely to affect the establishment success of invasive species equally as much as life history traits. Previous studies (Tayeh et al. 2015) have found that life history can evolve quickly during the invasion process and that this is not necessarily in favour of a faster reproductive strategy. As such, I further propose that future studies should investigate species in decline or species undergoing expansions at varying stages of these processes. Increasing the number of species for which adequate trait data is available, ensuring integration of different data sources (Webb & Vanhoorne, 2020; Feng et al. 2021) and improving accessibility of this data is another priority. This would allow for more assessments to be conducted by the IUCN on a wider range of taxa.

3.6. Supporting material

Appendix S3: Complete biological trait dataset of 1935 species used in Chapter 3.

Appendix S4: Biological trait dataset of 689 IUCN Red List Species used in Chapter 3.

4. Global analysis of thermal tolerance, latitude and depth zone of invasive and threatened marine molluscs

4.1. Abstract

Thermal tolerances vary considerably between species and according to latitude and vertical zonation, meaning that the impacts of increasing temperatures are not uniformly distributed within and between communities. Consequently, thermal traits may differ systematically between winners (e.g., non-threatened species, invasive species) and losers (threatened species) as a result of global climate change, however, global reviews across of the relationship between vertical zonation, latitude, and thermal tolerance across different risk groups remains scarce, particularly in marine invertebrates. To address this, I collected environmental data (thermal traits, latitude, and depth), and life history trait data (body size, longevity, maturity, fecundity, pelagic stage duration and egg size) for 1530 marine mollusc species which were classified according to risk status (Invasive, Native, Threatened, Non-threatened and Data Deficient). I used phylogenetic generalized least squares models to test for relationships between a) thermal tolerance breadth and latitude, b) thermal tolerance breadth and maximum temperature, and c) maximum temperature and absolute latitude with primary axis of life history variation. I observed a moderate phylogenetic signal in the relationship between both thermal tolerance breadth and absolute latitude ($\lambda = 0.443$), and thermal breadth and maximum temperature ($\lambda = 0.615$), suggesting that ectothermic species retain their ancestral climatic affinities through evolutionary time, making it difficult for such species to adapt to climates which differ considerable from those inhabited by their ancestors. Controlling for phylogeny, I further found a significant positive correlation between thermal breadth and maximum temperature in both the deep and shallow sea, with this relationship being strongest in shallow water invasive species compared to native or threatened species. My analysis indicates that life-history variation across benthic marine molluscs is largely consistent with Thorson’s rule. In the warmer, lower latitude environments, species which are smaller bodied and produce numerous offspring favoured, whereas in colder environments at higher latitudes, larger bodied species which produce fewer eggs, delay reproduction, and mature later in life are favoured.

4.2. Introduction

Predicting how species and communities will respond to increasing temperatures is key to understanding the wider consequences of global climate change (Webb et al. 2020). Temperature is among the most important abiotic factor in determining a species distribution (Somero 2005), critically influencing its physiology, behaviour, and abundance (Sunday et al. 2011). As temperature shifts further from a species' optimal range, the ability of individuals to grow and reproduce is reduced (Pörtner & Farrell 2008; Crozier & Hutchings 2014). Thermal tolerances and thermal breadths (that is, the range of temperatures at which a species can survive and thrive) vary considerably between species, however, meaning that these impacts are not uniformly distributed within and between communities. A central tenet of macroecology is that physiological processes of organisms are linked to large scale geographic patterns in environmental conditions (Sunday et al. 2011). Species at higher latitudes, for instance, experience greater seasonal variation in temperatures and consequently can withstand greater temperature extremes (Sunday et al. 2011, 2012, 2019). Nearer to the equator, where seasonal variation in temperature is minimal, thermal tolerance breadths are relatively narrow in comparison (Sunday et al. 2011, 2019). In the marine environment, the vertical zonation of species further affects their thermal tolerances, with increasing temperatures likely to first affect species occurring in the upper ocean within coastal areas or on the continental shelf (Brown & Thatje 2014). Such links between physiology and large-scale geography likely also have considerable implications in understanding the relative vulnerability of different species to climate change (Sunday et al. 2011, Parmesan & Yohe 2003).

One consequence of this is that thermal traits (including upper thermal tolerance and thermal breadth) may differ systematically between winners (e.g., non-threatened species, invasive species) and losers (threatened species) in the Anthropocene. For instance, eurythermality, the ability to maintain physiological functions across a wide range of temperatures, is a trait which has been widely theorized as a mechanism of ectotherm invasion success (Bates et al. 2013; Kelley 2014), while stenothermality, the ability to tolerate only small temperature ranges, may be a trait more commonly associated with threatened, endemic, or cold-dwelling species (Somero 2005; Somero 2011). Ultimately, species with a greater ecological generality, and an ability to tolerate more extreme abiotic conditions, have an increased capacity to survive transportation and successfully establish within a novel environment (Bates et al. 2013). Invasive species, therefore, are expected to have a larger thermal breadth, be highly plastic, or have a high adaptive potential when faced with new environments that are climatically different to where they evolved (Zerebecki & Sorte, 2011; Tepolt & Somero 2014; da Silva et al. 2021). As a result of these traits, invasive species are likely to have an increased capacity to cope with a warming climate compared to species with stable or contracting distributions (such as many threatened species) (Bates et al. 2013). Although it is expected that this greater thermal tolerance and larger thermal breadth are cornerstones of an invasive phenotype, the extent to which this is true is not well established empirically (Kelley 2014).

Species with narrow thermal tolerances, on the other hand, are expected to be more vulnerable to climate change. This is likely to be most pronounced for ectotherms in the tropics living near to their upper thermal limits (Sunday et al. 2011; Kellermann et al. 2012, Waldock et al. 2019; Webb et al. 2020) with narrow thermal tolerances or a low capacity to acclimatize to thermal change, and consequently limited latitudinal ranges (Comte & Olden 2016; da Silva et al. 2021; Tepolt & Somero 2014, Zerebecki & Sorte 2011). Thermal tolerances may also influence vulnerability indirectly through correlations with other life history and biological traits such as body size (Rubalacaba & Olalla-Tárraga 2020; Peralta-Maraver & Rezende 2020), growth rate (Angilletta et al. 2004) and reproductive traits (e.g., reproductive mode and fecundity) (Baer et al. 2000; Iossa et al. 2019; Heerwaarden & Sgró 2021; Xing & Zhao 2022).

Whether these expected systematic differences in thermal traits between threatened and non-threatened species are generally observed, however, remains unknown, as few studies have compared the physiological and environmental tolerance of taxonomically similar species that differ in the extent to which they can extend their distributions (Zerebecki & Sorte 2011). In part, this is because of the difficulty in obtaining experimental derivations of thermal tolerance (Eme & Bennett 2009, Comte & Olden 2016). However, there is now good evidence that the "realized thermal niche" of a species - the environmental temperatures at which individuals are actually observed to occur in the wild (Magnuson, Crowder & Medvick 1979) – provides a good proxy for physiological thermal limits, especially in marine species (Sunday et al. 2019, Webb et al. 2020), and metrics derived from species realized thermal niches can be used to predict changes in marine communities at both the species and ecosystem level (Day et al. 2018). This is encouraging as such metrics can be derived from data that is much more widely available, for a far greater range of species, than experimentally derived thermal tolerance limits (Webb et al. 2020).

In this study, I take advantage of the ready availability of realised thermal tolerance estimates to undertake a global analysis of thermal tolerance, latitudinal range and depth zonation of invasive, threatened (those listed as critically endangered, endangered and vulnerable on the IUCN Red List of Threatened Species (IUCN 2022) non-threatened (those listed as near threatened and least concern by the IUCN), 'native' (frequently observed species which are not invasive and have not been Red List assessed), and data deficient marine molluscs. Over 50,000 valid marine mollusc species are recognised (WoRMS Editorial Board 2022), making them the second largest marine animal phylum. In this study, I focus specifically on gastropods and bivalves, two groups of taxa which include some of the most ecologically and economically damaging invasives (Tang & Aldridge 2019) and which have also been more comprehensively IUCN assessed than many other invertebrate groups (Lydeard et al. 2004; Cowie et al. 2017). Gastropods and bivalves provide essential ecosystem services including habitat structuring, food for benthic organisms and purification of water through filtration (Parker et al. 2013), and even sub-lethal impacts on these molluscs due to climate change may have considerable consequences for marine ecosystems (Parker et al. 2013). However, to my knowledge, there are no global reviews that attempt to determine the relationship between vertical zonation, latitude, and thermal tolerance across different risk groups of molluscs, while controlling for phylogeny.

I collated occurrence-derived thermal tolerance traits for 1279 benthic gastropods and 251 benthic bivalve species from 37 orders encompassing 212 invasive alien species and 436 species which have had their conservation status formally assessed by the IUCN, of which 36 are considered to be threatened with extinction. I further classified species into depth strata (shallow and deep sea). I used this dataset to test whether invasive species have a larger thermal breadth, wider latitudinal range, and higher upper thermal limit then either native or threatened species (objective 1). I also examined the relationships between thermal breadth, thermal affinity, maximum thermal limit, latitude, and depth strata, across different species statuses (objective 2). Finally, I used data on mollusc life history traits (see Chapter 2) to explore the relationship between thermal traits and latitudinal distribution with the primary axes of life history variation, with the prediction that larger bodied and slower maturing species will have a lower maximum temperature as theory predicts that organisms should grow to be larger in colder environments (Angilletta et al. 2003; 2004), while fecundity will correlate positively with a higher thermal tolerance as organisms tend to grow and mature faster in warmer environments (Angilletta et al. 2004; 2006) (objective 3). I also predict that, in accordance with

Thorson's Rule, lower latitude species will produce many offspring, smaller eggs and will have longer pelagic stage durations (Thorson 1957).

4.3. Materials and Methods

4.3.1. Biological data

A total of 1530 macrobenthic species were investigated, 1279 gastropods and 251 bivalves from 37 orders, 205 families and 658 genera (see Appendix S5). These species fall into one of five categories according to their distributional status at a global scale. Invasive alien species (n = 212) are those which have been introduced, either accidentally or deliberately, outside of their native range, typically with negative consequences for their recipient environment. The invasive dataset was downloaded from the World Register of Introduced Marine Species on the 1st September 2020 (Rius et al. 2022). The search was completed at the species level selecting for any global origin and any measure of invasiveness. On the same date, the Red List dataset (n = 436) was downloaded from the IUCN Red List of Threatened Species (IUCN 2022) using the advanced search option to select for gastropod and bivalve molluscs from all marine regions. I use the Red List data to classify species into one of three categories; Threatened species (n = 36) which are those listed as Critically Endangered (CR, n = 5), Endangered (EN, n = 10), or Vulnerable (VU, n = 21); Non-threatened species (n = 357) which are those considered to be either Near Threatened (NT, n= 6) or Least Concern (LC, n = 351); and Data Deficient species (DD, n = 43) which are those with insufficient information for an adequate assessment of conservation status. The final group of species I term 'Native species' (n = 882) which includes species which are widespread and/or frequently observed, but which are not invasive and have not been Red List assessed. The native species dataset which was compiled on the 13th October 2020 by downloading accepted marine gastropod and bivalve species across all marine regions with the greatest number of occurrence records from the Ocean Biodiversity Information System (OBIS 2022). This method of selecting native species minimises the chance of including species that would be classified as threatened if formally IUCN assessed, as species with many distribution records are more likely to be non-threatened and threatened (albeit this trend is rather weak; Webb & Vanhoorne 2020) Additionally, any native species which already occurred on the Invasive, Threatened or Non-threatened lists were excluded(Webb & Vanhoorne 2020). Given, that the goal of this investigation is to identify broad relationships and signals of status, this study should thus be robust to a few outlying cases where species groups overlap. All species names were matched to WoRMS (WoRMSEditorialBoard, 2022), allowing us to assign a valid WoRMS Aphia ID to each species.

4.3.2. Occurrence records

Data on where marine species occur can be found using the Ocean Biodiversity Information System (OBIS 2022), a large, open access, global repository of >100M occurrence records of >120,000 marine species. Each occurrence record is accompanied by spatial (longitude and latitude) and temporal (month, year) information, with depth also sometimes being available. Occurrence records for each species were obtained from OBIS using the robis package v2.1.10 (Provoost & Bosch 2019). Only species with ≥ 1 occurrence record were kept for the purpose of this study (hence only 1530 species, rather than the 1935 species in Chapter 2) Of these 1530 species, 42 Red List species (CR n =1, EN n= 1, VU n = 6, LC n = 26, NT n =2, DD n = 6), and 16 invasive species have only 1 record. Of the whole dataset of 1530 species, 87% have ≥ 10 records and 70% have ≥ 100 records, including all native species (Table 9). In total, across the 1530 species, there were 1,768,647 occurrence records.

Table 9: Summary of OBIS occurrence records available for the 1530 marine molluscs included. Both total number and percentages (in parenthesis) are shown.

	<10 records	≥10 records	≥100 records	≥500 records	≥1000 records	Total
Invasive	43 (20%)	169 (80%)	106 (50%)	37 (18%)	22 (10%)	212
Native	0 (0%)	882 (100%)	882 (100%)	387 (44%)	216 (25%)	882
Threatened	18 (50%)	18 (50%)	5 (14%)	3 (8%)	1 (3%)	36
Non-threatened	116 (32%)	241 (68%)	81 (23%)	13 (4%)	3 (<1%)	357
Data Deficient	28 (65%)	15 (354%)	0 (0%)	0 (0%)	0 (0%)	43
Total	**205 (13%)**	**1325 (87%)**	**1074 (70%)**	**440 (29%)**	**242 (16%)**	**1530**

4.3.3. Environmental data

Occurrence records from OBIS typically lack any in situ measures of environmental temperature, so I used the workflow derived by Webb et al. (2020) to obtain occupancy-derived thermal affinities by matching OBIS occurrences to the Bio-ORACLE (Assis et al. 2018; Tyberghein et al. 2012) global sea bottom temperature layers using the sdmpredictors package v0.2.8 (Bosch 2018) to import the temperature data as raster layers in R v4.2.1 (R Core Team

2022). The full workflow was implemented using the tidyverse v1.2.1 suite of packages (Wickham 2017). Summary statistics were then derived which describe the realized thermal affinity of each species. I calculated a range of measures of 'thermal affinity' including measures of both central tendency and upper and lower bounds of the temperatures at which species have been recorded to occur. Specifically for each species I calculated the mean, minimum, maximum, median, and 5th and 95th quantiles of each temperature measure. I used sea bottom temperature as species in this study are all benthic according to WoRMS. I used the Bio-ORACLE layers maximum sea water temperature at mean bottom depth, mean sea water temperature at mean bottom depth, and minimum sea water temperature at mean bottom depth (SBT, °C, mean from monthly climatologies 2002-2014 at mean bottom depth). Occurrence records for which I could not obtain a temperature match were excluded from calculations of thermal affinity. I further extracted from OBIS the maximum, minimum, mean and range of latitude, longitude, and sample depth for each species. Separate minimum and maximum depth records were also obtained for each species using published literature sources and trait databases, primarily SeaLifeBase (Palomares & Pauly 2022) and BIOTIC (Biological Traits Information Catalogue) (MarLIN 2006).

Thermal tolerance breadth was calculated using the 95th quantile for maximum temperature at mean depth minus the 5th quantile for minimum temperature at mean depth while absolute latitude was calculated using the absolute value of mean latitude. Interpretation of any results must, however, take into consideration the measurement error associated with thermal breath. Global gridded bathymetry datasets, for instance, fail to incorporate any subgrid scale variation in depth and temperature, as a result there are likely to be inherent and unresolvable measurement errors in occurrence records which result in imperfect values for temperature at depth points. These errors are likely to be more pronounced in studies of deep-sea and benthic species rather than pelagic species.

Species were also split into one of two depth zones depending on their upper depth limit. Shallow sea species were those which had a minimum depth of ≤100 meters, while deep-sea species had a minimum depth of >100 meters. Of the 1530 species, 94% occurred in the shallow sea with 6% in the deep sea (84% and 16% for data deficient species, 98% and 2% for invasive species, 96% and 4% for native species, 92% and 8% for non-threatened species and 50% and 50% for threatened species). See Figure S4 of the Supplementary Material for the relationship between the minimum depths of OBIS generated depths and minimum depths of literature generated depths which shows a strong correlation. For the purpose of this study, the literature generated depths are used for any measure of minimum depth as they incorporate expert judgement which likely helps to overcome sampling biases in OBIS occurrence records. See also Figure S5 for the number of OBIS occurrence records against both thermal breadth and maximum temperature, split by risk category. Figure S5 highlights that native species typically have the greatest number of occurrence records in OBIS and that all risk categories display a wide range of maximum temperatures and most risk categories, except for threatened, display a wide range of thermal breadths.

4.3.4. Trait data

As I wanted to explore the relationship between thermal tolerance and biological and life history traits the following six traits were included in the dataset for each species: body size (in cm, defined as the maximum linear dimension), lifespan (defined as the maximum number of years an organism lives), age at maturation (the time taken for an organism to become sexual mature, in years), annual fecundity (defined as the total number of eggs or offspring produced in one year), egg size (defined as the mean diameter of mature ovarian oocytes in micrometres), and pelagic stage duration (the length of time offspring spend in the water column before settling, in days). Life history and biological traits were collected from a variety of online published sources (Chapter 2). For invasive species this included trait databases such as BIOTIC (Biological Traits Information Catalogue) (MarLIN 2006), NEMESIS (National Exotic Marine and Estuarine Species Information) (Fofonoff et al. 2018), CABI (Invasive Species Compendium) (CABI 2022) and SeaLifeBase (Palomares & Pauly 2022). For Red List species the IUCN Red List of Threatened Species (IUCN 2022) and The Conus Biodiversity Website (https://biology.burke.washington.edu) proved useful, while for native species GBIF (the Global Biodiversity Information Facility) (https://www.gbif.org), BIOTIC, The Natural History Museum of Wales (https://naturalhistory.museumwales.ac.uk) and the Animal Diversity Web (Myers et al. 2022)) were frequently consulted. In addition, data from a large range of dispersed expert knowledge within both published and unpublished literature proved useful in filling all three datasets.

Similar to other studies using biological and life-history traits (Tyler et al. 2012; Liu et al. 2016), I initially lacked a complete trait dataset, and so I used imputation to fill gaps, as documented fully in Chapter 2. Briefly, in order to complete the datasets Trait Explorer (https://www.marine-ecosystem.org.uk/Trait_Explorer) was used to fill in the gaps by applying "automated expert judgement", to estimate missing trait values based on their taxonomic relationships and patterns of covariation between traits (see Bruggeman et al. 2009 for a full explanation of the methods). Following this extrapolation additional ground-truthing was performed ensuring for example that age of maturity is always less than lifespan. The dataset used in this study is fully documented in the University of Sheffield's Online Research Data repository (Appendix S5).

4.3.5. Data Analysis

Statistical analysis was carried out in R version 4.2.1. (R Core Team 2021). I relied on phylogeny from the Open Tree of Life using the 'rotl' package (Michonneau et al. 2016) which produces branched and rooted phylogenetic trees built by combining taxonomic information with published phylogenies. After dropping unmatched taxa 1382 molluscs were included in the phylogenetic analysis. For these species branch lengths were computed using the Grafen method (see Grafen 1989 for more details). Although these are not definite phylogenies, they provide a useful framework, and the comparative analysis I conduced are robust to small inaccuracies in phylogeny (Symonds & Blomberg 2014).

As species are not independent data points for analysis due to a shared evolutionary history, generalized least squares models which incorporated phylogeny (PGLS) were used to investigate the relationship between both species' environmental tolerance traits and risk status, to address Objectives 1 and 2 and species' environmental tolerance traits and life-history traits, in order to address Objective 3. PGLS analysis accounts for the non-independence of data due to shared ancestry (Pagel 1999; Freckleton et al. 2002) and fits a linear regression to investigate the impact of one or more predictor variables on a single response variable while controlling for potential phylogenetic signal in the response. I followed Revell (2010), Böhm et al. (2017) and Wang et al. (2017) and optimized Pagels (λ), a branch length transformation indicating the strength of the phylogenetic signal, in each PGLS model using the maximum likelihood method (lambda = "ML"). Models were run without an intercept to determine the coefficient for each risk level.

Four PGLS models were run. I began the analysis by fitting Model 1 to investigate the relationship between thermal tolerance breadth, risk, depth, and absolute latitude to address objective 1:

Thermal tolerance breadth ~ Risk + Depth + Absolute latitude + Risk : Absolute latitude + Depth : Absolute latitude + Risk : Depth + Risk : Depth : Absolute latitude

Model 2 was then used to explore the relationship between maximum temperature, risk, depth, and thermal tolerance to address objective 2:

Thermal tolerance breadth ~ Risk + Depth + Maximum temperature + Risk : Maximum temperature + Depth : Maximum temperature + Risk : Depth + Risk : Maximum temperature : Depth

To explore the relationship between thermal traits and latitudinal distribution with primary axis of life history variation (PC1 and PC2), I ran two PGLS models. Model 3 investigated the relationships between maximum temperature, risk, depth, PC1 and PC2:

Maximum temperature ~ Risk + PC1 + PC2 + Depth + Risk : PC1 + Risk : PC2 + Risk : Depth + Depth : PC1 + Depth : PC2 + Risk : Depth : PC1 + Risk : Depth : PC2

Model 4 investigated the relationships between absolute latitude, risk, depth, PC1 and PC2:

Absolute latitude ~ Risk + PC1 + PC2 + Depth + Risk : PC1 + Risk : PC2 + Risk : Depth + Depth : PC1 + Depth : PC2 + Risk : Depth : PC1 + Risk : Depth : PC2

The function “pgls” was used within the package “caper” to run the models (Orme et al. 2013). This function has been found to outperform other comparative methods when the phylogenetic tree includes a large number (>100) taxa (Graber 2013; Caviedes-Solis et al. 2020). For visualisation of the model outputs, I refitted the models using the function ‘gls’ within the package “nlme” (Pinheiro et al. 2013), with phylogenetic distances determining the variance-covariance matrix. Coefficient estimates are effectively identical using the two approaches, however the gls method could be plotted using the ggeffects package (v1.1.2.1) (Lüdecke 2018).

4.4. Results

4.4.1. Thermal tolerance breadth and absolute latitude if invasive and threatened species

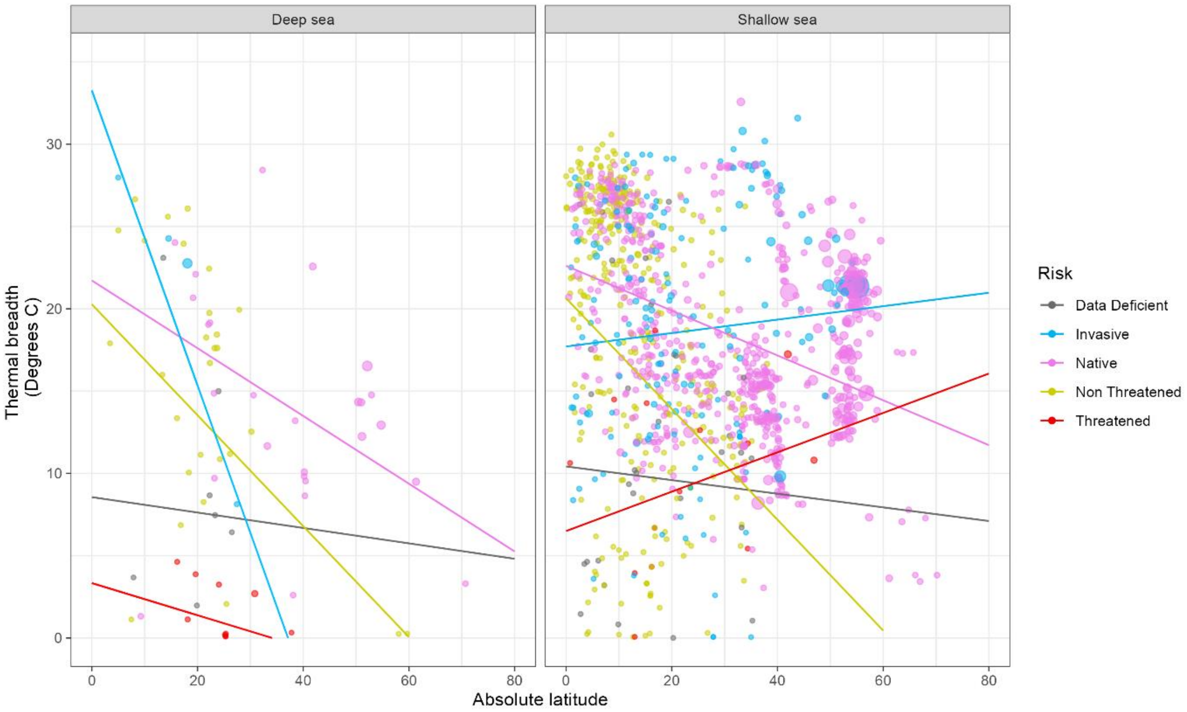


Figure 9: Thermal breadth against absolute latitude, colour coded for each risk level and split by depth strata. Lines show fits from a generalized least squares model which accounts for phylogeny. Thermal breadth is calculated using the 95th quantile of maximum temperature at mean depth minus the 5th quantile minimum temperature at mean depth. Points are scaled to the number of OBIS occurrence records per species.

Overall, model 1 (fitted in Figure 9) was highly significant ($F_{19, 1301} = 16.6$, $\lambda = 0.443$, adjusted $R^2 = 0.183$, p = < 0.0001) (Table 10). There was a significant relationship between thermal tolerance breadth and absolute latitude ($F_{19, 1301} = 102.5$, $p < 0.0001$), between thermal tolerance breadth and depth strata (($F_{19, 1301} = 17.3$, $p < 0.0001$), and between thermal tolerance breadth and risk ($F_{19, 1301} = 29.8$, p = < 0.0001) with a steeper negative slope in deep sea invasive species (-0.90 ± 0.54) and non-threatened species (-0.34 ± 0.40) compared to native (-0.20 ± 0.40) and threatened species (-0.10 ± 0.52) (which are all also negative) (Table 10). There was also a steeper negative slope in shallow sea non-threatened species (-0.34 ± 0.40) compared to all other risk categories, particularly in comparison to threatened species which had a strong positive slope (0.12 ± 0.52). Similar differences were obsered between invasive and native species, the former of which had a positive slopes (0.04 ± 0.54), while the latter a negative slope (-0.13 ± 0.40. There were further significant interactions between risk and absolute latitude with thermal tolerance breadth ($F_{19,\ 1301}$ = 14.9, p = < 0.0001) (Table 10). At low latitudes in the deep sea, threatened species typically had the lowest thermal breadth (Figure 9) and this declined with increasing latitude (slope of -0.10 ± 0.52), whereas in the shallow sea, the thermal tolerance of threatened species increased with absolute latitude (slope = 0.12 ± 0.52). There was a negative relationship between thermal tolerance and absolute latitude in both deep sea (-0.21 ± 0.40) and shallow sea native species (-0.14 ± 0.40). The PGLS analysis showed a moderate phylogenetic signal in the relationship between thermal breadth and absolute latitude (λ = 0.443), however the model does have relatively low explanatory power (adjusted R^2 = 0.183) (Table 10).

Table 10: Results of the Phylogenetic Least Squares Model showing the relationship between thermal tolerance breadth, risk, depth, and absolute latitude. Models are fitted with lambda = ‘ML’ (Maximum likelihood) and without an intercept.

	Coefficient estimate	**SE**	**t-value**	**Pr(>|t|)**	**P-value**	**Model adjusted R^2**	**Lambda [ML]**	**Lambda 95% CI (lower, upper)**
Thermal tolerance breadth ~					<0.001	0.1833	0.443	0.123, 0.700
Data Deficient	8.558	8.363	1.023	0.306				
Invasive	33.270	7.177	4.635	0.000				
Native	21.722	3.948	5.502	0.000				
Non-Threatened	20.274	3.709	5.466	0.000				
Threatened	3.336	8.881	0.376	0.707				
Shallow Sea	1.863	8.193	0.227	0.820				
Absolute Latitude	-0.047	0.389	-0.120	0.904				
Invasive : Absolute Lat	-0.849	0.538	-1.577	0.115				
Native : Absolute Lati	-0.159	0.397	-0.401	0.689				
Non-threatened : Absolute Lat	-0.290	0.402	-0.721	0.471				
Threatened : Absolute Lat	-0.051	0.516	-0.099	0.921				
Shallow Sea : Absolute Lat	0.005	0.401	0.013	0.989				
Invasive : Shallow Sea	-17.425	10.670	-1.633	0.103				
Native : Shallow Sea	-0.973	8.802	-0.111	0.912				
Non-threatened : Shallow Sea	-1.497	8.593	-0.174	0.862				
Threatened : Shallow Sea	1.297	12.402	0.105	0.917				
Invasive: Shallow Sea : Absolute Lat	0.932	0.548	1.701	0.089				
Native: Shallow Sea : Absolute Lat	0.064	0.409	0.157	0.875				
Non-threatened: Shallow Sea: Absolute Lat	-0.005	0.415	-0.012	0.991				
Threatened: Shallow Sea : Absolute Lat	0.212	0.542	0.391	0.696				

4.4.2. Maximum temperature and thermal tolerance breadth of invasive and threatened species

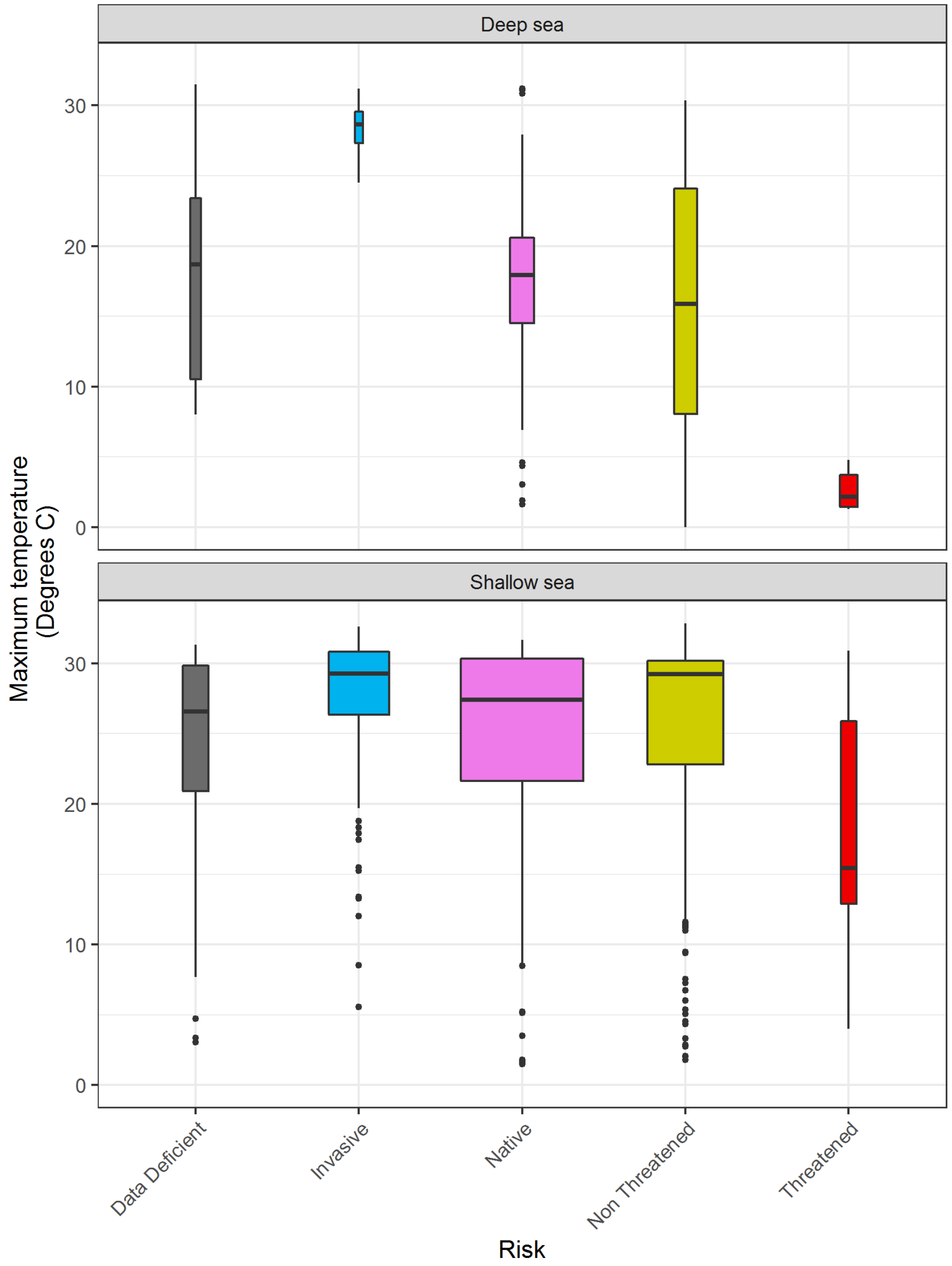


Figure 10: Boxplots showing the relationship between risk status and maximum temperature at which a species has been recorded to occur (95th quantile), for shallow (≤100m) and deep (>100m) water species. Width of boxes are scaled to the number of species.

Threatened species have the lowest maximum temperature in both the deep and shallow sea (median of ~2°C and ~16°C, respectively) and the greatest range of maximum temperatures in the shallow sea (~13°C- 26°C) (Figure 10). In the deep sea, invasives have the highest maximum temperature of ~28°C whereas in the shallow sea, this is true of non-threatened species with a maximum temperature of ~29.5°C, closely followed by invasive species with a maximum temperature of ~29°C. In the deep sea, non-threatened species have the greatest range of maximum temperatures (~8°C-24°C) whereas threatened species have the narrowest range. In the shallow sea, threatened and non-threatened species show the greatest difference in median maximum temperature.

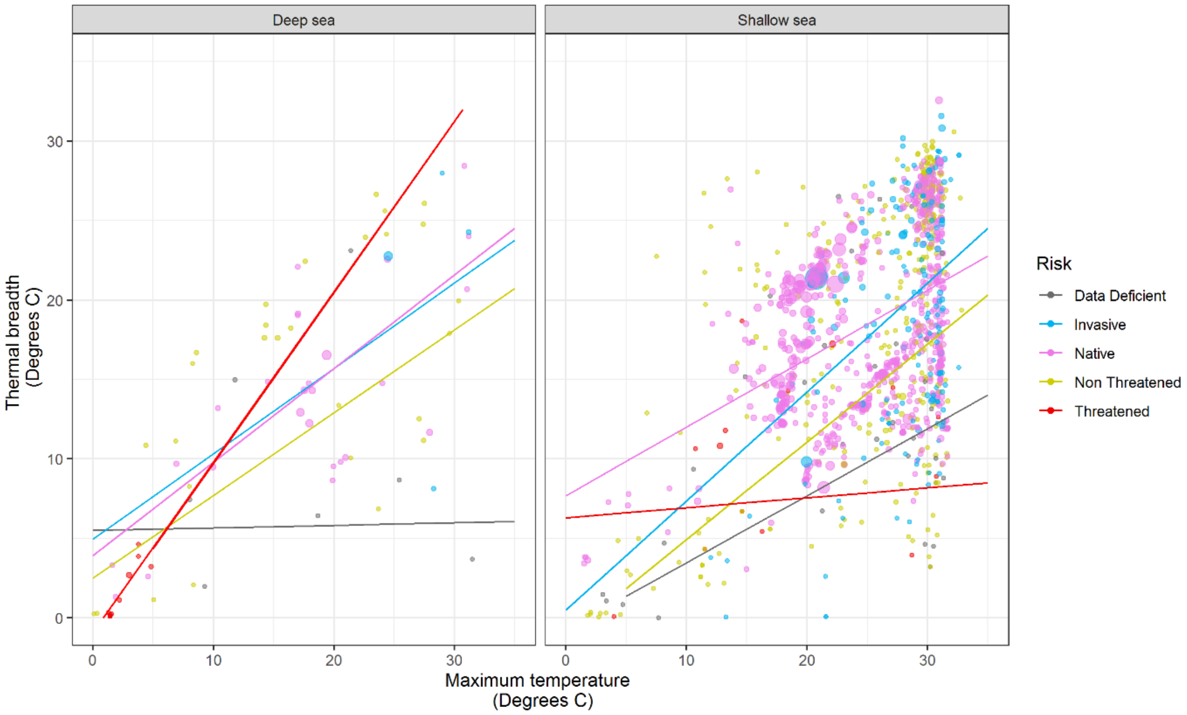


Figure 11: Maximum temperature against thermal breadth, colour coded for each risk status and split by depth strata. Lines show fit from a generalized least squares model which accounts for phylogeny. Thermal breadth is calculated using the 95th quantile of maximum temperature at mean depth minus the 5th quantile minimum temperature at mean depth. Points are scaled to the number of OBIS occurrence records per species.

Overall, model 2 was highly significant ($F_{19, 1301} = 27.06$, $\lambda = 0.615$, adjusted $R^2 = 0.273$, p = <0.0001) (Figure 11, Table 11). There was a significant interaction between both depth strata and thermal tolerance breadth ($F_{19, 1303} = 17.20$, p = <0.0001), and between risk and maximum temperature with thermal tolerance breadth ($F_{19, 1301} = 3.38$, p = 0.009). There was a more positive slope in deep sea threatened species (1.08 ± 1.53) compared to non-threatened species (0.52 ± 0.31) and other risk categories in the deep sea (all of which were also positive). Deep sea invasive and native species, however, showed very similar patterns. With regards to shallow sea species, invasives showed a more positive slope (0.69 ± 1.18) compared to native species (0.43 ± 0.31) and other risk categories (which again all showed positive slopes). Shallow water threatened species showed the shallowest slope (0.06 ± 1.53), compared to shallow water non-threatened species (0.311 ± 0.31). There is a moderate phylogenetic signal in the relationship between thermal breadth and maximum temperature ($\lambda = 0.615$) and, overall, this model had a moderate explanatory power (adjusted $R^2 = 0.273$) (Table 11).

Table 11: Results of the Phylogenetic Least Squares Model showing the relationship between thermal tolerance breadth, risk, depth, and maximum temperature. Models are fitted with lambda = 'ML' (Maximum likelihood) and without an intercept.

	Coefficient estimate	**SE**	**t-value**	**Pr(>|t|)**	**P-value**	**Model adjusted R^2**	**Lambda [ML]**	**Lambda 95% CI (lower, upper)**
Thermal tolerance breadth ~					<0.001	0.2728	0.615	0.327, 0.758
Data Deficient	5.503	6.345	0.867	0.386				
Invasive	4.954	32.552	0.152	0.879				
Native	3.917	3.907	1.003	0.316				
Non-threatened	2.501	3.769	0.664	0.507				
Threatened	-1.041	5.088	-0.205	0.838				
Shallow Sea	-6.251	6.149	-1.017	0.310				
Max Temperature	0.016	0.283	0.057	0.955				
Invasive : Max Temperature	0.521	1.176	0.443	0.658				
Native : Max Temperature	0.573	0.314	1.824	0.068				
Non-threatened: Max Temperature	0.505	0.308	1.639	0.102				
Threatened : Max Temperature	1.060	1.527	0.694	0.488				
Shallow Sea : Max Temperature	0.406	0.304	1.338	0.181				
Invasive : Shallow Sea	1.795	33.138	0.054	0.957				
Native : Shallow Sea	10.028	6.764	1.483	0.138				
Non-threatened : Shallow Sea	2.522	6.644	0.380	0.704				
Threatened : Shallow Sea	13.591	8.526	1.594	0.111				
Invasive : Shallow Sea :Max Temperature	-0.257	1.186	-0.217	0.828				
Native : Shallow Sea : Max Temperature	-0.564	0.335	-1.685	0.092				
Non-threatened : Shallow Sea : Max Temperature	-0.311	0.331	-0.941	0.347				
Threatened : Shallow Sea : Max Temperature	-1.419	1.546	-0.918	0.359				

4.4.3. Environmental correlates of the primary axis of life history variation

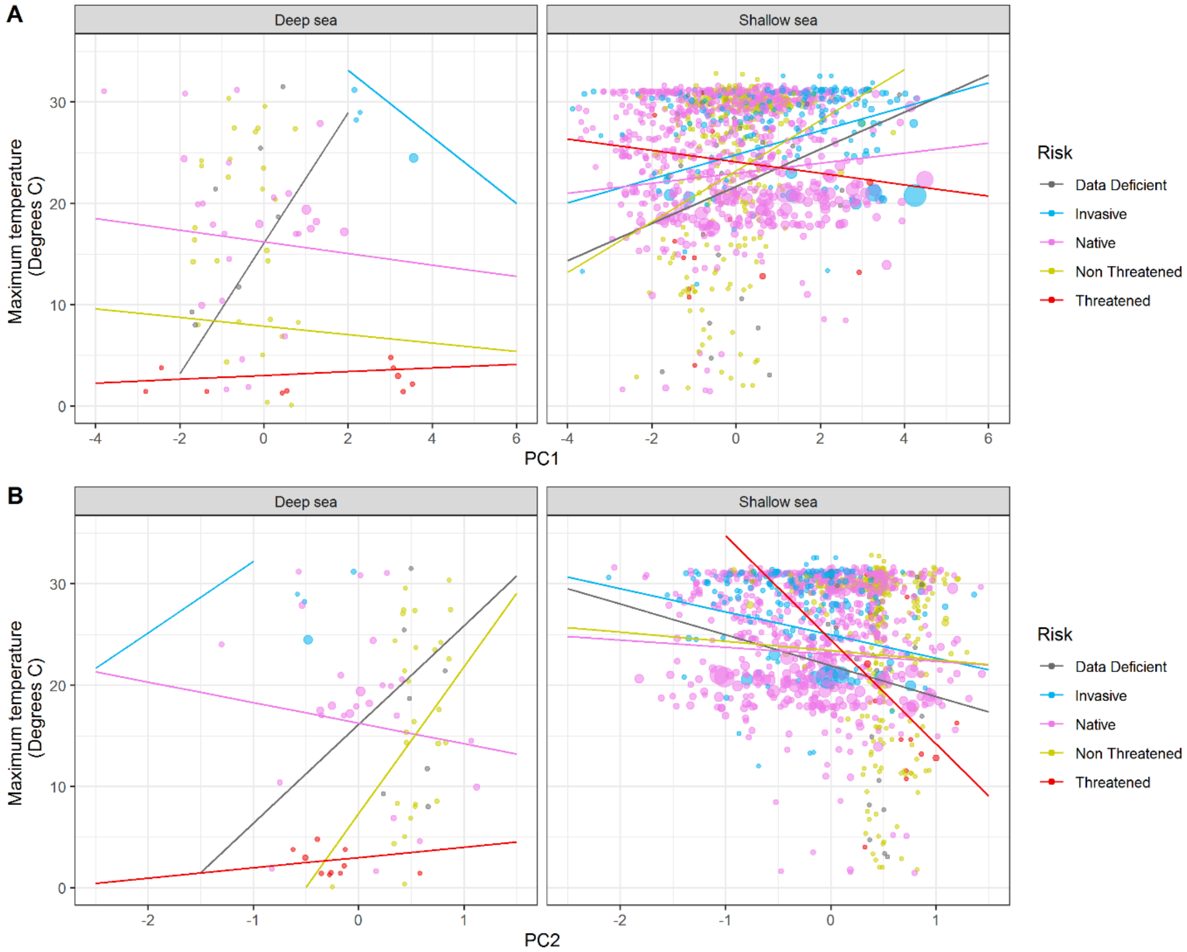


Figure 12: Maximum temperature by risk category, split according to depth strata, against A) PC1 effective in separating species according to annual fecundity and B) PC2 effective in separating species according to pelagic stage duration, age at maturity, longevity, and body size. Points are scaled to the number of OBIS records per species. All fitted with a generalized least squares model which accounts for phylogeny.

Overall, model 3 was highly significant ($F_{29, 1291}$ =10.26, $\lambda = 0.862$, adjusted R^2 =0.169, p = < 0.0001) (Figure 12, Table 12). There were significant relationships between risk and maximum temperature ($F_{29, 1291}$ = 27.30, p = < 0.0001), between depth and maximum temperature ($F_{29, 1291}$ = 57.01, p = <0.0001) and between PC1 (which splits species according to annual fecundity, see Figure S6 and Table S8) and maximum temperature ($F_{29, 1291}$ = 29.37, p = < 0.0001). There were also significant three-way interactions between risk, PC1, depth and maximum temperature ($F_{29, 1291}$ = 2.66, p = 0.0311) and between risk, PC2 (which splits species according to pelagic stage duration, age at maturity, lifespan and body size, see Figure S6 and

Table S8) depth and maximum temperature ($F_{29, 1291}$ = 5.11, p = 0.0004). Likewise, there were also significant interactions between risk and PC1 with maximum temperature ($F_{29, 1291}$ = 11.29, p = <0.0001), and, to a lesser extent, between PC1 and depth strata with maximum temperature ($F_{29, 1291}$ = 4.12, p = 0.0426). With regards to PC1 for deep sea species, only data deficient and threatened species showed a positive slope (0.28 ± 2.80 for threatened species) compared to non-threatened species (0.94 ± 3.00), while the steepest negative slope was in invasive species. However, considering there are very few deep-sea invasive species (n=4), this has resulted in a lack of precision in parameter estimates (95% confidence intervals ranging from -40.49 to 83.84 for invasive deep-sea species on Figure 12b) that are likely further impacted by the phylogenetic correctness in the fitted PGLS. This means that the fitted lines for this group in Figure 12b and 13b specifically are not a good fit to the data and, therefore, this group was no longer considered further in the interpretation of the results Considering PC1 for shallow water species, only threatened species showed a negative slope while the steepest positive slope was in non-threatened species (2.72 ± 2.96). For shallow water species with regards to PC1, invasives showed a more positive slope (1.062 ± 4.95) than native species (0.37 ±2.74). With regards to PC2 for deep sea species, all risk categories, except for natives (-0.38 ± 12.31), showed a positive slope, the steepest of which was in non-threatened species (21.36 ± 12.98) and the shallowest of which was in threatened species (2.99 ± 13.70). Considering PC2 for shallow species, all risk categories showed negative slopes, the steepest of which was in threatened species (-10.58 ± 13.7) and the shallowest of which was in non-threatened species (-0.79 ± 12.98) and native species (-0.24 ± 12.31), compared to invasives (-1.05 ± 16.21) PGLS analysis showed that there is a strong phylogenetic signal in both PC1 and PC2 when considered alongside maximum temperature (λ = 0.862), however again the model has relatively low explanatory power (adjusted R^2 =0.169) (Table 12).

Table 12: Results of the Phylogenetic Least Squares Model showing the relationship between maximum temperature, risk, PC1, PC2 and depth. Models are fitted with lambda = 'ML' (Maximum likelihood) and without an intercept.

	Coefficient estimate	**SE**	**t-value**	**Pr(>|t|)**	**P-value**	**Model adjusted R^2**	**Lambda [ML]**	**Lambda 95% CI (lower, upper)**
Maximum Temperature ~					<0.001	0.169	0.862	0.810, 0.897
Data Deficient	17.769	8.488	2.093	0.037				
Invasive	33.674	11.210	3.004	0.003				
Native	22.986	4.278	5.373	0.000				
Non-threatened	7.365	4.954	1.487	0.137				
Threatened	4.997	4.685	1.066	0.286				
PC1	6.842	2.647	2.585	0.010				
PC2	8.655	12.197	0.710	0.478				
Shallow Sea	5.660	7.453	0.759	0.448				
Invasive : PC1	-7.316	4.952	-1.477	0.140				
Native : PC1	-7.035	2.738	-2.569	0.010				
Non-threatened : PC1	-5.898	2.958	-1.994	0.046				
Threatened : PC1	-6.564	2.796	-2.348	0.019				
Invasive : PC2	-2.187	16.209	-0.135	0.893				
Native : PC2	-9.036	12.313	-0.734	0.463				
Non-threatened : PC2	12.701	12.979	0.979	0.328				
Threatened : PC2	-5.664	13.704	-0.413	0.679				
Invasive : Shallow Sea	-11.212	12.803	-0.876	0.381				
Native : Shallow Sea	-0.655	7.513	-0.087	0.931				
Non-threatened : Shallow Sea	12.550	7.966	1.575	0.115				
Threatened : Shallow Sea	16.716	8.980	1.862	0.063				
PC1 : Shallow Sea	-5.059	2.749	-1.841	0.066				
PC2 : Shallow Sea	-11.765	12.486	-0.942	0.346				
Invasive : PC1 : Shallow Sea	6.597	5.009	1.317	0.188				
Native : PC1 : Shallow Sea	5.627	2.837	1.983	0.048				
Non-threatened: PC1: Shallow Sea	6.835	3.081	2.218	0.027				
Threatened : PC1 : Shallow Sea	4.947	3.012	1.642	0.101				
Invasive : PC2 : Shallow Sea	4.243	16.433	0.258	0.796				
Native : PC2 : Shallow Sea	11.906	12.598	0.945	0.345				
Non-threatened : PC2 : Shallow Sea	-10.380	13.350	-0.778	0.437				
Threatened : PC2 : Shallow Sea	-1.807	15.173	-0.119	0.905				

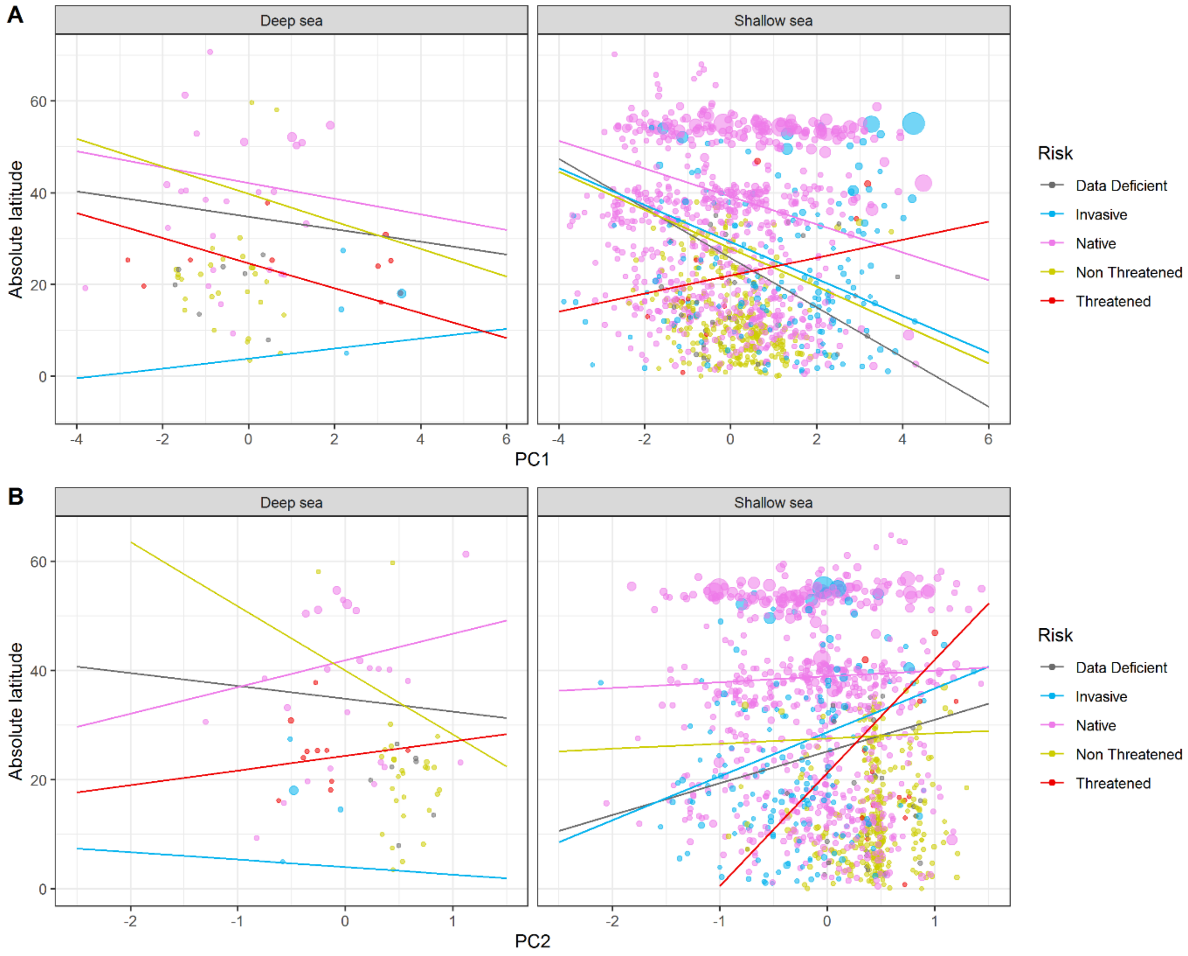


Figure 13: Absolute latitude by risk category, split according to depth strata, against A) PC1 effective in separating species according to annual fecundity and B) PC2 effective in separating species according to pelagic stage duration, age at maturity, longevity, and body size. Points are scaled to the number of OBIS occurrence records per species. All fitted with a generalized least squares model which accounts for phylogeny.

Overall model 4 was highly significant ($F_{29, 1291} = 10.30$, $\lambda = 0.402$, adjusted $R^2 = 0.170$, $p = < 0.0001$) (Figure 13, Table 13). There were significant interactions between PC1 and absolute latitude ($F_{29, 1291} = 92.19$, $p = <0.0001$), and between risk and PC2 with absolute latitude ($F_{29, 1291} = 4.97$, $p = 0.0006$). For PC2 there was a steeper positive slope in shallow water threatened species (20.73 ± 32.66) compared to non-threatened (6.282 ± 30.55) and all other risk categories (which for shallow water species were all positive). With regards to PC2 there was also a steeper positive slope in both deep sea threatened (2.68 ± 32.66) and native (4.88 ± 28.55) species compared to non-threatened (-11.77 ± 30.55) which has the steepest negative slope of all risk categories. With regards to PC1, deep sea species all had negative slopes (except for invasive species), the steepest of which were in non-threatened (-3.01 ± 6.87) and threatened species (2.72 ± 6.33). Considering PC1, shallow water species all have negative slopes except for threatened species which was positive (1.96 ± 6.33) compared to non-threatened species (-4.18 ± 6.87). Although both negative, shallow water invasive species (-4.02 ± 12.60) had a steeper negative slope than natives (-3.04 ± 6.28) PGLS showed that for both PC1 and PC2 when considered against absolute latitude, model 4 has the lowest phylogenetic signal ($\lambda = 0.402$), but again, the model has a low explanatory power (adjusted $R^2 = 0.170$) (Table 13).

Table 13: Results of the Phylogenetic Least Squares Model showing the relationship between absolute latitude, risk, PC1, PC2 and depth. Models are fitted with lambda = 'ML' (Maximum likelihood) and without an intercept.

	Coefficient estimate	SE	t-value	Pr(>|t|)	P-value	Model adjusted R^2	Lambda [ML]	Lambda 95% CI (lower, upper)
Absolute latitude ~					<0.001	0.170	0.402	0.262, 0.539
Data Deficient	34.921	16.940	2.061	0.039				
Invasive	3.918	28.633	0.137	0.891				
Native	41.985	5.217	8.047	0.000				
Non-threatened	40.223	8.063	4.988	0.000				
Threatened	24.551	6.885	3.566	0.000				
PC1	-1.376	5.956	-0.231	0.817				
PC2	-2.345	28.161	-0.083	0.934				
Shallow Sea	-9.360	16.596	-0.564	0.573				
Invasive : PC1	2.460	12.598	0.195	0.845				
Native : PC1	-0.339	6.276	-0.054	0.957				
Non-threatened : PC1	-1.630	6.869	-0.237	0.812				
Threatened : PC1	-1.346	6.326	-0.213	0.831				
Invasive : PC2	0.976	41.539	0.023	0.981				
Native : PC2	7.225	28.555	0.253	0.800				
Non-threatened : PC2	-9.421	30.547	-0.308	0.758				
Threatened : PC2	5.025	32.666	0.154	0.878				
Invasive : Shallow Sea	34.406	32.809	1.049	0.295				
Native : Shallow Sea	6.530	16.806	0.389	0.698				
Non-threatened : Shallow Sea	-3.019	17.961	-0.168	0.867				
Threatened : Shallow Sea	5.964	20.003	0.298	0.766				
PC1 : Shallow Sea	-4.036	6.287	-0.642	0.521				
PC2 : Shallow Sea	8.173	29.228	0.280	0.780				
Invasive : PC1 : Shallow Sea	-1.070	12.768	-0.084	0.933				
Native : PC1 : Shallow Sea	2.707	6.599	0.410	0.682				
Non-threatened: PC1 : Shallow Sea	2.859	7.231	0.395	0.693				
Threatened : PC1 : Shallow Sea	8.715	7.020	1.242	0.215				
Invasive : PC2 : Shallow Sea	1.241	42.294	0.029	0.977				
Native : PC2 : Shallow Sea	-11.988	29.609	-0.405	0.686				
Non-threatened: PC2 : Shallow Sea	4.533	31.732	0.143	0.886				
Threatened : PC2 : Shallow Sea	9.874	36.303	0.272	0.786				

4.5. Discussion

This study is the first to investigate on a global scale the relationship between thermal traits (specifically thermal tolerance breadth and maximum temperature), absolute latitude, vertical zonation and life histories of marine gastropod and bivalve molluscs, while accounting for phylogeny. Understanding the extent to which phylogeny constrains the ability of species to adapt to warming climates is crucial for anticipating climate-related impacts on the marine environment (Comte & Olden 2016). I observed a moderate phylogenetic signal in the relationship between both thermal tolerance breadth and absolute latitude and thermal breadth and maximum temperature. This is supported by the previous work of Comte and Olden (2016) who observed a strong phylogenetic signal in the thermal tolerance of freshwater fish and Nati et al. (2021) who found a strong phylogenetic signal in the upper thermal temperature limits of fish. Several studies (Weines et al. 2010; Bennett et al. 2011; Huey et al. 2012) have suggested that ectothermic species retain their ancestral climatic affinities through evolutionary time making it difficult for such species to adapt to climates which differ considerable from those inhabited by their ancestors.

The analyses presented here support previous findings from a range of taxa including fish and marine benthic invertebrates that a broad range of temperature tolerances (larger thermal breadth) is associated with a higher upper thermal tolerance threshold, and that this relationship is more positive in invasives than natives (Kelley 2014; Zerebecki & Sorte 2011; Moyle and Marchetti 2006). In my investigation I observed that there is a strong positive correlation between thermal breadth and maximum temperature in both the deep and shallow sea and that for the shallow sea, this relationship is stronger in invasive species than either native or threatened species (Figure 11). Eurthermality, the ability to maintain function across a wide range of temperatures, has been previously theorized as a mechanism of invasion success (McMahon 2002, Zerebecki & Sorte 2011; Bates et al. 2013) and species which experienced a broader ancestral thermal width may be better equipped, or preadapted, for survival if they are introduced to novel environments (Kelley 2014). As well as a wider thermal breadth, invasive species have previously been found to inhabit locations with a higher maximum temperature than native species (Zerebecki & Sorte 2011), mirroring my findings for both deep sea and shallow sea species whereby invasives have a higher maximum temperature than either native or threatened species (Figure 10). Invasive species are therefore expected be more successful than native and endemic or threatened species as temperature increases with climate change (Zerebecki & Sorte 2011; da Silva et al. 2021). The flipside of this is that species with the lowest thermal tolerances are likely to be the most susceptible to global warming (Zerebecki & Sorte 2011) and I observed that for both the deep and shallow sea, threatened species typically have the lowest maximum temperature.

My study showed that the thermal tolerance of deep-sea species declines with distance from the equator, with this relationship being stronger in invasive species and weaker in threatened species (Figure 9). However, because my investigation uses the latitudinal midpoint to determine absolute latitude, it potentially conflates latitudinal positions with latitudinal range. Nevertheless, my findings largely contradict the previously observed pattern that in ectothermic animals, thermal tolerance breadth increases with latitude (Shah et al. 2017; Rohr et al. 2018). In shallow water species, however, the thermal tolerance of both invasive and threatened species increases with distance from the equator, while the opposite is true for other risk groups (Figure 9), partially supporting the macroecological pattern observed in previous studies (Payne & Smith 2016). Janzen's extension of the climate variability hypothesis for instance, suggests that higher latitudes experience greater seasonal variation than lower latitudes and as such these locations favour a larger thermal breadth in temperate organisms compared to their tropical counterparts (Shah et al. 2017). Previous studies, however, have shown that that there is a lower rate of increase in thermal tolerance breadth with latitude in marine species than terrestrial species, with marine species commonly displaying a poleward decrease in upper thermal limits (Sunday et al. 2011). This may be because Janzen's hypothesis is more relevant to species occupying shallow seas rather than deeper water as seasonality in temperature is much greater in shallow water compared to deep water (Webb 2012)

Although surprisingly few studies have attempted to link thermal tolerance traits of species to their IUCN threat status, Rohr et al. (2018) found that threatened ectothermic species encompassing fungi and marine, freshwater, and terrestrial invertebrates tended to have narrower thermal breadths and acclimated more slowly to rising temperatures. They further found that thermal acclimation capacity (the degree to which organisms can alter their optimal temperature and critical thermal limits) increases with latitude (Rohr et al. 2018). In this investigation, I found that at low latitudes in both the shallow and deep sea, threatened species typically had the lowest thermal breadth of all risk categories (Figure 9). Rohr et al. (2018) further found that threat level decreased as latitude increased. In agreement with this, I only found threatened species in the deep sea at absolute latitudes <40°, however no such pattern was observed in the shallow sea (Figure 9).

The relationship between life history traits and environmental temperature in ectotherms has puzzled ecologists for decades due to the paradoxical effects of temperature on growth rate, body size and size at maturity (Angilletta et al. 2004). While most optimization models predict that in colder environments which stunt growth individuals will be smaller bodied and reach maturity at a smaller size, in reality, lower temperatures typically cause ectotherms to grow slower and mature at a larger body size (Angilletta et al. 2004). This suggests that despite their slow growth rates, individuals inhabiting colder environments prolong their growth and delay reproduction in order to reach larger sizes (Angilletta et al. 2004). After accounting for shared ancestry, I observed significant relationships between life history principal components and maximum temperature for each risk category.

Pelagic stage duration, age at maturity, lifespan and body size were all strongly loaded on PC2 (see Chapter 3) which, in all shallow sea risk categories, was negatively related to maximum temperature (Figure 12). Thus, for shallow sea species, as maximum temperature decreased, pelagic stage duration decreased while, age at maturity, lifespan and body size all increase, with this relationship particularly pronounced for threatened species (Figure 12). The relationships between life history principal components and absolute latitude further support this: across all shallow sea risk categories PC2 was positively related to absolute latitude (Figure 13), such that the traits associated with low maximum temperature are also associated with higher latitudes. These trends are less pronounced in the deep sea, with positive relationships between PC2 and absolute latitude only observed in native and threatened species, possibly because temperature and latitude are less tightly correlated in deeper water (e.g., Webb 2012). In general, my results support previous conclusions that in colder environments marine ectotherms are larger bodied, live longer, and reach maturity later in life (Angilletta et al. 2004; Moss et al. 2016; Ibanez et al. 2018). One explanation could be that a longer lifespan may be a consequence of a decrease in disturbance frequency with high latitudes which allows species to not only live longer and grow larger, but also to delay the onset of reproduction for years, or in some cases, decades (Moss et al. 2016).

Despite the caveat of low explanatory power, the analysis highlighted significant interactions between the principal components of life history variation and absolute latitude. With regards to PC1 (which split species according to annual fecundity) all deep-sea species (except for those considered to be invasive) and all shallow water species (except for those which are threatened) showed negative correlations between annual fecundity and absolute latitude (Figure 13) suggesting fecundity declines with distance from the equator. In the shallow sea, this relationship is likely linked to the fact that water temperature typically declines from lower to higher latitudes. My analysis further showed a significant relationship between PC1 (annual fecundity) and maximum temperature in the shallow sea whereby each risk category showed a positive relationship between annual fecundity and maximum temperature except shallow sea threatened species (Figure 12). In the deep sea, this relationship was less clear with only threatened and data deficient species showing a positive relationship between annual fecundity and maximum temperature (Figure 12). Nevertheless, this suggests that, generally, fecundity increases and maximum temperature increases, particularly in shallow sea species. These patterns lend support to Thorson's rule which posits that benthic marine invertebrates at low latitudes tend to be highly fecund and produce many eggs which develop into widely dispersing, pelagic large whereas at high latitudes such organisms tend to produce fewer offspring which are typically brooded rather than pelagic. Previous studies (Clark 1992; Gallardo & Penchaszadeh 2001) have further confirmed that Thorson's Rule holds well for gastropod molluscs with the original work by Thorson being based on gastropod molluscs from Thailand, Denmark, and Greenland (Thorson 1936;1950).

In summary, my analysis seems to agree that life-history variation across benthic marine molluscs is largely consistent with Thorson's rule. In the warmer, highly stochastic, lower latitude environments, species which are smaller bodied, produce numerous offspring are favoured, whereas in colder environments at higher latitudes, larger bodied species which produce fewer eggs, delay reproduction, and mature later in life are favoured. Typically, the traits displayed by species occupying lower latitudes are consistent with an r-selected strategy whereas the traits displayed by species occurring in higher latitudes are more consistent with a K-selected strategy.

Findings must be considered in light of the fact that my method of collecting environmental data, specifically the grid-scale temperature values assigned to each occurrence record from Bio-Oracle, involves using approximations from imperfect data and is thus an imprecise estimate of the temperature experienced by the individual (Webb et al. 2020). This is especially true for species occupying certain habitats such as the intertidal zone or deep sea near seamounts, where both bathymetry and temperature arranged over the grid scale (approximately 9km) may not accurately reflect the conditions experienced by organisms living there. Although the values for maximum temperature and thermal breadth of species should be interpreted with this in mind, given the scale and speed at which climate change is impacting marine species, making best use of available data and including as many species as possible into the analysis to allow predictions to be made with regards to the impact of warming oceans on benthic marine molluscs is imperative (Webb et al. 2020).

Although the analysis presented here provide an important step in understanding how thermal traits are distributed according to latitude, depth, life history characteristics and risk status, the knowledge that a large proportion of variation can be attributed to phylogenetic inertia implies that thermal tolerances are constrained by phylogeny. Thus, a species response to climate change is likely to be limited by genetic constraints, with these constraints seemly affecting certain groups (those which are threatened), more so than others (those which are invasive). Ultimately, my results indicate that invasive species, particularly those occurring in shallow waters, may be better poised than threatened species to thrive under increasing temperatures as a consequence of global climate change, largely due to their higher maximum temperature and larger thermal tolerances. This work emphasises the importance of studying invasive and threatened species in tandem to clearer delineate the trait profiles of each and to understand, and potentially predict, their likely response to warming temperatures. It is hoped that future studies will take this work further by considering biotic factors, such as competition and predation, alongside life history traits and environmental affinities to better determine the species most at risk of becoming invasive or extinct. This would allow for clearer management action to prevent either species loss or species establishment. An ongoing priority should also be to increase the number of species for which we have adequate trait data and to ensure accessibility and integration of such information (Webb & Vanhoorne 2020). This would allow for an increased number of assessments to be conducted by the IUCN, meaning more accurate comparisons could be made between different risk categories.

4.6. Supporting Material

Figure S4: The minimum depth of species using depth data collected from various online sources including SeaLifeBase, BIOTIC, published, and unpublished literature, against minimum depth calculated using depth summaries from OBIS. Points are scaled to the number of OBIS records per species and split according to each risk category.

Figure S5: Number of OBIS occurrence records (log transformed) against A) thermal breadth (calculated using the maximum mean temperature at mean depth minus the minimum mean temperature at mean depth) and B) maximum temperature. Colour coded for each risk category.

Figure S6: A) Principal Component Analysis (PCA) of 1530 marine molluscs split by five risk categories (Data deficient (n = 43), Invasive (n = 212), Native (n = 882), Non-threatened (n = 357), and Threatened (n = 36)) defined by the first two principal components (PC1 and PC2). PCA is a form of multivariate data analysis which is used to reduce the dimensionality of the data in order to provide a set of summary indices. Arrows indicate mean loadings (directions and weighing) of each life history in the PCA. Each point represents the position of a species within two-dimensional space. B) Boxplot of each risk category against PC1. C) Boxplot of each risk category against PC2. Width of the boxplots are scaled to the number of observations.

Table S8: Summary of the Principal Component Analysis (PCA) of trait data for marine molluscs (n = 1530).

Appendix S5: Biological trait dataset of 1530 mollusc species used in Chapter 4

5. General Discussion

Throughout this thesis I have investigated the macroecology of biological, ecological, and life-history traits of invasive, native, and threatened marine invertebrates with the aim of attempting to identify which traits predispose species to a heightened risk of invasion or extinction and to determine whether traits can be used to help predict and manage both species in decline and species on the move. Here, I summarise the key findings of this research (Section 5.1) and discuss them in relation to trait-based approaches and trait-based predictions (Section 5.2) and the incorporation of phylogeny into studies of extinction and invasion risk (Section 5.3). I then go on to consider future avenues of research which could build on the work presented here (Section 5.4.).

5.1. Key Findings

i. After assembling a trait database of 85 non-indigenous species and 302 native species I showed that the typical non-indigenous marine invertebrate is a mid-sized, long-lived, highly fecund suspension feeder which either broods its offspring or has a pelagic stage duration of 1-30 days and is either attached-sessile or burrows to a depth of 5cm (Chapter 2). This helped to answer one of the most pressing questions in invasion biology: what allows an invader to be successful?

ii. I further showed that the main traits discriminating between non-indigenous and native species were body size, lifespan, annual fecundity, offspring protection, burrowing depth and, to a lesser extent, pelagic stage duration (Chapter 2), and that these traits could distinguish between non-indigenous and native species with an accuracy of 78%. My findings thus add to the growing evidence that non-indigenous species possess a greater affinity for certain traits than do native species.

iii. Using this dataset (Chapter 2) I was able to propose a method based on trait profiles which can be used to predict native species with a tendency for invasion. These “potentially invasive” native species were able to be predicted from the wider native species dataset, using only biological traits, with an accuracy of 78%. This method may, therefore, be used to aid targeted surveillance and proactive management of species which are likely to become invasive if they were to successfully establish in a new environment.

iv. A second trait database of 1935 gastropod and bivalve molluscs highlighted that risk status in both gastropods and bivalves is more driven by phylogeny than by traits (Chapter 3). I found that while phylogeny may be used to predict risk status in marine molluscs, the inclusion of trait data adds very little to the predictive power of the models.

v. I further found that extinction risk and invasiveness are not randomly distributed across families and instead certain families contain a greater proportion of either threatened or invasion prone species than others. This is likely due to the strong phylogenetic component to extinction and invasion risk whereby species which share an evolutionary lineage, or geographic range are more like to have certain endangerment or expansion promoting traits than others. This finding means that families more at risk, such as pen shells (*Pinnidae*) and deep-water dwelling snails and limpets (*Provannidae* and *Peltospiridae*) can be made the focus of management action to prevent their declines further (Chapter 3).

vi. I did not find strong support for the hypothesis that individual traits predispose species to becoming threatened or invasive, or that invasive and threatened species lay at opposite ends of the life-history continuum. I did find, however, that species belonging to different risk categories display contrasting life histories with regards to certain traits and thus lay at varying, although not opposite, positions within the POSE framework. Considering where a species' life history falls on the POSE spectrum can help to diagnose vulnerability to human exploitation and can also indicate which species may be poised for invasion success were they to be transported beyond their native range (Chapter 3). It should be noted, however, that the exploratory power of my PGLS models is typically quite low suggesting a degree of unexplained variation. Therefore, these findings are general trends rather than strong patterns.

vii. I supplemented the species-trait dataset collected in Chapter 3 with environmental data including thermal traits, latitude and depth and used phylogenetic generalized least squares models to show that there is a moderate phylogenetic signal in the relationship between thermal tolerance breadth and absolute latitude and between thermal tolerance breadth and maximum temperature (Chapter 4). This indicates that ectothermic species retain their ancestral climatic affinities through evolutionary time, potentially making it difficult for such species to adapt to climates which differ considerably from those inhabited by their ancestors.

viii. Controlling for phylogeny, I also found a significant positive correlation between thermal breadth and maximum temperature in both the deep and shallow sea. This relationship was strongest in shallow water invasive species compared to either native or threatened species. This suggests that invasive species occurring in shallow waters may be better poised than native or threatened species to survive under increasing temperatures from global climate change.

ix. Analysis indicated that life history variation across benthic marine molluscs is largely consistent with Thorson’s rule. In the warmer, lower latitude environments, species which are smaller-bodied and produce numerous offspring are favoured, whereas in colder environments at higher latitudes, larger bodied species which produce fewer eggs, delay reproduction, and mature later in life are favoured. Again, however, the exploratory power of my PGLS models is typically quite low which should be considered when interpreting the strength of these patterns.

5.2. The Trait-Based Approach and Traits-Based Predictions

Traditionally, the impacts of invasive species have been studied with regards to species composition and species abundance. Although in certain circumstances this approach is desirable, for example, documenting the change in abundance of a commercially important species, it has been argued that considering the impact of invasive species on the composition of life-history, biological and functional traits is of increasing importance, thus requiring us to embrace the ‘trait-based approach’ (McGill et al. 2006; Mouillot et al. 2013; Bremner et al. 2005). There has been a recent proliferation in trait-based research across numerous disciplines: from evolutionary science (Salguero-Gómez et al. 2018) to global patterns of biodiversity (Díaz et al. 2013) and the relationship between ecosystem functions and species assemblages (Bello et al. 2010; Mouillot et al. 2013) which has resulted in a shift from the previously common species-centred approach. This shift has meant that groups of individuals are able to be categorised instead according to their biological, life history or functional traits.

A trait-based approach is commonly used in the marine environment (Degen et al. 2018), specifically with regards to species invasions. For instance, such approaches are used to assess the response of communities and ecosystems to species invasions in European seas (see Hewitt et al. 2016 and Weigel et al. 2015 for invasive polychaetes in the northern Baltic Sea), to assess the potential of certain species to become invasive (Cardeccia et al. 2018; Geburzi &

McCarthy 2018) and to understand the effects of climate change on ecosystem functioning (Suding et al. 2008) and species vulnerability (Butt et al. 2022; Green et al. 2022). Here, I have investigated the traits typical of non-indigenous species and identified traits which discriminate between native and non-indigenous marine invertebrates.

I observed that the typical profile of a non-indigenous marine invertebrate is one in which the species is a mid-sized, long-lived, highly fecund suspension feeder which either broods its offspring or has a pelagic stage duration of 1-30 days and is either attached-sessile or burrows to a depth of 5cm. Additionally, I highlighted that body size, lifespan, annual fecundity, offspring protection, burrowing depth and, to a lesser extent, pelagic stage duration are the main traits discriminating between native and non-indigenous marine invertebrates. Since the publication of this work, van Kuijk et al. (2021) investigated traits which enable crayfish invasion success in the Netherlands and found that traits associated with higher reproductive output, including high fecundity and continuous reproduction, long distance dispersal and migration, higher aggression levels and broader environmental tolerances are key to distinguishing successful from failed invaders. Similarly, Leitz (2022) investigated the traits which predict invasion success in the Laurentian Great Lakes and found that non-indigenous fish species with higher fecundities, longer lifespans and higher ages at maturity were capable of invading further than species which lacked these traits. Recent work, therefore, confirms that fecundity is likely to be a key trait enabling the success of invasive species, potentially acting as a major determinant of a species ability to spread beyond the point of introduction.

I further proposed a method based on trait profiles which can be used to predict non-indigenous species likely to cause the greatest impact and native species with tendency for invasion. This resulted in a list of 59 potentially invasive native species. Predictive tools such as the one presented in Chapter 2 of this thesis, which can forecast native species likely to become invasive, would greatly benefit detection programmes worldwide and would help to provide an insight into invasion dynamics. Post hoc analysis of these 59 potentially invasive native species revealed that 13 of these species are currently known to be invasive outside of their native Western European region. This research builds on the work of Rejmanek & Richardson (1996) who were among the first to apply quantitative statistical analysis to invasive species prediction and Kolar & Lodge (2002) who led one of the earliest investigations evaluating species traits across more than one invasion stage. Rejmanek & Richardson (1996) investigated twenty-four species in the genus Pinus across the Northern Hemisphere, twelve of which were invasive and twelve non-invasive (despite plantings on multiple continents they have had no reported spread). For each species, they gathered information on 10 life history characteristics and used discriminant function analysis (DFA) to assign each species to one of two groups (invader or non-invader). DFA correctly classified all species, suggesting that mean seed mass and minimum juvenile period were among the three characteristics most important for discriminating between the two (Rejmanek & Richardson 1996). This simple tool remains one of the better methods for predicting invasive species (Lockwood et al. 2013) and has been built-upon by Kolar & Lodge who developed a risk-assessment protocol for non-native fishes in the North American Great Lakes over three invasion stages (establishment, spread and impact). They identified 24 established species (split into fast spreading species with negative impacts and slower dispersing species with minimal impacts) and 21 introduced species and collected data on 24 traits including those associated with life-history, ecology, and invasion history (Kolar & Lodge 2002). They then conducted DFA and categorical and regression tree analysis (CART) on both establishment and spread data and found that they could discriminate between successful and failed invasions with an 87-94% accuracy, between fast and slow spreading invaders with a 94% accuracy and between high and low impact invaders with 89% accuracy (Kolar & Lodge 2002). Using these models Kolar & Lodge (2002) then created a list of 22 species predicted by both DFA and CART to pose a high risk of establishment in the Great Lakes.

The work presented in this thesis further lends to the more recent approaches of Fournier et al. (2019) who used ecological characteristics to predict ant species likely to invade and those with the most detrimental impacts. This was done by matching ecological profiles of known invasive species to currently native species to suggest which native species are poised to become the next global invaders. Since publication of this work, Chen et al. (2021) has also shown that specific traits such as prior invasion success, lower fecundity, higher tropic level, and involvement in the aquarium trade can be useful predictors of freshwater fish invaders in Southeast Asia. They propose that incoming freshwater species should be screened for these traits to allow the arrival of likely invaders to be prohibited.

5.3. Incorporating Phylogeny into Predictions of Extinction and Invasion Risk

In Chapters 3 and 4 I incorporated phylogeny to investigate which traits correlate more strongly with extinction risk and invasiveness and to compare the response of invasive, native, threatened, non-threatened and data deficient species to thermal stress. My analysis revealed that there is a strong phylogenetic signal in invasion and extinction risk whereby species which share an evolutionary lineage are more likely to have certain invasive promoting or endangerment promoting traits. There has been a wealth of recent studies linking phylogeny to both extinction risk and invasion success. Suhonen et al. (2022) for instance, investigated dragonflies and damselflies from Central Finland. They applied PGLS models, much like the ones I used in Chapters 3 and 4, to show that species relatedness, i.e., phylogenetic signal, did not affect local extinction risk. They further found that incorporating phylogeny into the analysis did not improve the use of functional traits in predicting local species extinctions (Suhonen et al. 2022). Contrastingly, Koppel et al. (2022) investigated phylogenetic patterns of climate-driven phenology shifts in bumblebee species across Canada and found that these shifts in phenology were strongly structured according to phylogeny. Similarly, Chen et al. (2022) used PGLS models to determine the key predictors of extinction across cetacean species and found that nearly all predictors of extinction showed significant phylogenetic signals, with a Pagels λ of close to 1.

With regards to predicting invasiveness using phylogeny, in contrast to my findings, Shao-Peng et al. (2019) investigated laboratory bacterial communities and revealed that phylogeny was not found to be a reliable predictor of invasion success and that instead fitness hierarchy between invasive and native species played a greater role. Park et al. (2020) on the other hand, investigated the evolutionary relatedness between native and non-native plants and found that this relatedness can be used to predict invasion success, particularly across large spatial scales. Similarly, Sol et al. (2022) also investigated the longstanding theory that invasion risk can be predicted based on phylogenetic relatedness between non-native and native species. They found that in the case of global bird communities, the ecological niches of species are phylogenetically conserved, and that invasion success increases when native and invasive species are more phylogenetically similar. Any interpretation of phylogenetic signal in invasive species, however, must be considered alongside the knowledge that introduced species themselves are not randomly selected, that is, human-induced invasions tend to involve specific clades such as those of commercial interest, or, in the case of marine species, those occurring in shallow coastal waters easily transported by maritime traffic (Sol et al. 2022). Similarly, the phylogenetic conservatism of ecological niches suggested by Sol et al. (2022), likely supports the notion proposed in Chapter 4, that species retain their ancestral climatic or ecological niches throughout evolutionary time, meaning species may have a predisposition to being able to expand their range, or not. Furthermore, my finding that invasion risk in non-randomly distributed across families concurs with a slightly older study by Pigot et al. (2018) which, when investigating birds on a global level, found that introductions were non-random, with a strong phylogenetic bias towards wide-ranging species from specific clades and regions.

Ultimately, the use of phylogeny to predict either invasion success or threat status relies on the assumption that phylogeny is indicative of meaningful differences between species. Thus, studies which combine species traits alongside phylogeny, such as in this thesis, are likely to predict invasiveness and extinction risk more accurately. Additionally, the incorporation of information regarding the environmental context of species is likely to aid in the usefulness of such predictions.

Therefore, in Chapter 4 I further identified a moderate phylogenetic signal in the relationship between thermal tolerance breadth and absolute latitude and thermal tolerance breadth and maximum temperature. This is mirrored by the recent work of Nati et al. (2021) which investigated the thermal tolerances of tropical and temperate fishes. They found that the variation in maximum temperature among fish shows a strong phylogenetic signal and that this may indicate an evolutionary constraint to adapting to rising global temperatures (Nati et al. 2021). Likewise, Faria et al. (2020) investigated crab species from tropical to sub-Antarctic South America and found that the physiological traits exhibited at upper thermal limits evolved in a phylogenetic manner, whereas traits linked to lower thermal limits evolved to be more plastic. This suggests that both trait inheritance and thermal environment help to explain thermal tolerances in both warmer and colder environments.

5.4. Limitations

There are four main limitations of the work presented here: missing trait data, the use of trait imputation methods, the biases in IUCN assessments and the approximations of Bio-Oracle temperature records. I will discuss each of these in turn, staring with missing trait data.

Although traits have been widely used in ecological and phylogenetic comparative studies for decades now, often trait data is unavailable for many species of interest (Johnson et al. 2020). Thus, despite the importance of these trait-based approaches, their use is limited due to a heavily dependence on the availability and compatibility of trait data in addition to the level of taxonomic and regional coverage they provide (Schneider et al. 2019). Trait datasets are thus largely underexploited as they typically suffer from a lack of standardization and heterogeneity in data formats, meaning it can be difficult to combine trait information compiled by multiple data providers (Schneider et al. 2019). One commonly cited limitation of trait databases is that while some traits may be largely static, such as feeding method, others, such as burrowing behaviour, may be highly variable. Thus far, there is no consistent framework in place to determine how often during the day, or year, a species must exhibit a particular trait in order to assign that species to a specific burrowing behaviour, movement or feeding method for instance. For this reason, a fuzzy coding approach was taken for non-indigenous species in Chapter 2 which allowed for species to display an affinity towards multiple trait modalities. Traditionally, species with missing trait data were simply excluded without further analysis, however, the estimation of missing trait values using imputation techniques is becoming more standard practice to deal with this issue (Johnson et al. 2020).

Therefore, as a result of incomplete trait datasets, in Chapters 2 and 3 I used Trait Explorer to estimate missing trait information for species in my dataset. Trait Explorer works by inferring traits values for species listed in the World Register of Marine Species, it applies "automated expert judgement" to estimate missing trait values based on species taxonomic relationships and patterns of covariation between traits (Bruggeman et al. 2009). The trait values estimated by Trait Explorer reflect the accuracy and amount of information fed into it. For instance, in Chapter 2 only 2.4 % of species were missing body size data, therefore Trait Explorer was able to provide more accurate inferences for this trait, whereas 59% of species were missing any value for 'burrowing depth', meaning imputed values for this trait are likely much less certain. Similarly, in Chapter 3 the mean proportion of missing trait data across the six traits investigated was 68.4% for Red List species, 65.3% for native species and 54.9% for invasive species. Again, body size had the most data available, missing only 1.5% in total, while age at maturity was missing for 87.9% of species.

One benefit of using Trait Explorer is that is uses the phylogenetic relatedness of species to estimate these missing trait values, as it is expected that more closely related species will display similar traits (Bruggeman et al. 2009). Error is reduced by not only looking at the single parent species, which may have trait values which are missing or inaccurate, but by considering more distantly related species in the phylogeny (Bruggeman et al. 2009). Trait Explorer, therefore, provides an estimation of trait values weighed according to phylogenetic proximity to closely related species with known traits (Bruggeman et al. 2009). One criticism of this approach, however, is that the accuracy of Trait Explorer's phylogenetic predictions depends on the underlying 'Brownian motion' model of evolution which assumes values change through genetic drift (Bruggeman et al. 2009). It has been suggested that this model overemphasises the randomness of trait value changes in both direction and distance over time, as opposed to more directional change due to natural selection (Bruggeman et al. 2009). Nevertheless, the Brownian motion model has been shown to provide a robust model for phylogenetic analysis in cases where no information is known about the exact process which governed the evolutionary change (Bruggeman et al. 2009), as is the case in this thesis.

An initial concern regarding the analysis performed in Chapters 3 and 4 was the circularity of the analysis i.e., fitting an evolutionary model (PGLS) to traits generated using an evolutionary model (that which is applied when using Trait Explorer). However, in principal inputting data using a method such as Trait Explorer, so long as it is robust, will likely reduce possible bias within the PGLS model. Subsequently, I decided to proceed with this method of analysis, considering the usual caveats of reliability over imputation methods when a large quantity of trait data is missing.

In Chapter 3 I incorporate IUCN assessed species into my analysis to better understand the drivers of invasion and extinction and to determine whether invasive and threatened species lay at opposite ends if the life history continuum. One inherent limitation of this is that there are taxonomic biases in the assessments of both threat status, and, to a lesser extent, invasiveness. IUCN assessments for instance, have not been conducted on a phylogenetically random subset of species and there is a clear taxonomic bias to well-studied species (Donaldson et al. 2016). As a result, the finding that extinction and invasion risk are not randomly distributed across families and instead certain families contain a greater proportion of either threatened or invasion prone species than others, may in some part be due to this taxonomic bias.

In addition, the marine realm is still poorly covered by the IUCN Red List, with $< 15\%$ of species assessed. Invertebrates are also largely under-assessed with $<2\%$ of the known species (IUCN 2018) currently evaluated. In my investigation, I found that IUCN Red List assessments overwhelmingly targeted certain taxa (e.g., the 600 species of *Conus*; Peters et al. 2013), which thus likely conflates the traits of *Conus* species with the traits of Red List species. Given the biased taxonomic coverage in evaluated species, it follows that many species which may be considered threatened have currently not been assessed or have been deemed to be data deficient. Currently only 7% of the world’s described species have had their extinction risk assessment completed. This lack of comprehensive coverage within the IUCN Red List likely limits its usefulness in large scale analysis of threat status. Hence, the IUCN Red List now has a goal to assess at least 160,000 species (currently 147,500 have been assessed). Yet with no date stated for this goal to be met, it is likely that the taxonomic coverage may not be improved for some time. Furthermore, although phylogenetic clustering has been found to be much weaker in studies of invasiveness (Lambdon 2007; Pigot et al. 2018), it is still the case that assessments of invasive species are highly taxonomically biased and not phylogenetically random (Jelbert et al. 2019). Given that this non-randomness in species sampling is commonplace in phylogenetic studies of both invasiveness and extinction risk (Hau & Lanfear 2018), mine being no exception, the estimates of phylogenetic signal found in both invasiveness and IUCN assessment status are likely to overstate the true signal across all molluscs. This is also likely true of the phylogenetic signals found between thermal tolerance breadth and absolute latitude and between thermal tolerance breadth and maximum temperature in Chapter 4.

Individual traits have also been shown to differ in their degree of phylogenetic signal (Blomberg et al. 2003; Maitner et al. 2021) meaning that in cases where invasion success is determined by traits which have a weak phylogenetic signal, phylogeny may not be a useful metric. The traits used in all chapters however, were decided after much exploration of the literature to determine the traits most appropriate for discriminating between a) non-indigenous and native species b) invasive and threatened species and c) invasive, native, threatened, non-threatened and data deficient species with regards to abiotic factors. Nevertheless, the phenotypic plasticity of traits, that is- the ability of individuals to express different phenotypes in response to changing environmental conditions- can also weaken the usefulness of phylogeny as a trait proxy (Maitner et al. 2021; Relyea et al. 2018), this is likely to be particularly relevant with regards to Chapter 4 whereby species occur at a variety of different geographical locations subject to varying environmental conditions.

In Chapter 4 I collect environmental data, specifically grid-scale temperature values from Bio-Oracle, which are assigned to each OBIS occurrence record. This was necessary given that very few occurrence records have in situ measures of environmental temperature recorded alongside them, meaning that it becomes necessary to match the occurrence records to environmental temperatures post hoc. Currently, however, no standard protocol exists for doing this. Additionally, because occurrence records from OBIS are known to contain spatial, temporal, and taxonomic biases, there are potential sources of error when combining these occurrence records with temperature records to generate species level thermal affinities.

Consequently, the findings of Chapter 4 must be considered in light of the fact that this method of collecting environmental data involves using approximations from imperfect data and thus is an imprecise estimate of the temperature experienced by the individual. Therefore, interpretation of any results, must also take into consideration the measurement error associated with thermal breadth. The use of Bio-Oracle gridded temperature records also introduces several sources of error. For instance, given that global gridded bathymetry datasets fail to incorporate any subgrid scale variation in depth and temperature, there is likely to be inherent and unresolvable measurement errors in records which result in imperfect values for temperature at depth points. This is especially true for species occupying certain habitats such as the intertidal zone or the deep sea near seamounts, where both bathymetry and temperature arranged over the grid scale (approximately 9km) may not accurately reflect the conditions experienced by organisms living there. Although the values for maximum temperature and thermal breadth of species should be interpreted with this in mind, given the scale and speed at which climate change is impacting marine species, making best use of available data, and including as many species as possible into the analysis to allow predictions to be made with regards to the impact of warming oceans on benthic marine molluscs is imperative (Webb et al. 2020). As such, the usefulness of open access databases such as OBIS and Bio-ORACLE should not be underestimated (Webb et al. 2020).

5.5. Future Directions

Coordinated research through databases such as WoRMS, OBIS, and BioOracle will likely offer a promising avenue for furthering our knowledge of the key traits of invasive, non-indigenous and threatened species. It is likely that as biological trait information becomes more widely available, standardized, and centralized, there will be a greater ability to detect differences between native and NIS and threatened and invasive species to provide a clear delineation of an invader profile. Primary data collection through fieldwork and observational experiments will likely be needed, focusing on species identified by the IUCN to be threatened or data deficient to better understand their life history traits and environmental tolerances. Species identified as being potentially invasive in Chapter 2 should also be further investigated to enable predictions to be made regarding both the regions they are likely to invade and their impacts. Once additional information is collated, present lines of enquiry explored in this thesis should be readdressed.

Several avenues of further research are available which are suggested as a continuation of the work presented in this thesis. These avenues are centred around three main themes: the temporal and spatial patterns of traits, environmental traits, and behavioural and personality traits:

a) Temporal and Spatial Patterns of Traits

- Do the traits important for invasion success differ at each stage of the invasion process (e.g., are the traits important during the initial uptake stage different from those which enable success during the transport, establishment and spread stages?)
- How do the traits driving an organism's response to environmental variability differ between the stages of invasion? (e.g., is a large thermal breadth the primary trait conveying success of the transportation stage?)
- How do the traits of species (either those which are invasive or threatened) change ontogenically (e.g., from larval, to post larval to adulthood) and over shorter timescales (e.g., diurnally)?
- To what extent can prior invasion history be used as a predictor of future invasion success?
- How do the traits of invasive marine molluscs differ between their native and invaded regions?

b) Environmental Traits

- To what extent is there intraspecific variation in the environmental traits of species, and how does this differ between invasive, native, and threatened species?
- What impact does temperature have on the interactions between native and invasive species? Previous studies have shown examples of condition-specific competition whereby invasive species are more likely to displace native species at higher temperatures (Carmona-Catot et al. 2013).

c) Behavioural and Personality Traits

- How do the dominant behavioural and personality traits (e.g., aggression, boldness, exploratory activity, sociability) differ between native, invasive, and threatened species?

- Do these behavioural and personality traits also differ within invasive species? (e.g., are certain traits more important during the transport stage with others e.g., increased boldness or exploratory activity, more important during the spread phase?
- Finally, how do these behaviours and personalities mediate an organism's response to climate change?

5.6. Concluding Remarks

The work presented in this thesis provides a foundation for future comparative macroecological studies aimed at understanding how the traits of invasive, native, and threatened marine invertebrates differ and how phylogeny and environmental factors (e.g., temperature, latitude, and depth) interact to determine climate change vulnerability. The work presented in this thesis provides a unique contribution to understanding the traits of marine invertebrates, specifically molluscs. By building on the work of Rejmanek & Richardson (1996), Kolar & Lodge (2002), and Cardeccia et al. (2018), I have been able to provide the first comprehensive comparison of the biological traits of native and non-indigenous marine invertebrate species throughout Western European Seas. This work goes beyond traditional biological trait analysis by using such attributes to estimate species invasiveness applied to a dataset of currently non-invasive species, complimentary to the work of Fournier et al. 2019. From this, I have developed a method based on trait profiles which can be used to predict non-indigenous species likely to cause the greatest impact and native species with tendency for invasion. Predictive tools such as the one presented in this thesis, which can forecast native species likely to become invasive, would greatly benefit detection programmes worldwide and would help to provide an insight into invasion dynamics. My research has further shown the relevance of combining a traits-based approach with phylogeny and existing life history frameworks to build on the previous work of Liu et al. (2017) and Kindsvater et al. (2016). Moreover, this thesis comprises the first global review of the relationship between vertical zonation, latitude, and thermal tolerance across risk groups of molluscs while also controlling for phylogeny and sets the stage for future trait-based assessments of marine invasive and threatened benthic invertebrates.

6. References

Alcaraz, C., Vila-Gispert, A., García-Berthou, E. (2005). Profiling invasive fish species: The importance of phylogeny and human use. *Diversity and Distributions,* 11(4), 289-298.

Allen, W., Street, S., Capellini, I., Letters, E. (2017). Fast life history traits promote invasion success in amphibians and reptiles. *Ecological Letters,* 20, 222-230.

Alonso, A., Castro-Díez, P. (2008). What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)? *Hydrobiologia,* 614, 107-166.

Alpert, P. (2006). The advantages and disadvantages of being introduced. *Biological Invasions*, 8(7), 1523-1534.

Alvarez-Yépiz J., Búrquez, A., Martínez-Yrízar, A., Dovciak, M. (2019). A trait-based approach to the conservation of threatened plant species. *Oryx*, 53(3), 429-435.

Anderson, S.C., Farmer, R.G., Ferretti, F., Houde, A.L.S. & Hutchings, J.A. (2011). Correlates of vertebrate extinction risk in Canada. *BioSciences,* 62, 538-549.

Angilletta, M & Dunham, A. (2003). The Temperature-Size Rule in Ectotherms: Simple Evolutionary Explanations May Not Be General. *The American Naturalist,* 162 (3), 332-342.

Angilletta, M., Oufiero, C & Leache A. (2006). Direct and Indirect Effects of Environmental Temperature on the Evolution of Reproductive Strategies: An Information-Theoretic Approach. *The American Naturalist,* 168 (4), 123-135.

Angilletta, M., Steury, T & Sears, M. (2004). Temperature, Growth Rate and Body Size in Ectotherms: Fitting Pieces of a Life-History Puzzle. *Integrative and Comparative Biology,* 44 (6), 498-509.

Anton, A., Geraldi, N., Lovelock, C., Apostolaki, E., Bennett, S., Cebrian, J., Krause-Jensen, D., Marba, N., Martinetto, P., Pandolfi, J., Ssntana-Garcon, J., Duarte, C. (2019). Global ecological impacts of marine exotic species. *Ecology and Evolution,* 3, 787-800.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E., De Clerck, O. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography, 27, 277-284.

Baer, C. & Travis J. (2000). Direct and correlated responses to artificial selection on acute thermal stress tolerance in livebearing fish. *Evolution*, 52, 238-244.

Baker, K., Devine, J., Haedrich, R. (2009). Deep-sea fisheries in Canada's Atlantic: Population declines and predicted recovery times. *Environ. Biol. Fishes*, 85, 79-88.

Barnosky AD, Matzke N, Tomiya S et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57.

Bates, A., McKelvie, C., Sorte, C., Morley, S., Jones, N., Mondon, J., Bird, T., Quinn., G. (2013). Geographical range, heat tolerance and invasion success in aquatic species. *Proceedings: Biological Sciences,* 280, 1-7.

Beauchard, O., Mestdagh, S., Koop, L., Ysebaert, T., Herman, P.M.J. (submitted). Marine benthic synecology in a soft sediment shelf: habitat contrasts and assembly rules of life strategies. About to be resubmitted to Marine Ecology Progress Series.

Beauchard, O., Veríssimo, H., Queirós, A.M., Herman, P.M.J. (2017). The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecological Indicators,* 76, 81-96.

Bello, F., Lavorel, S., Diaz, S., et al., (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*. 19, 2873-2893.

Belmaker, J., Parravicini, V., Kulbicki, M. (2013). Ecological traits and environmental affinity explain Red Sea fish introductions into the Mediterranean. *Global Change Biology*, 19, 1373-1382.

Bennett, J., Sunday, J., Calosi, P., Villalobos, F., Martinez, B., Molina-Venegas, R., Araujo, M., Algar, A., Clusella-Trullas, S., Hawkins, B., Kieth, S et al., (2021). The evolution of critical thermal limits of life on Earth. *Nature Communications,* 12, 1198.

Bennett, P.M. & Owens, I. (1997). Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London, Series B: Biological Sciences,* 264 (1380), 401-408.

Bielby, J., Cunningham, A. & Purvis, A. (2006). Taxonomic selectivity in amphibians: ignorance, geography or biology? *Animal Conservation,* 9 (2), 135-143.

Blackburn, T. (2019). Macroecology and invasion biology. Global Ecology and Biogeography. 28(1), 28-32.

Blackburn, T. M. & Jeschke, M. J. (2009). Invasion success and threat status: two sides of a different coin? *Ecogeography,* 31 (1), 83-88. *Global Ecology and Biogeography,* 25 (4), 391-405.

Blomberg, S., Garland, T., Ives, A. (2003). Testing for phylogenetic signal in comparative data: behavioural traits are more labile. *Evolution,* 57(4), 717-745.

Böhm, M., Kemp, R., Williams, R., Davidson, A., Garcia, A., McMillan, K., Bland, L., Bramhall, H. & Collen B. (2017). Rapoport's rule and determinants of species range size in snakes. Diversity and Distribution, 23 (12), 1472-1481.

Böhm, M., Williams, R., Bramhall, H., McMillan, K., Davidson, A., Garcia, A., Bland, L., Bielby J. & Collen B. (2016). Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. *Global Ecology and Biogeography,* 25 (4), 391-405.

Bolam, S.G., Garcia, C., Eggleton, J., Kenny, A.J., Buhl-Mortensen, L., Gonzalen-Mirelis, G., van Kooten, T., Dinesen, G., Hansen, J., Hiddink, J.G., et al., (2017). Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Marine Environmental Research* Elsevier Ltd, 126: 1–13.

Bosch, S. (2018) sdmpredictors: Species distribution modelling predictor datasets. Retrieved from: https://CRAN-R-project.org/packages=sdmpredictors.

Bougeard, S & Dray, S. (2018). "Supervised Multiblock Analysis in R with the ade4 Package." *Journal of Statistical Software,* 86(1), 1-17.

Bradshaw, C. J. A., Giam, X., Tan, H. T.W., Brook, B. W. & Sodhi, N. S. (2008). Threat or invasion status in legumes is related to opposite extremes of the same ecological and life history attributes. *Journal of Ecology,* 96 (5), 869-883.

Brandner, J., Cerwenka, A., Schliewen, U., Geist, J. (2018). Invasion strategy in round goby (*Neogobius melanostomus*): Is bigger really better? *PLoS ONE* 13 (1), e0190777.

Bremner, J. (2005). Assessing ecological functioning in marine benthic communities. Ph.D thesis, University of Newcastle upon Tyne, UK

Brown, A. & Thatje S (2014). The effects of changing climate on faunal depth distributions determine winners and losers. Global Change Biology, 21 (1), 173-180.

Brown, J. H. (1995). Macroecology. Chicago, IL: University of Chicago Press.

Brown, J., Maurer, B.A. (1989). Macroecology: the division of food and space among species on continents. Science. 243, 1145-1150.

Bruggeman, J., Heringa, J. & Brandt, B.W. (2009). PhyloPars: estimation of missing parameter values using phylogeny. Nucleic Acid Research, 37, 179-184.

Brun, P., Payne, M., Kiørboe, T. (2016). A trait database for marine copepods. PANGAEA, https://doi.pangaea.de/10.1594/PANGAEA.862968

Butt, N., Halpern, B., O'Hara, C., Allcock, A., Polidoro, B., Sherman, S., Byrne, M., Birkeland, C., Dwyer, R., Frazier, M., et al., (2022). A trait-based framework for assessing the vulnerability of marine species to human impacts. *Ecosphere,* 13(2), e3919.

CABI (2021). *Ficopomatus enigmaticus*. In: Invasive Species Compendium. Wallingford, UK: CAB International. https://www.cabi.org/isc/datasheet/108338

CABI (2022) Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc

Cadotte, M. W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology,* 48(5), 1079-1087.

Caldeira, K., Wickett, M.E. (2003). Oceanography: anthropogenic carbon and ocean pH. *Nature,* 425:365.

Capellini, I., Baker, J., Allen, W. L., Street, S. E. & Venditti, C. (2015). The role of life history traits in mammalian invasion success. *Ecology Letters,* 18 (10), 1099-1107.

Capinha, C., Ess,l F., Seebens, H., Moser, D., Pereira, H. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science,* 348, 1248–1251.

Cardeccia, A., Marchini, A., Occhipinti-Ambrogu, A., Galil, B., Gollasch, S., Minchin, D., Narščius, A., Olenin, S., Ojaveer, H. (2018). Assessing biological invasions in European Seas:

Biological traits of the most widespread non-indigenous species. *Estuarine, Coastal and Shelf Science,* 201, 17-28.

Cardillo, M. (2003). Biological determinants of extinction risk: why are smaller species less vulnerable? *Animal Conservation,* 6, 63-69.

Cardillo, M., Mace, G., Jones, K., Bielby, J., Bininda-Emonds, O., Sechrest, W., Orme D. & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Nature.* 309 (1538), 1239-1241.

Cardoso, P., Borges, P., Triantis, K., Ferraandez, M & Martin, J. (2011). Adapting the IUCN Red List criteria for invertebrates. *Biological Conservation*, 114, 2431-2440.

Carlton, J. (1993). Neoextinctions in marine invertebrates. *American Zoologist,* 33: 499–507.

Carlton, J., Vermeij, G., Lindberg, D., Carlton, D., Dudley, E. (1991). The first historical extinction of a marine invertebrate in an ocean basin: the demise of the eelgrass limpet Lottia alveus. *Biological Bulletin,* 180: 72–80.

Carmona, C., Tamme, R., Partel, M., de Bello, F., Brosse, S., Capdevila, P., Gonzalez, R., Gonzalez-Suarez, M., Salguero-Gomez, R., Vasquez-Valderrama, M. & Toussaint, A. (2021). Erosion of global functional diversity across the tree of life. *Science Advances,* 7 (13), eabf2675.

Carmona-Catot, G., Magellan, K., García-Berthou, E. (2013). Temperature-specific competition between invasive mosquitofish and an endangered cyprinodontid fish. *PLoS ONE,* 8(1), e54734.

Cassey, P., Blackburn, T., Russel, G., Jones, K., Lockwood, J. (2004). Influences on the transport and establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world. *Global Change Biology*, 10, 417-426.

Castilla, J., Uribe, M., Bahamonde, N., Clarke, M. et al. (2005). Down under the southeastern Pacific: marine non-indigenous species in Chile. *Biological Invasions,* 7, 213-232.

Catford, J.A., Jansson, R., Nilsson, C. (2008). Reducing redundancy in invasion ecology by integrating hypothesis into a single theoretical framework. *Diversity and Distributions,* 15, 22-40.

Caviedes-Solis, I.W., Kim, N. & Leaché. (2020). Species IUCN threat status level increases with elevation: a phylogenetic approach for Neotropical tree frog conservation. Biodiversity and Conservation, 29, 2515-2537.

Cazalis, V., Marco, M.D., Butchart, S.H.M, Akcakaya, H.R. Gonzalez-Suarez, M. et al. (2022). Bridging the research-implementation gap in IUCN Red List assessments. *Trends in Ecology & Evolution. In Press.*

CBD (2020). Update of the zero draft of the Post-2020 Global Biodiversity Framework (provided in document CBD/POST2020/PREP/2/1) Convention on Biological Diversity. [accessed 28 June 2021]

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M. & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances,* 1, e1400253.

Chan, F & Briski, E. (2017). An overview of recent research in marine biological invasions. *Marine Biology*, 164(121).

Chen, C., Chen, C. & Wang, Y. (2019). Ecological correlates of extinction risk in Chinese amphibians. *Diversity and Distributions,* 25 (10), 1586-1598.

Chen, C., Jefferson, T., Chen, B., Wang, Y. (2022). Geographic range size, water temperature, and extrinsic threats predict the extinction risk in global cetaceans. *Global Change Biology,* 28, 16385.

Chen, J., Zeng, J., Yeo, D.C. (2021). Invasive species trait-based risk assessment for non-native freshwater fishes in a tropical city basin in Southeast Asia. *PLoS ONE*, 16(3), e0248480.

Chevenet,F., Dolédec, S., Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology,* 31(1), 295-309.

Chichorro, F., Juslén, A. & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, 237, 220-229.

Chichorro, F., Urbano, F., Teixeira, D., Vare, H., Pinto, T., Brummitt, N., He, X., Hochkirch, A., Hyvonen, J., Kalia, L., Juslen, A., Cardoso, P. (2020). Species traits predict extinction risk across the Tree of Life. Pre-Print.

Clark, A. (1992). Reproduction in the cold: Thorson revisited. *Invertebrate Reproduction & Development,* 22:175-184.

Cleland, E. (2011). Trait divergence and the ecosystem impacts of invading species. *New Phytologist,* 189(3), 649-652.

Colautti, R.I., Alexander, J.M., Dlugosch, K.M., Keller, S.R. & Sultan, S.E. (2017). Invasions and extinctions through the looking glass of evolutionary ecology. *Philosophical Transactions of the Royal Society B.* 372 (1712), 20160031.

Collins, K., Edie, S., Hunt, G., Roy, K., Jablonski, D. (2018). Extinction risk in extant marine species integrating palaeontological and biodistributional data. *Proceedings of the Royal Society B*, 285(1887).

Comte, L & Olden, J. (2016). Climate vulnerability of the world's freshwater and marine fishes. *Nature Climate Change,* 7, 718-722.

Costello, M.J., Claus, S., Dekeyzer, S., Vandepitte, L., Tuama, E., Lear, D., Tyler-Walters, H. (2015). Biological and ecological traits of marine species. *PeerJ* 3: e1201.

Cowie, R.H., Régnier, C., Fontaine, B. & Bouchet, P. (2017). Measuring the Sixth Extinction: what do mollusks tell us? *The Nautilus,*131 (1), 3-41.

Crozier, L & Hutchings, J. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications,* 7 (1), 68-87.

Cuttelod, A., Seddon, M. & Neubert, E. (2011). European Red List of Non-marine Molluscs. Luxembourg: Publications Office of the European Union.

Czerniejewski, P. (2013). Realized fecundity in the first brood and size of eggs of Chinese Mitten crab (*Eriocheir sinensis*)- Laboratory Studies. *International Journal of Biological Sciences,* 2(2), 1-6.

da Silva, C., Bearman, J., Dorey, J., Barker, S., Congedi, N., Elmer, M., Galvin, S., Tuiwawa, M., Stevens, M., Alton, L., Schwarz, M & Kellermann, V. (2021). Climate change and invasive species: a physiological performance comparison of invasive and endemic bees in Fiji. *Journal of Experimental Biology,* 224 (1), jeb230326.

Daehler, C. (2001). Two ways to be an invader, but one is more suit-able for ecology. *ESA*

Bulletin, 82, 101–102.

Darling, E., Green, S., O'Leary, J., Côté, I. (2011). Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. *Biological Invasions*, 13, 2045–2051.

Davidson, A.M., Jennions, M. & Nicotra, A.B. (2011). Do invasive species show higher phenotypical plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecological Letters*, 14, 419-431.

Davies, B., Stuart, V., Villiers, M. (1989). The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* (Fauvel)) and its effects on water quality in a coastal marina. *Estuarine, Coastal and Shelf Science*, 29, 613-620.

Davies, K. F., Margules, C. & Lawrence, J. F. (2004). A Synergistic Effect Puts Rare, Specialized Species at Greater Risk of Extinction. *Ecology*, 85 (1), 265-271.

Day, P., Smith, R., Edgar, G., Bates, A. (2018). Species' thermal ranges predict changes in reef fish community structure during 8 years of extreme temperature variation. *Diversity and Distributions*, 24, 1036-1046.

Degen, R., Aune, M., Bluhm, B., Cassidy, C., Kedra, M., Kraan, C., Vanderpitte, L., Zhulay, I., Albano, P., Bremner, J., et al., (2018). Trait-based approaches in rapidly changing ecosystems; A roadmap to the future polar oceans. *Ecological Indicators*, 91, 722-736.

Denney, N.H., Jennings, S, & Reynolds, J.D. (2002). Life-History Correlates of Maximum Population Growth Rates in Marine Fishes. *Proceedings of the Royal Society B: Biological Sciences*, 269 (1506), 2229-2237.

Devin, S. & Beisel, J.N. (2007). Biological and ecological characteristics of invasive species: A gammarid study'. *Biological Invasions*, 9(1), 13–24.

Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M.,Donoghue, M.J., Ewers, R.M, Jordano, P. & Pearse, W. (2013.) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, 3(9), 2958–2975.

Donaldson, M., Burnett, N., Braun, D., Suski, C., Hinch, S., Cooke, S., Kerr, J. (2016). Taxonomic bias and international biodiversity conservation research. *FACETS*, 1(1), 105-113.

Drakare, S., Lennon, J., Hillebrand, H. (2006). The impact of the geographical and ecological context on species-area relationships. *Ecological letters,* 9(2), 215-227.

Dubios, S., Cimmito, J., Oliver, F., Retière, C. (2006). Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. *Estuary Coast Shelf Science,* 68, 635-46.

Dulvy, N., Fowler, S., Musick, J., Cavanagh, R., Kyne, P., Harrison, L., Carlson, J., Davidson, L. et al., (2014). Extinction risk and conservation of the world's sharks and rays. eLife, 3: e00590.

Dulvy, N., Kindsvater, H. (2017). The Future Species of Anthropocene Seas. *Conservation for the Anthropocene Ocean,* 39-69.

Dulvy, N.K., Sadovy, Y. & Reynolds, J.D. (2003). Extinction vulnerability in marine populations. *Fish and Fisheries,* 4 (1), 25-64.

Early, R., Bradley, A., Dukes, J., Lawler, J., Olden, J., Blumenthal, D., Gonzalez, P., Grosholz, E., Ibanez, I., Miller, L., Sorte, C., Tatem, A. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications* 7:12485.

EEA (European Environment Agency) (2010). Invasive alien species in Europe. European Network on Invasive Alien Species, accessed: 17 February 2021, < https://www.eea.europa.eu/data-and-maps/indicators/invasive-alien-species-in-europe/invasive-alien-species-in-europe>

EEA (European Environment Agency) (2019). Trends in marine non-indigenous species. European Network on Invasive Alien Species, accessed: 8 December 2020, < https://www.eea.europa.eu/data-and-maps/indicators/trends-in-marine-alien-species-mas-3/assessment>

Elofsson, K. & Gren I. (2014). Regulating invasive species with different life history. *Journal of Bioeconomics,* 17, 113-136.

Eme, J & Bennett, W. (2009). Critical thermal tolerance polygons of tropical marine fishes from Sulawesi, Indonesia. *Journal of Thermal Biology,* 34 (5), 220-225.

Engelkes, T. & Mills, N. J. (2011). A conceptual framework for understanding arthropod predator and parasitoid invasions. *BioControl,* 56 (4), 383-393.

Eno, N.C., Clark, R.A., Sanderson, W.G. (1997). Non-native marine species in British waters: a review and directory. JNCC, Peterborough.

Essington, T., Moriarty, P., Froehlich H., Hodgson, E., Koehn, L., Oken, K., Siple, M. & Stawitz, C. (2015). Fishing amplifies forage fish population collapse. *PNAS*, 112 (21), 6648-6652.

Fang, X., Mestgagh, S., Ysebaert, T., Moens, T., Soetaert, K., van Colen. C. (2019). Spatio-temporal variation in sediment ecosystem processes and roles of key biota in the Scheldt estuary. *Estuarine and Coastal Shelf Science* 222, 21-31.

Faria, S., Bianchini, A., Lauer, M., Zimbardi, A., Tapella, F., Romero, K., McNamara, J. (2020). Living on the Edge: Physiological and Kinetic Trade-Offs Shape Thermal Tolerance in Intertidal Crabs from Tropical to Sub-Antarctic South America. *Front Physiol*, 11(312), PMID:32390860.

Faulwetter, S., Markantonatou, V., Pavloudi, C., Papageorgiou, N., Keklikoglou, K., Chatzinikolaou, E., Pafilis, E., Chatzigeorgiou, G., Vasileiadou, K., Dailianis, T., Fanini, L., Koulouri, P., Arvanitidis, C. (2014). Polytraits: A database on biological traits of marine polychaetes. *Biodiversity Data Journal*, 2, e1024.

Feng, X., Enquist, B., Park, D., Boyle, B., Breshears, D., Gallagher, R., Lien, A, Newman, E., Burger, J., Maitner, B, et al., (2021). A review of the heterogeneous landscape of biodiversity databases: opportunities and challenges for a synthesized biodiversity knowledge base. *Global Ecology and Biogeography*, 31 (7), 1242-1260.

Fisher, D. O. & Owens, I.P.F. (2004). The comparative method in conservation biology. *Trends in Ecology & Evolution*, 19 (7), 391-398.

Floerl, O., Pool, T., Inglis, G. (2004). Positive interactions between nonindigenous species facilitate transport by human vectors. *Ecological Applications*, 4, 798-807.

Fofonoff, P., Ruiz, G., Steve, B., Simkanin, C &Carlton, J. (2018). National Exotic Marine and Estuarine Species Information System. https://invasions.si.edu/nemesis

Fortes, R., Absalão, R. (2004). The applicability of Rapoport’s Rule to the American marine mollusks. *Journal of Biogeography*. 31(12), 1909-1916.

Fournier, A., Penone, C., Pennino, M., Courchamp, F. (2019). Predicting future invaders and future invasions. *Proceedings of the National Academy of Science of the United States of America*, 116(16), 7905-7910.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002). Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence. The American Naturalist, 166 (6), 712-726.

Friedman, H. (1989). Regularized Discriminant Analysis. *Journal of the American Statistical Association*, 84(405), 165–75.

Froese, R., Pauly, D. Editors (2022). FishBase. World Wide Web electronic publication. www.fishbase.org.

Gabrielová, J., Münzbergová, Z., Tackenberg, O. & Chrtek, J. (2013). Can we distinguish plant species that are rare and endangered from other plants using their biological traits? *Folia Geobot*, 48, 449–466.

Gallardo, C. & Penchaszadeh, P. (2001). Hatching mode and latitude in marine gastropods: revisiting Thorson’s paradigm in the southern hemisphere. *Marine Biology*, 138, 547-552.

García-Berthou, E. (2007). The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology,* 71, 33-55.

Gaston, K & Blackburn, T. (2000). Patterns and Processes in Macroecology, Wiley, Blackwell Science Ltd

Gaston, K. (2003). The structure and dynamics of geographic ranges. Oxford University press.

Gaston, K. J. & Blackburn, T.M. (1995). Birds, Body Size and the Threat of Extinction. *Philosophical Transactions of The Royal Society B Biological Sciences*, 347 (1320), 205-212.

GBIF.org (2022) GBIF Home Page. https://www.gbif.org

Geburzi, J & McCarthy, M. (2018). How do they do it?- Understanding the success of marine invasive species, In: Jungblut, S., Liebich, V., Bode, M. (eds) YOUMARES 8 – Oceans Across Boundaries: Learning from each other. Springer, Cham. https://doi.org/10.1007/978-3-319-93284-2_8

Gilbey, V., Attrill, M., Coleman, R. (2008). Juvenile Chinese mitten crabs (*Eriocheir sinensis*) in the Thames estuary: distribution, movement, and possible interactions with the native crab *Carcinus maenas*. *Biological Invasions*, 10, 67–77.

Global Invasive Species Database. (2021). Species profile: Littorina littorea. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=400 on 15-02-2021 (accessed 15 February 2021)

Goedknegt, A., Nauta, R., Markovic, M., Buschbaum, C., Folmer, E., Luttikhuizen, P., van der Meer, J., Waser, A., Wegner, M., Thieltges, D. (2019). How invasive oysters can affect parasite infection patterns in native mussels on a large spatial scale. *Oecologia* 190 (1), 10.1007/s00442-019-04408-x

Gollasch, S. (1996). Untersuchungen des Arteintrages durch den internationalen Schiffsverkehr unter besonderer Berücksichtigung nichtheimischer Arten. Diss., Univ. Hamburg; Verlag Dr. Kovac, Hamburg, 314 pp

Gollasch, S. (2006). Overview on introduced aquatic species in European navigational and adjacent waters. *Helgoland Marine Research*, 60, 84-89.

Gollasch, S., Haydar, D., Minchin, D., Wolff, W., Reise, K. (2009). Introduced aquatic species of the North Sea coasts and adjacent brackish waters. In: Rilov, G., Crooks, J. Biological Invasions in marine ecosystems: Ecological, management and geographic perspectives. Ecological Studies 204. Springer, Berlin, Heidelberg.

González-Suárez, M., Gomez, A., Revilla, E. (2013b). Which intrinsic traits predict vulnerability to extinction depends on the actual threatening process. *Ecosphere*, 4, 1-16.

González-Suárez, M., Revilla, E. (2013a). Variability in life-history and ecological traits is a buffer against extinction in mammals. *Ecology Letters,* 16, 242-251.

Graber, S. (2013). Phylogenetic comparative methods for discrete responses in evolutionary biology. Master Thesis in Biostatistics.

Grabowska, J & Przybylski, M. (2015). Life-history traits of non-native freshwater fish invaders differentiate them from natives in the Central European bioregion. *Reviews in Fish Biology and Fisheries*, 25, 165-178.

Grabowski, M., Bacela, K., Konopacka, A. (2007). How to be an invasive gammarid (Amphipoda: Gammaroidea) - comparison of life history traits. *Hydrobiologia,* 590, 75-85.

Grafen, A. (1989). The phylogenetic regression. Phil. Trans. R. Soc. Lond, 326, 119-157

Green, S., Brookson, C., Hardy, N., Crowder, L. (2022). Trait-based approaches to global change ecology: moving from description to prediction. *Proceedings of the Royal Society B,* 289(1971), e0071.

Grey, J., Bjorgesaeter A., Ugland, K., Frank, K. (2006). Are there differences in structure between marine and terrestrial assemblages? *Journal of experimental marine biology and ecology, 330*(1), 19-26.

Gribben, P., I'Ons, S., Phillips, N., Geange, S., Wright, J., Murray, B. (2013). Biogeographic comparisons of the traits and abundance of an invasive crab throughout its native and invasive ranges. *Biological Invasions,* 15(8), 1877–1885.

Grosholz, E., Ruiz, G. (2003). Biological invasions drive size increases in marine and estuarine invertebrates. *Ecological Letters,* 6(8), 700-705.

Guy-Haim, T., Lyons, D.A., Kotta, J., Ojaveer, H., Queirós, A.M., Chatzinikolaou, E., Arvanitidis, C., Como, S., Magni, P., Blight, A.J. (2018). Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: A global review and meta-analysis. *Global Change Biology,* 24 (3), 906–924.

Halpern, B.S., Frazier, M., Potapenko, J. et al. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications,* 6, 7615.

Hänfling, B & Kollmann, J. (2002). An evolutionary perspective of biological invasions. *Trends in Ecological Evolution,* 17, 545–546.

Hänfling, B., Edwards, F., Gherardi, F. (2011). Invasive alien Crustacea: dispersal, establishment and control. *Biological Control,* 56: 573-595.

Hanna, E. & Cardillo, M. (2013). A comparison of current and reconstructed historic geographic range sizes as predictors of extinction risk in Australian mammals. *Biological Conservation,* 158, 196-204.

Harvey, G., Henshar, A., Brasington, J., England, J. (2019). Burrowing invasive species: an unquantified erosion risk at the aquatic-terrestrial interface. *Review of Geophysics,* 57(3), 1018-1036.

Hastie, T., Tibshirani, R., Friedman, J. (2009). Elements of Statistical Learning (second edition, chapter 13), Springer, New York.

Hau, X & Lanfear, R. (2018). The influence of non-random species sampling on macroevolutionary and macroecological inference from phylogenies. *Methods in Ecology and Evolution,* 9 (5), 1352-1362.

Heerwaarden, B & Sgró, C. (2021). Male fertility thermal limits predict vulnerability to climate warming. *Nature Communications,* 12, 2214.

Herbert, R., Roberts, C., Humphreys, J., Fletcher, S. (2012). The Pacific Oyster (*Crassostrea gigas*) in the UK: Economic, Legal and Environmental Issues Associated with its Cultivation, Wild Establishment and Exploitation. Report for the Shellfish Association of Great Britain

Hevia, V., Martin-Lopez, B., Palomo, S., Garcia-Llorente, M., de Bello, F., Gonzalez, J. (2017). Trait-based approaches to analyze the links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. *Ecology and Evolution,* 7(3), 831-844.

Hewitt, J., Everett, R., Parker, N. (2009). Examples of Current International, Regional and national Regulatory Frameworks for Preventing and Managing Marine Bioinvasions in Biological Invasions in Marine Ecosystems

Hewitt, J., Juan, S.D., Lohrer, D., Townsend, M. & D'Archino, R. (2014). Functional traits as indicators of ecological integrity, Prepared for Department of Conservation, 1-41

Hewitt, J., Norkko, J., Kauppi, L., Villnäs, A., Norkko, A., Peters, D. (2016). Species and functional trait turnover in response to broad-scale changes in an invasive species. *Ecosphere,* 7(3), e01289.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am.Nat*, 163, 192-211.

Hobbs, R., Higgs, E., Harris, J. (2009). Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution*, 24(11), 599-605.

Hodgins, K., Bock, D., Rieseberg, L. (2018). Trait Evolution in Invasive Species. *Animal and Plant Reviews Online.* 1(2).

Hopkins, C.C.E. (2002). Introduced marine organisms in Norwegian waters, including

Svalbard. In: Leppäkoski, E., Gollasch, S., Olenin, S. (eds) Invasive aquatic species of Europe. Distribution, impacts and management. Kluwer, Dordrecht, pp 240–252.

Huey, R., Kearney, M., Krockenberger, A., Holtum, J., Jess, M., Williams, S. (2012). Predicting organismal vulnerability to climate warming: roles of beheaviour, physiology ad adaption. *Phiolos Trans R Soc Lond B Biol Sci*, 367(1597), 1665-1679.

Hughes, E., Edwards, D., Thomas, G. (2022). The homogenization of avian morphology and phylogenetic diversity under the global extinction crisis. Current Biology, In press.

Hui, C & Richardson, M. (2017). Invasion Dynamics. Oxford University Press, Oxford, UK .

Hulme, P. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46(1), 10-18.

Hulme, P.E & Bernard-Verdier, M. (2017). Comparing traits of native and alien plants: Can we do better? *Functional Ecology*, 32(1), 117–125.

Hutchings, J., Myers, R., García, V., Lucifora, L., Kuparinen, A. (2012). Life-history correlates of extinction risk and recovery potential. *Ecological Applications*, 22(4), 1061-1067.

Hutchings, J.A., Minto, C., Ricard, D.et al. (2010). Trends in the abundance of marine fishes. *Can J Fish Aquat Sci*, 67, 1205–1210.

Ibáñez, C., Rezende, E., Sepúlveda, R., Avaria-Llautureo, J., Herńandez, C., Sallanes, J., Poulin, E., Pardo-Gandarillas, C. (2018). Thorson's rule, life history evolution, and diversification of benthic octopuses (Cephalopoda: Octopodoidea). *Evolution*, 72(9), 1829-1839.

Iossa, G (2019). Sex-specific differences in thermal fertility limits. *Trends in Ecology and Evolution*, 34, 490-492.

Isaac, J. L. (2009). Effects of climate change on life history: Implications for extinction risk in mammals. *Endangered Species Research*, 7, 115-123.

Isaac, J.L. & Cowlishaw, G. (2004) How species respond to multiple extinction threats. *Proceedings of the Royal Society B: Biological Sciences*, 271 (1544), 1135-1141.

ISSG (2021). Global Invasive Species Database (GISD). In: Global Invasive Species Database (GISD): Invasive Species Specialist Group of the IUCN Species Survival Commission.

https://www.cabi.org/isc/datasheet/71177#04664bfd-c1ca-41c2-a544-1d3239f28d5b

IUCN (2018). Invasive Species. IUCN https://www.iucn.org/theme/species/our-work/invasive-species (accessed 11 November 2018)

IUCN (2021). The IUCN Red List of Threatened Species. Version 2021-1. https://www.iucnredlist.org Accessed: 07 June 2021

IUCN (2022) The IUCN Red List of Threatened Species. Version 2021-3. https://www.iucnredlist.org.

Jackson, J., Le Coeur, C., Jones, O. (2022). Life history predicts global population responses to the weather in terrestrial mammals. *eLife*, 11:e74161.

Jaspers, C., Marty, L., Kiørboe, T. (2018). Selection for life-history traits to maximize population growth in an invasive marine species. *Global Change Biology,* 24(3), 1164–1174.

Jelbert, K., Buss, D., McDonald, J., Townley, S., Franco, M., Scott, I., Jones, O., Salguero-Gomez, R., Buckley, Y., Knight, T., Silk, M., Sargent, F., Rolph, S., Wilson, P & Hodgeson, D. (2019). Demographic amplification is a predictor of invasiveness among plants. *Nature,* 10 (5602).

Jelbert, K., Buss, D., McDonald, J., Townley, S., Franco, M., Stott, I., Jones, O., Salguero-Gómez, R., Buckley, Y., Knight, T., et al. (2019). Demographic amplifications is a predictor of invasiveness among plants. *Nature Communications,* 10, 5602.

Jensen, K. & Knudsen, J. (2005). A summary of alien marine invertebrates in Danish waters. *Oceanological and Hydrobiological Studies,* 34 (Suppl 1), 137-162.

Jeschke, J. M. & Strayer, D. (2006). Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology,* 12, 1608-1619.

Jeschke, J. M. & Strayer, D. (2008). Are threat status and invasion success two sides of the same coin? *Ecography*, 31 (1), 124-130.

Jeschke, J. M. & Strayer, D. (2009). Determinants of invasion success in Europe and north America. *Global Change Biology*, 12 (9), 1608-1619.

Jetz, W. & Pyron R.A. (2018). The interplay pf past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology & Evolution*, 2, 850-858.

Johnson, T., Isaac, N., Paviolo. A., Gonzálex-Suárez, M. (2020). Handling missing values in trait data. *Global Ecology and Biogeography,* 30(1), 51-62.

Jones, K.R., Klein, C.J., Halpern, B.S. et al. (2018). The location and protection status of Earth's diminishing marine wilderness. *Current Biology*, 28, 2506–2512.

Jormalainen, V., Gagnon, K., Sjoroos, J., Rothausler, E. (2016). The invasive mud crab enforces a major shift in a rocky littoral invertebrate community of the Baltic Sea. *Biological Invasions*, 18, 409-419.

Joseph, A. (2017). Chapter 9- Oceans: Abode of Nutraceuticals, Pharmaceuticals, and Biotoxins. In: Investigating Seafloors and Oceans: From Mud Volcanoes to Giant Squid. Elsevier Inc. 493-554.

Juan-Jordá, M. J., Mosqueira, I., Freire, J. & Dulvy, N.K. (2015). Population declines of tuna and relatives depend on their speed of life. *Proceedings of the Royal Society B: Biological Sciences,* 282 (1811), 20150322.

Junior, D., Hoeinghaus, D., Bini, L., Agrostinho, A. (2015). Are non-native species larger in their invaded range? A test with tropical floodplain fish assembly following inundation of a biogeographoical barrier. *Biological Invasions,* 17 (11), 3263-3274.

Kaiser, B. & Burnett, K. (2010). Spatial economic analysis of early detection and rapid response strategies for an invasive species. *Resource Energy Economy*, 32(4), 566–585.

Kalogirou, S., Mittermayer, F., Pihl, L., Wennhage, H. (2012). Feeding ecology of indigenous and non-indigenous fish species within the family Sphyraenidae. *Journal of Fish Biology,* 80, 2528-2548.

Kassambara, A & Mundt, F. (2020). factoextra: Extract and Visualize the Results of Multivariate Data Analysis. R Package version 1.0.7.

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M.E., Oztürk, B., Grabowski, M., Golani, D., Cardoso, A.C. (2014). Impacts of Invasive Alien Marine Species on Ecosystem Services and Biodiversity: a pan-European Review. *Aquatic Invasions,* 9(4), 391-423.

Kattge, J., Bönisch, G., Diaz, S., Lavorel, S., Prentice, I., Leadley, P., Tautenhahn, S., Werner, G., Aakala, T., Abedi, M et al., (2022). TRY plant trait database- enhanced coverage and open access. *Global Change Biology,* 26(1), 119-188.

Keene, J. (1980). The importance of a reef-forming polychaete *Mercierella enigmatica* Fauvel, in the oxygen and nutrient dynamics of a hypereutrophic subtropical lagoon. *Estuarine, Coastal and Shelf Science,* 11(2), 167-178.

Keith, S., Webb, T., Isaac, N. (2012). What is macroecology? *Biological Letters,* 8(6), 904-906.

Keller, R., Drake, J., Lodge, D. (2007). Fecundity as a basis for risk assessment of nonindigenous freshwater molluscs. *Conservation Biology* 21, 191–200.

Keller, R.P., Geist, J., Jeschke, J.M., Kühn, I. (2011). Invasive species in Europe: Ecology, status, and policy, Environmental Sciences Europe. *Springer Open Ltd,* 23(1), 23.

Kellermann V., Overgaard, J., Hoffmann, A., Fiojgaard, C., Svenning, J., Loeschcke, V. (2012). Upper thermal limits of Drosphila are linked to species distributions and strongly constrained phylogenetically. *PNAS,* 109 (40), 16228-16233.

Kelley, A. (2014). The role thermal physiology plays in species invasion. *Conservation Physiology,* 2 (1), 1-14.

Kindsvater, H., Mangel, M., Reynolds, J., Dulvy, N. (2016). Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and Evolution,* 6(7), 2125-2138.

Kindsvater, H.K. & Otto, S. (2014). The Evolution of Offspring Size across Life-History Stages. *The American Naturalist,* 185(5), 543-555.

King, J.R., McFarlane, G.A. & Beamish, R.J. (2001). Incorporating the dynamics of marine systems into the stock assessment and management of sablefish. *Prog. Oceanography,* 49, 619-639.

Kohn, A & Anderson, T (2022). The Conus Biodiversity Website. https://biology.burke.washington.edu

Kolar, C.S. & Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends* *in Ecology and Evolution*, 16, 199-204.

Kolar, C.S. & Lodge, D.M. (2002). Ecological predictions and risk assessment for alien fishes in North America. *Science*, 298, 1233-1236.

Koppel, O. & Kerr, K. (2022). Strong phenological shifts among bumblebee species in North America can help predict extinction risk. *Biological Conservation*, 272, 109675.

Kort, H., Prunier, J., Ducatez, S., Honnay, O., Baguette, M., Stevens, M., Blanchet, S. (2021). Life history, climate and biogeography interactively affect worldwide genetic diversity of plants and animal populations. *Nature Communications*, 12(516).

Kotiaho, J., Kaitala, V., Komonen, A., Paivinen, J. (2005). Predicting the risk of extinction from shared ecological characteristics. *PNAS,* 102(6), 1963-1967.

Kritzer, J & Sale, P. (2006). Marine Metapopulations. Academic Press.

Krushelnycky, P.D. & Gillespie R. (2010). Correlates of vulnerability among arthropod species threatened by invasive ants. *Biodiversity and Conservation*, 19, 1971-1988.

Kulhanek, S., Ricciardi, A., Leung, B. (2011). Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species. *Ecological Applications*, 12(1), 189-202.

Kuparinine, A. & Hutchings, J. (2012). Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proc. Biol. Sci*, 279, 2571-2579.

Lagos, M., White, C., Marshall, D. (2017). Do invasive species live faster? Mass-specific metabolic rate depends on growth form and invasion status. *Functional Ecology,* 31(11), 2080-2086.

Lambdon, P. (2007). Is invasiveness a legacy of evolution? Phylogenetic patterns in the alien flora of Mediterranean islands. *Journal of Ecology,* 96 (1), 46-57.

Larson, E. R. & Olden, J. D. (2010). Latent extinction and invasion risk of crayfishes in the southeastern United States. *Conservation Biology*, 24, 1099-1110.

Le Cam, S., Pechenik, J., Cagnon, M., Viard, M. (2009). Fast versus slow larval growth in an invasive marine mollusc: does paternity matter? *Journal of Heredity,* 100(4), 455-464.

Leffler, A., James, J., Monaco, T., Sheley, R. (2014). A new perspective on trait differences between native and invasive exotic plants. *Ecology*, 95(2), 298-305.

Leishman, M., Thomson, V., Cooke, J. (2009). Native and exotic invasive plants have fundamental similar carbon capture strategies. *Journal of Ecology,* 98(1), 28-42.

Leitz, C. (2022). Which traits predict invasion success in lake and stream environments in the Laurentian Great Lakes Basin? PhD Thesis, University of Michigan.

Leppäkoski, E. & Olenin, S. (2000). Non-native species and rates of spread: Lessons from the brackish Baltic Sea. *Biological Invasions,* 2(2), 151–163.

Leppäkoski, E., Gollasch, S., Gruszka, P., Ojaveer, H., Olenin, S., Panov, V. (2002). The Baltic – A sea of invaders. *Canadian Journal of Fisheries and Aquatic Sciences,* 59(7), 1175-1188.

Leuzinger, S. & Rewald, B. (2021). The Who or the How? Species vs Ecosystem Function Priorities in Conservation Ecology. *Front Plant Sci*, 2(12), 758413.

Lewis, P., Hewitt, C., Riddle, M., McMinn, A. (2003). Marine introductions in the Southern Ocean: an unrecognized hazard to biodiversity. *Marine Pollution Bulletin,* 46(2), 213-223.

Lewis, S. & Maslin, M. (2015). Defining the Anthropocene. *Nature,* 519, 171-180.

Liu, C., Comte, L. & Olden, J. D. (2017). Heads you win, tails you lose: Life history traits predict invasion and extinction risk of the world's freshwater fishes. *Aquatic Conservation Marine and Freshwater Ecosystems,* 27 (4), 773-779.

Lockwood, J. L. (1999). Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. *Conservation Biology,* 13, 560-567.

Lockwood, J., Cassey, P., Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution,* 20(5), 223-228.

Lockwood, J., Cassey, P., Blackburn, T. (2009). The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions,* 15(5), 904-910.

Lockwood, J., Hoopes, M., Marchetti, M. (2013). Invasion Ecology, Wiley-Blackwell, UK

Lotze, H.K., Lenihan, H.S., Bourque, B.J. et al. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, 312, 1806–1809.

Lüdecke, D. (2018). “ggeffects: Tidy Data Frames of Marginal Effects from Regression Models”. *Journal of Open Source Software,* 3(36), 772.

Luypaert, T., Hagan, J., McCarthy, M., Poti, M. (2019). Status of Marine Biodiversity in the Anthropocene. In: Jungblut, S., Liebich, V., Bode-Dalby, M. (eds) YOUMARES 9 – The Oceans: Our Research, Our Future. Springer, Cham.

Lydeard, C., Cowie, R. H., Ponder, W. F., Bogan, A. E., Bouchet, P., Clark, S. A., Cummings, K. S., Frest, T, J., Gargominy, O., Herbert, D. G., Hershler, R., Perez, K., Roth, B., Seddon, M., Strong, E. E. & Thompson, F. G. (2004). The global decline of non- marine mollusks. BioScience, 54, 321-330.

MacArthur, R.H. (1960). On the relation between optimal predation and reproductive value. *Proc. Natl. Acad. Sci. USA,* 46, 143-145.

Magnuson, J., Crowder, L., Medvick, P. (1979). Temperature as an Ecological Resource. *American Zoologist,* 19 (1), 331-343.

Maitner, B., Part, D., Enquist, B., Dlugosch, K. (2021). Where we’ve been and where we’re going: the importance of source communities in predicting establishment success from phylogenetic relationships. *Ecogeography,* 6, e05406.

Marchetti, M., Moyle, P., Levine, R. (2004). Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology,* 49(5), 646-661.

Marchini, A., Munari, C., Mistri, M. (2008). Functions and ecological status of eight Italian lagoons examined using biological traits analysis (BTA). *Marine Pollution Bulletin*, 56(6), 1076–1085.

MarLIN. (2006). BIOTIC – Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. Available from: www.marlin.ac.uk/biotic

Mathakutha, R., Steyn, C., le Roux, P., Blom, I., Chown, S., Daru, B., Ripley, B., Louw, A., Greve, M. (2019). Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science,* 30(5), 994-1006.

McAlister, J. & Moran, A. (2012). Relationship among egg size, composition and energy: A comparative study of germinate sea urchins. *PLoS One,* 7(7), e41599.

McDonald, P., Jensen, G., Armstrong, D. (2001). The competitive and predatory impact sof the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer* magister Dana. *Journal of Experimental Marine Biology & Ecology,* 258 (1), 39–54.

McGill, B., Enquist, B., Weiher, E, Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution,* 21(4), 178-185.

McKnight, E., Garcia-Berthou, E. Srean, P., Rius, M. (2017). Global meta-analysis of native and nonindigenous trophic traits in aquatic ecosystems. *Global Change Biology,* 23(5), 1861-1879.

McMahon, R. (2002). Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance. *Canadian Journal of Fisheries and Aquatic Science,* 59, 1235–1244.

Michonneau, F., Brown, J. W. & Winter, D. J. (2016). rotl: an R package to interact with the Open Tree of Life data. *Methods in Ecology and Evolution*, 7 (12), 1476-1481.

Miller, A., Hewitt, C., Ruiz, G. (2002). Invasion success: does size really matter? *Ecological Letters,* 5(2), 159-162.

Miller, A.W. (2000). Assessing the importance of biological attributes for invasion success: Eastern oyster (Crassostrea virginica) introductions and associated molluscan invasions of Pacific and Atlantic coastal systems. D.Env. dissertation. University of California, Los Angeles 209 pp

Miller, A.W., Ruiz G.M. (2009). Differentiating Successful and Failed Invaders: Species Pools and the Importance of Defining Vector, Source and Recipient Regions. In: Rilov G., Crooks J.A. (eds) Biological Invasions in Marine Ecosystems. Ecological Studies (Analysis and Synthesis), vol 204. Springer, Berlin, Heidelberg.

Miller, J.A., Gillman, R., Carlton, J.T., Murray, C.C., Nelson, J.C., Otani, M., Ruis, G.M. (2018). Trait-based characterization of species transported on Japanese tsunami marine debris: Effect of prior invasion history on trait distribution. *Marine Pollution Bulletin Elsevier,* 132, 90–101.

Minchin, D & Gollasch, S. (2003). Fouling and ships' hulls: how changing circumstances and spawning events may result in the spread of exotic species. *Biofouling*, 19, 111-122.

Minchin, D. & Eno, C. (2002). Exotics of coastal and inland waters of Ireland and Britain. In: Leppäkoski, E., Gollasch, S., Olenin, S. (eds) Invasive aquatic species of Europe: distribution, impact and management. Kluwer, pp 267–275.

Minchin, D., Cook, E., Clark, P. (2013). Alien species in British brackish and marine waters. *Aquatic Invasions*, 8(1), 3-19.

Miranda, M., Miqueleiz, I., Darwall, W., Sayer, C., Dulvy, N., Carpenter, K., Polidoro, B., Dewhurst-Richman, N., Pollock, C., Hilton-Taylor, C., Freeman, R., Collen, B., Böhm, M. (2022). Monitoring extinction risk and threats of the world's fishes based on the Sampled Red List Index. *Reviews in Fish Biology and Fisheries*, 32, 975-991.

MolluscaBase eds. (2020). MolluscaBase. Accessed at http://www.molluscabase.org on 2020-12-02

Molnar, J., Gamboae, R., Revenga, C., Spalding, M. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6(9), 485-492.

Moss, D., Ivany, L., Judd, E., Cummings, P., Bearden, C., Kim, W., Artuc, E., Driscoll, J. (2016). Lifespan, growth rate, and body size across latitude in marine Bivalvia, with implications for Phanerozic evolution. *Proceedings of the Royal Society B Biological Sciences*. 238.

Mouillor, D., Graham, N., Villéger, S., Mason, N., Bellwood, D. (2013). A functional approach reveals community responses to disturbance. *Trends in Ecology and Evolution*, 28(3), 167-177.

Mouillot, D., Loiseau, N., Grenié, M., Algar, A., Allegra, M., Cadotte, M., Casajus, N., Denelle, P., Guéguen, M., Maire, A., Maitner, B., McGill, B., McLean, M., Mouquet, N., Munoz, F., Thuiller, W., Villeger, S., Violle, C., Auber, A. (2021). The dimensionality and structure of species trait spaces. *Ecological Letters*, 24(9), 1988-2009.

Moyle, P. B. & Marchetti, M. P. (2006). Predicting Invasion Success: Freshwater Fishes in Colorado as a Model. *BioScience*, 56 (6), 515-524.

Mullon, C., Freon, P., Cury, P. (2005). The Dynamics of Collapse in World Fisheries. *Fish and*

Fisheries, 6(2), 111-120.

Munday, P. L. (2004). Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology*, 10 (10), 1642- 1647.

Murray, B. R., Thrall, P. H. & Lepschi, B. J. (2002). Relating species rarity to life history in plants of eastern Australia. *Evolutionary Ecology Research*, 4, 937–950.

Myers, P., Espinosa, R., Parr, C., Jones, T., Hammond, G & Dewey, T. (2022). The Animal Diversity Webb. https;//animaldiversity.org.

Naeem, S & Bunker, D. E. (2009). TraitNet: furthering biodiversity research through the curation, discovery and sharing of species trait data. Biodiversity, ecosystem functioning and human wellbeing (ed. By D.E.B Shahid Naeem, D. Bunker, A. Hector, M. Loreau and C. Perrings), pp. 281-289. Oxford University Press, Oxford.

Nati, J., Svendsen, M., Marras, S., Killen, S., Steffensen, J.,McKenzie, D., Domenici, P. (2021). Intraspecific variation in thermal tolerance differs between tropical and temperate fishes. *Scientific Reports,* 11, 21272

Nati, J., Svendsen. M., Marras, S., Killen, S., Steffensen, J., McKenzie, S., Domenici, P. (2021). Intraspecific variation in thermal tolerances differs between tropical and temperate fishes. *Scientific Reports*, 11, 21272.

Nawrot, R., Chattopadhyay, D., Zuschin, M. (2015). What guides invasion success? Ecological correlates of arrival, establishment and spread of Red Sea bivalves in the Mediterranean Sea. *Diversity and Distribution*, 21(9), 1075-1086.

Nehring, S. (2002). Biological invasions into German waters: an evaluation of the importance of different human-mediated vectors for nonindigenous macrozoobenthic species. In: Leppäkoski, E., Gollasch, S. and Olenin, S (eds.) Invasive aquatic species of Europe – Distribution, impacts and management. Kluwer, Dordrecht, 373-383.

Nehring, S. (2005). International shipping — a risk for aquatic biodiversity in Germany. In: Nentwig W, Bacher S, Cock MJW, Dietz H, Gigon A, Wittenberg R (eds) Biological invasions – from ecology to control. *NEOBIOTA*, 6, 125–143.

Neigel, J.E. (2003). Species-area relationships and marine conservation. *Ecological Applications*, 13(1), 138-145.

OBIS (2022). Ocean biogeographic information system. Retrieved from www.obis.org

Ojaveer, J., Galil, B., Zaiko, A. (2018). Historical baselines in marine bioinvasions: Implications for policy and management. *PLoS ONE,* 13(8), e0202383.

Olden, J. D., Hogan, Z. S. & Zander, J. V. (2007). Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, 16 (6), 694-701.

Olden, J. D., Leroy, Poff. N, Bestgen, K. R. (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs,* 76(1), 25–40.

Olenin, S., Alemany, F., Cardoso, A.C., Gollasch, S., Goulletquer, P., Lehtinieml, M., McCollin, T., Minchin, D., Mlossec, L., Occhipinti-Ambrogu, A. (2010). Marine Strategy Framework Directive - Task Group 2 Report. Non-indigenous Species, 44. Office for Official Publications of the European Communities, Luxembourg.

Oliver, P., Holmes, A., Killeen, I., & Turner, J. (2016). Marine Bivalve Shells of the British Isles. Amgueddfa Cymru- National Museum of Wales. https://naturalhistory.museumwales.ac.uk/britishbivalves.

Orme, D., Freckleton, R.P., Thomas, G.H., Petzoldt, T., Fritz, S.A. & Isaac, N. (2013). CAPER: comparative analysis of phylogenies and evolution in R. *Methods in Ecology and Evolution*, 3, 145-151.

Orr, J.C., Fabry, V.J., Aumont, O. et al. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature,* 437, 681.

Owens, I.P.F. & Bennett, P.M. (2000). Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *PNAS,* 12144-12148.

Padilla, D. (2010). Context-dependent Impacts of a Non-native Ecosystem Engineer, the Pacific Oyster *Crassostrea gigas. Integrative and Comparative Biology.* 50(2), 213-225.

Paganelli, D., Marchini, A., Occhipinti-Ambrogi, A. (2012). Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): A study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). *Estuarine, Coastal and Shelf Science,* 96(1), 245–256.

Pagel, M.D. (1989). Comparative methods for examining adaption depend on evolutionary models. *Folia Primatologica,* 53, 203-220.

Palomares, M & Pauley, D. (2022). SeaLifeBase. World Wide Web electronic publication. www.sealifebase.org.

Park, D., Feng, X., Maitner, B., Enquist, B. (2020). Darwin's naturalization conundrum can be explained by spatial scale. *Proc Natl Acad Sci USA,* 117(20), 10904-10910.

Parker, J., Torchin, M., Hufbauer, R., Lemoine, N., Alba, C., Blumenthal, D., Bossdorf, O., Byers, J., Dunn, A., Heckman, R., et al., (2013). Do invasive species perform better in their new ranges? *Ecology,* 94(5), 985-994.

Parker, L., Ross, P., O'Connor, W., Portner, H., Scanes, E & Wright, J. (2013). Predicting the Response of Molluscs to the Impact of Ocean Acidification. *Biology,* 2, 651-692.

Parmesan, C & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* 421, 37-42.

Payne, J.L., Bush, A.M., Heim, N.A., Knope, M.L. & McCauley, D.J. (2016). Ecological selectivity of the emerging mass extinction in the oceans. *Science,* 353(6305), 1284-1286.

Payne, N., Smith, J. (2016). An alternative explanation for global trends in thermal tolerance. *Ecology Letters,* 20 (1), 70-77.

Pearson, R., Stanton, J., Shoemaker, K., Akcakaya, H. et al. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Clime Change,* 4(3), 217-221.

Peralta-Maraver, I & Rezende, E (2021). Heat tolerance in ectotherms scales predictably with body size. *Nature Climate Change,* 11, 58-63.

Perez, K. & Munch, S. (2010). Extreme selection on size in the early lives of fish. *Evolution,* 64 (8), 2450-2457.

Perrin, N. (1988). Why are Offspring Born Larger When It is Colder? Phenotypic Plasticity for Offspring Size in the Caldoceran Simoscephalus vetulus (Muller). *Functional Ecology,* 2 (3), 283-288.

Peters, H., O'Leary B., Hawkins, J., Carpenter, K & Roberts, C. (2013). Conus: First Comprehensive Conservation Red List Assessment of a Marine Gastropod Mollusc Genus. *PLoS ONE,* 8 (12), e83353.

Petruzzella, A., Rodrigues, T., Leeuwen, C., Esteves, F., Figueiredo-Barros, M., Bakker, E. (2020). Species identity and diversity effects on invasion resistance in tropical freshwater plant communities. *Scientific Reports,* 10(5626).

Pettitt-Wade, H., Wellband, K., Fisk, A. (2017). Inconsistency for the niche breadth invasion success hypothesis in aquatic invertebrates. *Limnology and Oceanology,* 63(1), 141-159.

Pigot, A., Dyer, E., Redding, D., Cassey, P., Thomas, G, & Blackburn, T. (2017). Species invasions and the phylogenetic signal in geographical range size. *Global Ecology and Biogeography*, 27, 1080-1092.

Pigot, A., Jetz, W., Sheard, C., Tobias, J. (2018). The macroecological dynamics of species coexistence in birds. *Nature Ecology & Evolution,* 2, 1112-1119.

Pincheira-Donoso, D., Harvey, L., Cotter S., Stark G., Mein S., Hodgeson D (2020). The global macroecology of brood size in amphibians reveals a predisposition of low-fecundity species to extinction. *Global Ecology & Biogeography,* 30, 1299-1310.

Pinheiro, J., Bates, D., R Core Team (2022). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-159. Retrieved from: https://CRAN.R-project.org/package=nlme

Pinsky, M.L. & Byler, D. (2015). Fishing, fast growth and climate variability increase the risk of collapse. *Proceedings of Royal Biological Society B,* 282, 20151053.

Pöckl, M. (2007). Strategies of a successful new invader in European fresh waters: fecundity and reproductive potential of the Ponto-Caspian amphpod *Dikerogammarus villosus* in the Austrian danube, compared with the indigenous *Gammarus fossarum* and *G. roeseli*. *Freshwater Biology,* 52(1), 50-63.

Pörtner, H & Farrell, A. (2008). Physiology and Climate Change. *Science,* 332 (5902), 690-692.

Powles, H., Bradford, M., Bradford, R., Doubleday, W., Innes, S., Levings, C. (2000). Assessing and protecting endangered marine species. *ICES Journal of Marine Science,* 57, 669-676.

Preisler, R., Wasson, K., Wolff, W., Tyrrell, M. (2009). Invasions of Estuaries vs the Adjacent Open Coast: A Global Perspective in Biological Invasions in Marine Ecosystems, In: Rilov G., Crooks, J.A. (eds). Biological Invasions in Marine Ecosystems, vol 204. Springer, Berlin, Heidelberg.

Prinzing, A., Durka, W., Klotz, S., Brandl, R. (2002). Which species become aliens? *Evol Ecol Res*, 4, 385–405.

Provoost, P., Bosch, S (2019). robis: R client to access data from the OBIS API. Retrieved from:https://cran-r-project.org/package=robis

Purvis, A., Gittleman J.L., Cowlishaw, G. & Mace, G. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B*, 267, 1947-1952.

Pysek, P., Richardson, D., Pergl, J., Jarosik, V., Sixtrova, Z & Weber E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, 23 (5), 237-244.

Qin, J., Xiang, M., Meixiang, J., Cheng, F., Shang, L., Schmidt, B., Liu, J., Xie, S. (2020). Combined opportunistic and equilibrium life-history traits facilitate successful invasions of the Shimofuri goby (Tridentiger bifasciatus). Aquatic Invasions, in press.

Queirós, A.M., Bruggeman, J., Stephens, N., Artioli, Y., Butenschön, M., Blackford, J.C., Widdicombe, C., Allen, J.I. & Somerfield, P.J. (2015). Placing biodiversity in ecosystem models without getting lost in translation. *Journal of Sea Research*, 98, 83–90.

Quell, F., Schratzberger, M., Beauchard, O., Bruggerman, J. & Webb, T. (2021). Biological trait profiles discriminate between native and non-indigenous marine invertebrates. *Aquatic Invasions,* 16 (4), 571-600.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

R Core Team (2021). R: A language and environment for statistical computing. Retrieved from: https://www.R-Porject.org

Raddaelli, D., Solan, M., Webb, T (2005). Do marine and terrestrial ecologists do it differently? *Marine ecology progress series,* 304, 283-289.

Reise, K., Gollasch, S., Wolff, W. (1998). Introduced marine species of the North Sea coasts. *Helgoländer Meeresuntersuchungen,* 52(3-4), 219-234.

Rejmanek, M. & Richardon, D. (1996). What attributes make some plant species more invasive? *Ecology*, 77, 1655-1661.

Relyea, R., Stephens, P., Hammond, J. (2021). Phylogenetic patterns of trait and trait plasticity evolution: Insights from tadpoles. *Evolution,* 75(10), 2568-2588.

Revell, L.J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, 1, 319-329.

Reynolds, J. D., Dulvy, N. K., Goodwin, N. B. & Hutchings, J. A. (2005). Biology of extinction risk in marine fish. *Proceedings of the Royal Society B Biological Sciences*, 275 (1579), 2337-2344.

Ricciardi, A. & Mottiar, M. (2006). Does Darwin's naturalization hypothesis explain fish invasions? *Biological Invasions,* 8, 1403-1407.

Ricciardi, A. (2003). Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. *Freshwater Biology*, 48(6), 972–981.

Ricciardi, A. (2015). 'Ecology of Invasive Alien Invertebrates' in Thorp and Covich's Freshwater Invertebrates. Fourth Edition, Elsevier Inc, 83-91.

Ricciardi, A., Atkinson, S. (2004). Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecological Letters*, 7(9), 781–784.

Ricciardi, A., Cohen, J. (2007). The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, 9, 309-315.

Richard, J., Huet, M., Thouzeau, G., Paulet, Y. (2006). Reproduction of the invasive slipper limpet, *Crepidula fornicata*, in the Bay of Brest, France. *Marine Biology,* 149, 789-801.

Richardson, D., Pysek, P., Rejmánek, M., Barbour, M., Panetta, F. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions,* 3(6), 14-93.

Rilov, G. & Crooks, J. (2009). Marine Bioinvasions: Conservation Hazards and Vehicles for Ecological Understanding, in Biological Invasions in Marine Ecosystems.

Rilov, G. (2009). The Integration of Invasive Species into Marine Ecosystemss. In: Rilov G., Crooks J.A. (eds) Biological Invasions in Marine Ecosystems. Ecological Studies (Analysis and Synthesis), vol 204. Springer, Berlin, Heidelberg.

Rius, M., Ahyong, S., Bieler, R., Boudouresque, C., Costello, M.,Downey, R.,Galil, B., Gollasch, S, Hutchings, P., Kamburska, L, et al., (2022). World Register of Introduced Marine Species (WiRMS). Accessed at https://www.marinespecies.org/introduced

Rodriguez, L. (2006). Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions,* 8 (4), 927–939.

Rohr, J., Civitello, D., Cohen, J., Roznik, E., Sinervo, B., Dell, A. (2018). The complex drivers of thermal acclimation and breadth in ectotherms. *Ecology Letters,* 21(9), 1425-1439.

Rothschild, B.J. (1986). The dynamics of marine fish populations. Harvard University Press, Cambridge, MA.

Roy, H., Bacher, S., Essl, F., Adriaens, T., Aldridge, D., Bishop, J., Blackburn, T., Branquar, E., Brodie, J., Carboneras, C. et al., (2018). Developing a list of invasive alien species likely to threaten biodiversity and ecosystems in the European Union. *Global Change Biology,* 25(3), 1032-1048.

Roy, K., Jablonski, D., Valentine, J. (2002). Body size and invasion success in marine bivalves. *Ecological Letters*, 5(2), 163–167.

Rubalcaba, J & Olalla-Tárraga, M. (2020). The biogeography of thermal risk for terrestrial ectotherms: Scaling of thermal tolerance with body size and latitude. *Journal of Animal Ecology,* 89 (5), 1277-1285.

Ruiz, G., Fofonoff, P., Carlton, J., Wonham, M., Hines, A. (2000). Invasions of Coastal Marine Communities in North America: Apparent Patterns, Processes and Biases. *Annual Review of Ecology and Systematics,* 31, 481-531.

Ruiz, G., Rawlings, T., Dobbs, E., Drake, F., Mullady, T., Huq, A., Colwell, R. (2000). Global spread of microorganisms by ships- ballast water discharged from vessels harbours a cocktail of potential pathogens. *Nature,* 408, 49-50.

Saeedi, H., Costello, M., Warren, D., Brandt, A. (2019). Latitudinal and bathymetrical species richness patterns in the NW Pacific and adjacent Arctic Ocean. *Scientific Reports,* 9, 9309.

Sakai, A.K., Allenford, F.W., Holt, J.S., Lodge, D.M., Molofsky, J.K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C. et al., (2001). The Population Biology of Invasive Species.

Review of Ecology and Systematics, 32, 305-332.

Salguero-Gómez, R., Violle, C., Gimenez, O., Childs, D. (2018). Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. *Functional Ecology,* 32(6), 1424-1435.

Salice, C. J. (2009). Amphibian life history and extinction risk in an uncertain and stressful world. Conference: 94th ESA Annual Convention 2009.

Sarremejane, R., Cid, N., Stubbington, R., Datry, T., Alp, M., et al. (2020). DISPERSE, a trait database to assess the dispersal potential of European aquatic macroinvertebrates. *Scientific Data,* 7(386).

Schindler, D., Knapp, R., Leavitt, P. (2001). Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. *Ecosystems,* 4, 308-321.

Schneider, F., Fichtmueller, D., Gossner, M. et al. (2019). Towards an ecological trait-data standard. *Methods in Ecology and Evolution*, 10(12), 2006-2019.

Seddon, M. B., Killeen, I. J. & Fowles, A. P. (2014). A Review of the Non-Marine Mollusca of Great Britain: Species Status No. 17. NRW Evidence Report No: 14, 84pp, Natural Resources Wales, Bangor.

Seebens, H., Essl, F., Dawson, Y., Fuentes, N., Moser, D., Pergl, J., Pysek, P., Kleunen, M., Weber, E., Winter, M., Blasius, B. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology,* 21(11), 4128–4140.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. & Muller, J. (2015). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe: beetle extinction and forest degradation. *Conservation Biology,* 29, 382-390.

Shah, A., Gill, B., Encalada, A., Flecker, A., Funk, C., Guayasamin, J., Kondratieff, B., Poff, L., Thomas, S., Zamudio, K., Ghalambor, C. (2017). Climate variability predicts thermal limits of aquatic insects across elevation and latitude. *Functional Ecology,* 31 (11), 2118-2127

Shao-Peng, L., Tan, J., Yang, X., Ma, C., Jiang, L. (2019). Niche and fitness differences determine invasion success and impact in laboratory bacterial communities. *ISME,* 13(2), 403-412.

Smiseth P, Kolliker M, Royle N 'What is parental care?', in Smiseth P, Kolliker M, Royle N (2012). The Evolution of parental care. Oxford University Press

Sodhi, N.S., Koh, L.P., Peh., K.S., Tan. H.T.W., Chazdon, R.L., Corlett, R.T., Lee, T,M., Colwell, R.K et al (2008). Correlates of extinction proneness in tropical angiosperms. *Diversity and Distributions*, 14, 1-10.

Sol, D., Garcia-Porta, J., González-Lagos, C., Pigot, A., Trisos, C., Tobias, J. (2022). A test of Darwin's naturalization conundrum in birds reveals enhanced invasion success in the presence of close relatives. *Ecology Letters*, 25(3), 661-672.

Sol, D., Maspons, J., Vall-Ilosera, M., García-Peña, G., Piñol, J., Freckleton, R. (2012). Unravelling the Life History of Successful Invaders. *Science*, 337, 580-583.

Somero, G. (2005). Linking biogeography to physiology: Evolutionary and acclimatory adjustments of thermal limits. *Frontiers in Zoology*, 2 (1), https://doi.org/10.1186/1742-9994-2-1

Somero, G. (2011). Comparative physiology: a "crystal ball" for predicting consequences of global change. *Am J Physiol Regul Integr Comp Physiol*, 301 (1), 21430078.

Statzner, B., Bonada, N. & Dolédec, S. (2008). Biological attributes discriminating invasive from native European stream macroinvertebrates. *Biological Invasions*, 10(4), 517–530.

Stavert, J., Pattemore, D., Gaskett, A., Beggs, J., Bartomeus, I. (2017). Exotic species enhance response diversity to land-use change but modify functional composition. *Proceedings of the Royal Society B Biological Sciences*, 284. 20170788.

Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., Ludwig, C. (2015). The trajectory of the Anthropocene: The great acceleration. *Anthropocene Review*, 2(1), 81–98.

Stohlgren, T. & Schnase, J. (2006). Risk analysis for biological hazards: what we need to know about invasive species. *Risk Analysis*, 26, 126-173.

Suding, K., Larvorel, S., Chapin, F., Cornelissen, J., Dias, S., Gardier, E., Goldberg, D., Hooper, D., Jackson, S., Navas, M. (2008). Scaling environmental change through community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, 14, 1125-1140.

Suhonen, J., Ilvonen, J., Korkeamaki, E., Nokkala, C., Salmela, J. (2022). Using functional traits and phylogeny to understand local extinction risk in dragonflies and damselflies (Odonata). *Ecology & Evolution,* 12(3), e8648.

Sunday, J., Bates, A & Dulvy, N. (2011). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, 278 (1713), 1823-1830.

Sunday, J., Bates, A & Dulvy, N. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change,* 2, 686-690.

Sunday, J., Bennett, J., Calosi, P., Clusella-Trullas, S., Gravel, S., Hargreaves, A., Leiva, F., Verberk, W., Olallo-Tárraga, M & Morales-Castilla, I. (2019). Thermal tolerance patterns across latitude and elevation. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 374: 20190036.

Swart, C., Visser, V., Robinson, T.B. (2018). Patterns and traits associated with invasions by predatory marine crabs. *NeoBiota,* 39, 79–102.

Symonds, M. & Blomberg, S. (2014). A Primer on Phylogenetic Generalised Least Squares. In: Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology. Springer-Verlag Berlin Heidelberg. Garamszegi, L.Z.

Tang, F. & Aldridge, D. C. (2019). Microcapsulated biocides for the targeted control of invasive bivalves. *Scientific Reports*, 9 (18787).

Tayeh, A., Hufbauer R, Estoup, A., Ravinge, V., Frachon L. & Facon, B. (2015). Biological invasion and biological control select for different life histories. *Nature Communications,* 7268.

Tepolt, C & Somero, G. (2014). Master of all trades: thermal acclimation and adaption of cardiac function in a broadly distributed marine invasive species, the European green crab, Carcinus maenas. *Journal of Experimental Biology,* 217 (7), 1129-1138.

Terzopoulou, S., Rigal, F., Whittaker, R., Borges, P., Triantis, K. (2015). Drivers of extinction: the case of Azorean beetles. *Biology Letters*, 11(6), 20150273.

Theoharides, K.A, & Dukes, J.S. (2007). Plant invasion across space and time: Factors affecting nonindigenous species success during four stages of invasion. *New Phytologist,* 176(2), 256–273.

Thomas, N. & Thorp, C. (1994). Cyclical changes in the fauna associated with tube aggregates of Ficopomatus enigmaticus (Fauvel). *Mémoires de Muséum National d'Histoire Naturelle,* 162, 575-584.

Thorson, G. (1936). The larval development, growth and metabolism of Arctic marine bottom invertebrates compared with those of other seas. *Meddelingen on Grönland*, 100, 1-155.

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews,* 25(1), 1-45.

Thorson, G. (1957). Bottom communities (sublittoral or shallow shelf). In “Treatise on Marine Ecology and Paleoecology” (Ed J.W.Hedgpeth), pp. 461-535. Geological Society of America.

Tingley, R., Hitchmough, R. A. & Chapple, D. G. (2013). Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. *Biological Conservation*, 165, 62-68.

Torchin, M., Lafferty, K., Kuris, A. (2001). Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasion,* 3, 333–345.

Torres-Romero, E., Moreales-Castilla, I., Olalla-Tárraga, M. (2016). Bergmann’s rule in the oceans? Temperature strongly correlates with global interspecific patterns of body size in marine mammals. Global Ecology and Biogeography, 25(10), 1206-1215.

Tricarico, E., Junqueira, A., Dudgeon, D. (2016). Alien species in aquatic environments: a selective comparison of coastal and inland waters in tropical and temperate latitudes. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 26(5), 872-891.

Tyberghein, L., Verbruggen, J., Pauly, K., Troupin C., Mineur, F., De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography,* 21, 272-281.

Tyler, E. H. M., Somerfield, P. L., Berghe, E. V., Bremner, J., Jackson, J., Langmead, O., Palomares, M. L. D. & Webb, T. J. (2012). Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. Global Ecology and Biogeography, 21 (9), 922-934.

Van Allen, B., Dunham, A., Asquith, C., Rudolf, V. (2012). Life history predicts risk of species declines in a stochastic world. *Proc. R. Soc. B*, 279, 2691-2697.

van Kleunen, M., Weber, E., Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13(2), 235–245.

van Kluenen, M. & Richardson, D. M. (2007). Invasion biology and conservation biology: time to join forces to explore the links between species traits and extinction risk and invasiveness. *Progress in Physical Geography*, 31 (4), 447-450.

van Kuijk, T., Biesmeiher, J., van der Hoorn, B., Verdonschot, P. (2021). Functional traits explain crayfish invasion success in the Netherlands. *Scientific Reports,* 11, 2772.

Várbíró, G., Borics, G., Novais, M., Morais, M., Rimet, F., Bouchez, A., Tapolczai, K., Bácsi, I., Usseglio-Polatera, P., Béres, V. (2020). Environmental filtering and limiting similarity as main forces driving diatom community structure in Mediterranean and continental temporary and perennial streams. *Science of The Total Environment,* 741, 140459.

Verberk, W., Noordwijk, C., Hildrew, A. (2013). Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science,* 32(2), 531-347.

Verde, A. L. (2016). Biases, gaps, and opportunities in mammalian extinction risk research. *Mammal Research,* 46, 17-29.

Vermeij, G.J. (2005). Invasion as expectation. In: DF Sax, JJ Stachowicz, SD Gaines, eds. Species invasions: insights into ecology, evolution and biogeography. Sunderland, MA, USA: Sinauer Associates, 315– 339.

Vilà, M., Basnou, C., Pysek, P., Joseffson, M., Genovesi, P., Gollaschm, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P., et al., (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and Environment,* 8(3), 135–144.

Vila-Gispert, A., Alcaraz, C. & García-Berthou, E. (2005). Life-history traits of invasive fish in small Mediterranean streams. *Biological Invasions*, 7 (107).

Waldock, C., Stuart-Smith, R., Edgar, G., Bird, T., Bates, A. (2019). The shape of abundance distributions across temperature gradients in reef fishes. *Ecology Letters,* 22 (4), 685-696.

Wang, Y., Si, Xingfeng, Bennett, P. M., Chen, Chuanwu., Zeng, D., Zhao, Y. & Ping Ding, Y.U. (2017) Ecological correlates of extinction risk in Chinese birds. Ecogeography, 41 (5), 782-794.

Webb, J.K., Brook, B.W. & Shine, R. (2002). What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecological Research*, 17, 59-67.

Webb, T & Vanhoorne, B. (2020). Linking dimensions of data on global marine animal diversity. *Philosophical Transactions B,* 375, 20190445.

Webb, T. (2012). Marine and terrestrial ecology: unifying concepts, revealing differences. *Trends in Ecology & Evolution*, 27(10), 535-541.

Webb, T., Dulvy, N., Jennings, S., Polunin, N. (2011). The birds and the seas: body size reconciles differences in the abundance-occupancy relationship across marine and terrestrial vertebrates. *Oikos,* 120 (4), 537-549.

Webb, T., Lines, A & Howarth, L. (2020). Occupancy-derived thermal affinities reflect known physiological thermal limits of marine species. *Ecology and Evolution*, 10 (14), 7050-7061.

Webb, T., Mindel, B. (2015). Global Patterns of Extinction Risk in Marine and Non-Marine Systems. *Current Biology*, 26(4), 506-511.

Weigel, B., Blenckner, T., Bonsdorff, E. (2016). Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos,* 125, 1421-1433.

Weis, J. (2010). The role of behaviour in the success of invasive crustaceans. *Marine and Freshwater Behaviour and Physiology,* 43(2), 83-98.

Weiss, K. & Ray, C. (2019). Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides. *Ecogeography,* 42(12), 2012-2020.

Whitman, J. & Roy, K. (2009). Marine Macroecology. Chicago University Press.

Wickham, H (2017). tidyverse: Easily install and Load the “Tidyverse”. Retrieved from https://CRAN.R-project.org/package=tidyverse

Wiens, J., Ackerly, D., Allen, A., Anacker, B., Buckley, L., Cornell, H., Damschen, E., Davies J., Grytnes, J., Harrison, S et al., (2010) Niche conservatism as an emerging principal in ecology and conservation biology. *Ecology Letters,* 13 (10), 1310-1324.

Williamson, M. & Fitter, A. (1996). The characteristics of successful invaders. *Biological Conservation,* 78, 163-170.

Wilman, H., Belmaker, J., Simpson, J., Rosa, C., Rivadeneira, M., Jelts, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology,* 95(7), 2027-2027.

Winemiller, K. (2005). Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences,* 62(4), 872-885.

Wolff, W.J. (2005). Non-indigenous marine and estuarine species in the Netherlands. *Zool Meded Leiden,* 79, 1–116.

WoRMS Editorial Board (2022). World Register of Marine Species. Available from https://www.marinespecies.org at VLIZ. Accessed 2022-07-13. doi:10.14284/170

Wright, P.J. (2014). Are there useful life history indicators of stock recovery rates in gaddoids? *ICES J. Mar. Sci.,* 71, 1393-1406.

Xing, K., Zhao, F (2022). Acclimation effects of natural daily temperature variation on longevity, fecundity, and thermal tolerance of the diamondback moth (*Plutella xylostella).* *Insects*, 13(4), 309.

Yannelli, F. A., Koch, C., Jeschke, J. M., Kollmann, J. (2017). Limiting similarity and Darwin's naturalization hypothesis: understanding the drivers of biotic resistance against invasive plant species. *Oecologia,* 183, 775-784.

Yannelli, F., Hughes, P., Kollmann, J. (2017). Preventing plant invasions at early stages of revegetation: The role of limiting similarity in seed size and seed density. *Ecological Engineering,* 100, 286-290.

Yessoufou, K & Davies, T. (2016). Reconsidering the Loss of Evolutionary History: How Does Non-random Extinction Prune the Tree-of-Life? In: Pellens, R & Grandcolas, P (eds) Biodiversity Conservation and Phylogenetic Systematics. Topics in Biodiversity and Conservation, vol 14. Springer, Cham.

Young, A & Larson, B. (2011). Clarifying debates in invasion biology: a survey of invasion biologists. *Environmental Research*, 111(7), 893-898.

Yu G (2022). *Data Integration, Manipulation and Visualization of Phylogenetic Treess*, 1st edition edition. Chapman and Hall/CRC. https://www.amazon.com/Integration-Manipulation-Visualization-Phylogenetic-Computational-ebook/dp/B0B5NLZR1Z/.

Zenetos, A., Çinar, M. E., Crocetta, F., Golani, D., Rosso, A., Servello, G., Shenkar, N., Turon, X., Verlaque, M. (2017). Uncertainties and validation of alien species catalogues: The Mediterranean as an example. *Estuarine, Coastal and Shelf Science*, 191, 171–187.

Zerebecki, R & Sorte, C. (2011). Temperature Tolerance and Stress Proteins as Mechanisms of Invasive Species Success. *PLoS ONE*, 6(4), e14806.

Zong, Y., Chen, C. & Wang, Y. (2021). Biological and extrinsic correlates of extinction risk in Chinese lizards. *Current Zoology*, 1-9.

Zwerschke, N., van Rein, H. C., Reddin, C., Emmerson, M., Roberts, D., O'Connor, N. (2018). Compeition between co-occurring invasive and native consumers switch between habitats. *Functional Ecology*, 32(12), 2717-2729.

7. Supporting Material

Table S1: The proportion of each phyla included in the native and non-indigenous species dataset. The total number is given, with the percentages in parenthesis.

	Non-indigenous species	Native species	All species
Annelida	13 (15.3%)	50 (16.6%)	63 (16.3%)
Arthropoda	27 (31.8%)	80 (26.5%)	107 (27.5%)
Bryozoa	2 (2.4%)	20 (6.6%)	22 (5.7%)
Chordata	5 (5.9%)	20 (6.6%)	25 (6.5%)
Cnidaria	5 (5.9%)	22 (7.3%)	27 (7%)
Mollusca	32 (37.5%)	101 (33.4%)	133 (34.4%)
Platyhelminthes	1 (1.2%)	9 (3%)	10 (2.6%)

Table S2: The most important positive and negative loadings of trait modalities on dimension 1 and dimension 2 of the bidimensional plot encompassing the whole non-indigenous species dataset (Table 1, Figure 2b).

	Modality	**Dim1**	**Modality**	**Dim2**
Positive				
	L1 (<1year)	0.611	Am2 (1-3years)	0.516
	B1 (<1cm)	0.608	F5 (Omnivore)	0.459
	O1 (eggs)	0.539	M2 (Craw-Swim)	0.454
	Af1 (<100)	0.452	Bd2 (5-15cm)	0.389
	Af2 (100-1000)	0.452	L2 (1-3years)	0.372
Negative				
	B3 (3-10cm)	-0.528	M6 (Atta-Sessile)	-0.488
	F2 (Suspension)	-0.556	L1 (<1year)	-0.525
	Os2 (100-500um)	-0.558	M3 (Swimmer)	-0.552
	Af5 (>100,000)	-0.640	Bd4 (None)	-0.613
	O3 (Larvae)	-0.644	P1 (1-15days)	-0.614

Table S3: List of fifty-nine potentially invasive native species. * signifies those identified through RDA, ** indicates those which share 6-9 traits with a known NIS, *** represents those share 10-11 traits with a known NIS, and bold indicates those with identical trait profiles to a known NIS. Invasive refers to whether these native European species are themselves invasive elsewhere.

Species	Phylum	Invasive
*Chaetopterus variopedatus***	Annelida	Yes
*Goniada maculata****	Annelida	No
*Lanice conchilega***	Annelida	No
*Hediste diversicolor***	Annelida	No
*Hydroides norvegica***	Annelida	No
*Lepidonotus squamatus***	Annelida	No
*Poecilochaetus serpens***	Annelida	No
*Pygospio elegans***	Annelida	Yes
*Spiophanes bombyx***	Annelida	No
*Streblospio shrubsolii***	Annelida	No
*Thelepus cincinnatus***	Annelida	No
*Adna anglica****	Arthropoda	No
*Anthura gracilis***	Arthropoda	No
*Calanoides carinatus****	Arthropoda	No
*Chirona hameri****	Arthropoda	No
*Conilera cylindracea***	Arthropoda	No
*Eurydice pulchra***	Arthropoda	No
*Eurydice spinigera****	Arthropoda	No
*Eurydice truncate****	Arthropoda	No
*Pisidia longicornis***	Arthropoda	No
*Portumnus latipes***	Arthropoda	No
*Semibalanus balanoides****	Arthropoda	Yes
*Upogebia deltaura**	Arthropoda	No
*Chorizopora brongniartii****	Bryozoa	No
*Escharella ventricosa****	Bryozoa	No
*Microporella ciliate****	Bryozoa	No
*Porella concinna****	Bryozoa	No
*Ciona intestinalis****	Chordata	Yes
*Dendrodoa grossularia***	Chordata	No
Polycarpa pomaria	Chordata	No
*Polycarpa scuba**	Chordata	No
*Actinothoe sphyrodeta***	Cnidaria	No
*Clava multicornis***	Cnidaria	Yes
*Ectopleura larynx***	Cnidaria	No
*Hydractinia echinate***	Cnidaria	No
*Aequipecten opercularis***	Mollusca	Yes
*Anomia ephippium**	Mollusca	No
Atrina pectinate	Mollusca	No
*Corbula gibba***	Mollusca	Yes
*Diodora graeca***	Mollusca	No
Euspira catena	Mollusca	No
*Littorina littorea***	Mollusca	Yes
*Littorina obtusata***	Mollusca	No
*Lutraria lutraria***	Mollusca	No
*Mimachlamys varia***	Mollusca	No
*Modiolus adriaticus****	Mollusca	No
*Modiolus modiolus****	Mollusca	No
*Mytilus edulis***	Mollusca	Yes
*Nucella lapillus***	Mollusca	Yes
*Ocenebra erinaceus***	Mollusca	No
*Ostrea edulis***	Mollusca	Yes
*Palliolum tigerinum***	Mollusca	No
*Phaxas pellucidus***	Mollusca	No
*Propeamussium lucidum**	Mollusca	No
*Pteria hirundo***	Mollusca	Yes
*Similipecten similis***	Mollusca	No
*Solen marginatus**	Mollusca	Yes
*Steromphala umbilicalis***	Mollusca	No
*Talochlamys pusio***	Mollusca	No

Table S4: References for the native ranges of non-indigenous species used in the study.

Scientific name	**Native range**	**Reference**
Acartia tonsa	Indo-Pacific	Leppäkoski E., Olenin S. (2000). Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biological invasions, 2(2), 151-163.
Acartia omorii	Indo-Pacific	Galil B.S., Clark P.F., Carlton J.T. (Eds.). (2011). In the wrong place-alien marine crustaceans: distribution, biology and impacts (Vol. 6). Springer Science & Business Media.
Ammothea hilgendorfi	NW Pacific	Eno, N.C., Clark, R.A. & Sanderson, W.G. (eds). (1997). Non-native marine species in British waters: a review and directory, JNCC, Peterborough.
Amphibalanus amphitrite	Indo-Pacific	Cohen A.N. (2005). Guide to the Exotic Species of San Francisco Bay. San Francisco Estuary Institute, Oakland, CA.
Amphibalanus eburneus	NW Atlantic	Galil B.S., Clark P.F., Carlton J.T. (Eds.). (2011). In the wrong place-alien marine crustaceans: distribution, biology and impacts (Vol. 6). Springer Science & Business Media.
Amphibalanus improvisus	NW Atlantic	Shalaeva, E (2022). Balanus Improvisus. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.
Anomia chinensis	NW Pacific	Fofonoff PW, Ruiz GM, Steves B, Simkanin C, & Carlton JT. (2018). National Exotic Marine and Estuarine Species Information System.
Aulacomya atra	SE Pacific	Eno, N.C., Clark, R.A. & Sanderson, W.G. (eds). (1997). Non-native marine species in British waters: a review and directory, JNCC, Peterborough.
Austrominius modestus	SW Pacific	Jones D.S. (1992). A review of Australian fouling barnacles. Asian Marine Biology, 9, 89-100.
Bankia fimbriatula	Unknown	
Boccardia polybranchia	NE Atlantic	Goumri, M., Gillet, P., Chaouti, A., Chouikh, N., Maarouf, A., Cheggour, M., Mouabad, A. (2017) Journal of Materials and Environmental Science, 8 (10), 3606-3611.
Botrylloides violaceus	NW Pacific	Carver, C.E., Mallet, A.L., Vercaemer, B. (2006). Biological Synopsis of the Colonial Tunicates (Botryllus Schlosseri and Botrylloides Violaceus). Bedford Institute of Oceanography.
Brachidontes exustus	NW Atlantic	Abbott, R.T. & Morris, P.A. (1995). A Field Guide to Shells: Atlantic and Gulf Coasts and the West Indies. New York: Houghton Mifflin,17.

Bythocaris cosmetops	Unknown	
Callinectes sapidus	NW Atlantic	Zenetos, A., Gofas, S., Russo, G., Templado, J., Briand, F. (2003). CIESM Atlas of Exotic Species in the Mediterranean. Volume 3. Molluscs.
Calyptraea chinensis	Mediterranean	Kerckhof, F., Haelters, J & Gollasch, S. (2007). Alien species in the marine and brackish ecosystem: the situation in Belgian waters. Aquatic Invasions. 2(3), 243-257.
Caprella mutica	NW Pacific	NOBANIS. (2022) Available from http://www.NOBANIS.org. Data of access 9/9/2022.
Clymenella torquata	NW Atlantic	Leidy, J. (1855). Contributions towards a knowledge of the marine Invertebrate fauna of the coasts of Rhode Island and New Jersey. Journal of the Academy of Natural Sciences of Philadelphia. 3(2) no. 11: 135-152, pls. 10-11.
Corambe obscura	NW Atlantic	Reise K., Gollasch S., Wolff W.J. (1999). Introduced marine species of the North Sea coasts. Helgoländer Meeresuntersuchungen, 52(3), 219-234.
Corella eumyota	Indian	Millar, R.H. (1982). The marine fauna of New Zealand: Ascidiacea. New Zealand Oceanographic Institute Memoirs, 85, 1-117.
Crassostrea rhizophorae	NW Atlantic	Carpenter, K.E. (ed.) 2002 The living marine resources of the Western Central Atlantic. Volume 1: Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes, and chimaeras. FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5, Rome. 600pp
Crassostrea virginica	NW Atlantic	Buroker, N. E. (1983). Population genetics of the American oyster Crassostrea virginica along the Atlantic coast and Gulf of Mexico. Marine Biology 75:99-112.
Crepidula fornicata	NW Atlantic	Blanchard M. (1997). Spread of the slipper limpet Crepidula fornicata (L. 1758) in Europe. Current state and consequences. Scientia marina, 61(2), 109-118.
Dendostrea frons	NW Atlantic	Abbott, R.T. & Morris, P.A. (1995). A Field Guide to Shells: Atlantic and Gulf Coasts and the West Indies. New York: Houghton Mifflin, 35.
Desdemona ornata	Mediterranean	Bisby, F.A., M.A. Ruggiero, K.L. Wilson, M. Cachuela-Palacio, S.W. Kimani, Y.R. Roskov, A. Soulier-Perkins and J. van Hertum (2005). Species 2000 & ITIS Catalogue of

		Life: 2005 Annual Checklist. CD-ROM; Species 2000: Reading, U.K.
Diadumene cincta	NW Pacific	HELCOM. (2010). Revision of HELCOM list of non-indigenous, cryptogenic and harmful native species in the Baltic Sea and HELCOM target species.
Diadumene lineata	NW Pacific	Reitzel A.M., Darling J.A., Sullivan J.C., Finnerty J.R. (2008). Global population genetic structure of the starlet anemone Nematostella vectensis: multiple introductions and implications for conservation policy. Biological invasions, 10(8), 1197-1213.
Ensis leei	NW Atlantic	Abbott, R. T. & Morris, P. A. (1995). Shells of the Atlantic and Gulf Coasts and the West Indies., Boston, Peterson Field Guides, Houghton Mifflin Company.
Eriocheir sinensis	NW Pacific	Galil, B., Froglia, C., Noël, P. (2002). CIESM Atlas of Exotic Species in the Mediterranean. Vol. 2. Crustaceans: decapods and stomatopods. [F.Briand, Ed.]. 192 pages. CIESM Publishers, Monaco.
Eurytemora pacifica	NE Pacific	Jean-michel, B., Courcot, L., David, V., Sautour, B. (2016). Expansion of the North Pacific copepod Eurytemora pacifica Sato, 1913 (Copepoda: Calanoida: Temoridae) along the Atlantic coast of France. BioInvasions Records. 5. 245-250. 10.3391/bir.2016.5.4.09.
Eusarsiella zostericola	NW Atlantic	Faasse M. (2013). The North American ostracod Eusarsiella zostericola (Cushman, 1906) arrives in mainland Europe. BioInvasions Records, 2(1), 47-50.
Ficopomatus enigmaticus	Indo-Pacific	Jensen, K. R. (2010): NOBANIS – Invasive Alien Species Fact Sheet – Ficopomatus enigmaticus – From: Identification key to marine invasive species in Nordic waters – NOBANIS www.nobanis.org.
Fistulobalanus albicostatus	NW Pacific	Henry, D. P. & McLaughlin, P. A. (1975). The barnacles of the Balanus amphitrite complex (Cirripedia, Thoracica). Zoologische Verhandelingen, 141: 1-203.
Gibbula albida	Mediterranean	Zenetos, A.; Gofas, S.; Verlaque, M.; Cinar, M.; Garcia Raso, J.; Bianchi, C.; Morri, C.; Azzurro, E.; Bilecenoglu, M.; Froglia, C.; Siokou, I.; Violanti, D.; Sfriso, A.; San Martin, G.; Giangrande, A.; Katagan, T.; Ballesteros, E.; Ramos-Espla, A.; Mastrototaro, F.; Ocana, O.; Zingone, A.;

		Gambi, M.; Streftaris, N. (2010). Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. Mediterranean Marine Science. 11(2): 381-493
Goniadella gracilis	NW Atlantic	Eno, N.C., Clark, R.A. & Sanderson, W.G. (eds). 1997. Non-native marine species in British waters: a review and directory, JNCC, Peterborough.
Gonionemus vertens	NW Pacific	Tambs-Lyche H. (1964). Gonionemus vertens L. agassiz (limnomedusae)—A zoogeographical puzzle. Sarsia, 15(1), 1-8.
Grandidierella japonica	NW Pacific	Fofonoff PW, Ruiz GM, Steves B, Simkanin C, & Carlton JT. (2018). National Exotic Marine and Estuarine Species Information System. http://invasions.si.edu/nemesis.
Haliotis tuberculata	Mediterranean	Bouchet, P.; Gofas, S. (2012). Haliotis tuberculata Linnaeus, 1758. Accessed through: World Register of Marine Species
Hemigrapsus takanoi	NW Pacific	Asakura A., Watanabe S. (2005). Hemigrapsus takanoi, new species, a sibling species of the common Japanese intertidal crab H. penicillatus (Decapoda: Brachyura: Grapsoidea). Journal of Crustacean Biology, 25(2), 279-292.
Hexaplex trunculus	Mediterranean	Marzouk, Z., Chenuil, A., Blel, H & Saïd, K. (2016). Morphometric Variation of Fishery-Exploited Muricidae (Hexaplex trunculus) in the Mediterranean Sea and the Northeastern Atlantic Ocean: Implications for Stock Identification. Turkish Journal of Fisheries and Aquatic Sciences. 16(2), 327-338.
Homarus americanus	NW Atlantic	Van der Meeren, G, Støttrup J, Ulmestrand M, Øresland V, Knutsen JA, Agnalt AL (2010)NOBANIS – Invasive Alien Species Fact Sheet – Homarus americanus. – From: Online Database of the European Network on Invasive Alien Species - NOBANIS www.nobanis.org
Hydroides dianthus	NW Atlantic	Link H., Nishi E., Tanaka K., Bastida-Zavala R., Kupriyanova E.K., Yamakita, T. (2009). Hydroides dianthus (Polychaeta: Serpulidae), an alien species introduced into Tokyo Bay, Japan. Marine Biodiversity Records, 2, e87.
Hydroides ezoensis	NW Pacific	Link H., Nishi E., Tanaka K., Bastida-Zavala R., Kupriyanova E.K., Yamakita, T. (2009). Hydroides dianthus (Polychaeta: Serpulidae),

		an alien species introduced into Tokyo Bay, Japan. Marine Biodiversity Records, 2, e87.
Koinostylochus ostreophagus	NW Pacific	Eno, N.C., Clark, R.A. & Sanderson, W.G. (eds). (1997). Non-native marine species in British waters: a review and directory, JNCC, Peterborough.
Macromedaeus voeltzkowi	Indo-Pacific	Ghotbeddin, Negar & Naderloo, Reza. (2014). Confirming of the occurrence of three intertidal xanthid crabs (Crustacea: Decapoda: Brachyura: Xanthidae) in the Gulf of Oman. Marine Biodiversity Records. 7. 10.1017/S1755267214000712.
Maeotias marginata	Ponto-Caspian	Vainola R, Oulasvirta P. 2001. The first record of Maeotias marginata (Cnidaria, Hydrozoa) from the Baltic Sea: a Pontocaspian invader. Sarsia, 86: 401-404.
Magallana angulata	NW Pacific	Lapegue, S. (2004). Evidence for the presence of the Portuguese oyster, Crassostrea angulata, in northern China. Journal of Shellfisheries Research.
Magallana gigas	NW Pacific	Nehring, S. (2011): NOBANIS – Invasive Alien Species Fact Sheet – Crassostrea gigas. – From: Online Database of the European Network on Invasive Alien Species - NOBANIS www.nobanis.org
Magallana rivularis	NW Pacific	Wang, H., X. Guo, G. Zhang and F. Zhang 2004 Classification of jinjiang oysters Crassostrea rivularis (Gould, 1861) from China, based on morphology and phylogentic analysis. Aquaculture 242:137-155.
Marenzelleria neglecta	NW Atlantic	Paavola M., A. Olenin, E. Leppakoski. (2005). Are invasive species most successful in habitats of low native species richness across European brackish water seas? Estuarine, Coastal and Shelf Science, 64: 738-750.
Megabalanus tulipiformis	NE Atlantic	Quinteiro, J., Manent, P., Pérez-Diéguez, L., González, J., Almeida, C., Lopes, E., Araújo, R., Carreira, G., Rey-Méndez, M., González-Henríquez, N. (2015). Phylogeography of a Marine Insular Endemic in the Atlantic Macaronesia: The Azorean Barnacle, Megabalanus azoricus (Pilsbry, 1916). PLoS ONE. 10(4): e0124707.
Mercenaria mercenaria	NW Atlantic	Brown A., Heilmayer O., Thatje S. (2010). Metabolic rate and growth in the temperate bivalve Mercenaria mercenaria at a biogeographical limit, from the English Channel. Journal of the Marine Biological

		Association of the United Kingdom, 90(05), 1019-1023.
Molgula manhattensis	NW Atlantic	Calder, D. R., Brehmer, M. L. (1967). Seasonal occurrence of epifauna on test panels in Hampton Roads, Virginia., International Journal of Oceanology and Limnology 1(3): 149-164.
Monocorophium sextonae	SW Pacific	Eno, N.C., Clark, R.A. & Sanderson, W.G. (eds). (1997). Non-native marine species in British waters: a review and directory, JNCC, Peterborough.
Mya arenaria	NW Atlantic	Jensen, Kathe R. (2010): NOBANIS – Invasive Alien Species Fact Sheet – Mya arenaria – From: Identification key to marine invasive species in Nordic waters – NOBANIS www.nobanis.org
Mytilicola intestinalis	Mediterranean	NOBANIS. (2022). Available from http://www.NOBANIS.org. Data of access 9/9/2022.
Mytilicola orientalis	NW Pacific	Mori, T. (1935). Mytilicola orientalis, a new species of parasitic Copepoda. Zoological Magazine, Tokyo, 47:687-690.
Mytilopsis leucophaeata	NW Atlantic	Reise K., Gollasch S., Wolff W.J. (1999). Introduced marine species of the North Sea coasts. Helgoländer Meeresuntersuchungen, 52(3), 219-234.
Mytilus platensis	SE Pacific	SAUP Database (2006). SAUP Database. www.seaaroundus.org
Nemopsis bachei	NW Atlantic	Gittenberger A., Rensing M., Stegenga H., Hoeksema B. (2010). Native and non-native species of hard substrata in the Dutch Wadden Sea. Nederlandse Faunistische Mededelingen, 33, 21-75.
Neodexiospira brasiliensis	SW Atlantic	Knight-Jones, Phyllis, Knight-Jones, E. Wyn, Thorp, Clifford H., Gray, Peter W. G. (1975) Immigrant spirorbids (Polychaeta Sedentaria) on the Japanese Sargassum at Portsmouth, England, Zoologica Scripta 4: 145-149.
Ocinebrellus inornatus	NW Pacific	Kil, H. J., Yoon, S. H., Kim, W., Choe, B. L., Sohn, H. J., Park, J. (2005). Faunistic investigation for marine mollusks in Jindo Island., Korean Journal of Systematic Zoology Special Issue 5: 29-46.
Ostrea angasi	SW Pacific	GBIF (2015) Ostrea angasi G.B. Sowerby II, 1871. http://www.gbif.org/species/4373348
Ostrea chilensis	SE Pacific	CABI. (2022). Ostrea chilensis. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.
Ostrea denselamellosa	NW Pacific	Bernard, F.R., Cai, Y.Y., Morton, B. (1993). Catalogue of the living marine bivalve

		molluscs of China. Hong Kong University Press, Hong Kong. 121 p
Ostrea puelchana	NW Pacific	Rosenberg, G. (2009) Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca. [WWW database (version 4.1.1)] URL http://www.malacolog.org/.
Ostrea stentina	NW Atlantic	Lisha, Hu & Wang, Haiyan & Zhang, Zhen & li, Cui & Guo, Ximing. (2019). Classification of Small Flat Oysters of Ostrea stentina Species Complex and a New Species Ostrea neostentina sp. nov. (Bivalvia: Ostreidae). Journal of Shellfish Research. 38. 295. 10.2983/035.038.0210.
Palaemon macrodactylus	NW Pacific	Lavesque, N. (2010). First record of the successful invader Palaemon macrodactylus in Arcachon Bay and Charente estuary (SW France). In EMBS 45-European Marine Biology Symposium. 23-27 August, 2010, Heriot-Watt University, Edinburgh.
Penaeus japonicus	SW Pacific	Hayashi K, (1996) Bunrui to Bunpu (Taxonomy and Distribution), In: Kittaka, J, Takashima, F, Kanazwa, A, eds. Aquaculture of Crustaceans, Kouseishakouseikaku, Tokyo, Japan, pp. 1-32
Perophora japonica	Indo-Pacific	Baldock, B. & Bishop, J.D.D. (2001). Occurrence of the non-native ascidian Perophora japonica in the Fleet, southern England. Journal of the Marine Biological Association of the United Kingdom. 81.
Petricolaria pholadiformis	NW Atlantic	Abbott R.T. (1974). American seashells; the marine Mollusca of the Atlantic and Pacific coasts of North America 2.
Pileolaria berkeleyana	NW Pacific	Eno, N.C., Clark, R.A. & Sanderson, W.G. (eds). (1997). Non-native marine species in British waters: a review and directory, JNCC, Peterborough.
Polydora ciliata	Indo-Pacific	Johnston, G. (1838). Miscellanea Zoologica. III. — The British Ariciadae. Magazine of Zoology and Botany, Edinburgh. 2: 63-73, plates II-III., available online at https://biodiversitylibrary.org/page/40025966 page(s): 66-68, plate III figs. 1-6
Pseudomyicola spinosus	NW Atlantic	Cáceres-Martínez C, Chávez-Villalba J, Garduño-Méndez L. (2005). First record of Pseudomyicola spinosus in Argopecten ventricosus in Baja California, Mexico. J Invertebr Pathol, 89(2):95-100.
Rapana venosa	NW Pacific	NOBANIS. (2022). Available from http://www.NOBANIS.org. Data of access 9/9/2022.

Rhithropanopeus harrisii	NW Atlantic	Fowler A.E., Forsström T., von Numers M., Vesakoski O. (2013). The North American mud crab Rhithropanopeus harrisii (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. Aquatic Invasions, 8(1), 89-96.
Ruditapes philippinarum	NW Pacific	NOBANIS. (2022). Available from http://www.NOBANIS.org. Data of access 9/9/2022.
Streblospio benedicti	NW Atlantic	Carlton, J. T. (1979) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific Coast of North America., Ph.D. dissertation, University of California, Davis. Pp. 1-904.
Styela clava	NW Pacific	Carlisle, D. B. (1954). Styela mammiculata n.sp., a new species of ascidian from the Plymouth area. Journal of the Marine Biological Association of the United Kingdom. 33(2): 329-334.
Synidotea laticauda	NE Pacific	Carlton, J. T. (1979) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific Coast of North America., Ph.D. dissertation, University of California, Davis. Pp. 1-904
Terebella lapidaria	Mediterranean	Fishelson, L. (1971) Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea. Mar. Biol. 10:113-133.
Teredo navalis	Indo-Pacific	Reise K., Gollasch S., Wolff W.J. (1999). Introduced marine species of the North Sea coasts. Helgoländer Meeresuntersuchungen, 52(3), 219-234. Norman E. (1977). The geographical distribution and the growth of the wood-boring molluscs Teredo navalis L., Psiloteredo megotara (Hanley) and Xylophaga dorsalis (Turton) on the Swedish west coast. Ophelia, 16(2), 233-250.
Tricellaria inopinata	NW Atlantic	DAISIE (2009) Handbook of alien species in Europe. Springer, Dordrecht ISBN 978-1-4020-8279-5.
Urosalpinx cinerea	NW Atlantic	Carlton, J.T. (1979). History, Biogeography, and Ecology of the Introduced Marine and Estuarine Invertebrates of the Pacific Coast of North America. Ph.D. thesis, University of California, Davis, CA (pp. 384-394).
Victorella pavida	Ponto-Caspian	Carlton, J.T. (1979). History, Biogeography, and Ecology of the Introduced Marine and Estuarine Invertebrates of the Pacific Coast of North America. Ph.D. thesis, University of California, Davis, CA (pp. 384-394).

Table S5: Qualitative biological traits information for non-indigenous species. Red are the traits filled in using Trait Explorer.

Link available from ORDA: https://doi.org/10.15131/shef.data.21185953

Table S6: Raw data: Disjunctive table of trait modalities for NIS and native species. Trait codes correspond to the modalities listed in Table 2. The species number is its AphiaID in the World Register of Marine Species.

Link available from ORDA: https://doi.org/10.15131/shef.data.21185953

Table S7: Raw data: fuzzy coded data for non-indigenous species. Trait codes correspond to the modalities listed in Table 2. The species number is its AphiaID in the World Register of Marine Species.

Link available from ORDA: https://doi.org/10.15131/shef.data.21185953

Appendix S1: Reference list for the trait data of non-indigenous species used in Chapter 2.

Anders, P., Tøttrup, Benny., Chan, K., Koskinen, H., Høeg, J. (2010). ‘Flying barnacles’: implications for the spread of non-indigenous species. *Biofouling*, 26:5, 577-582, DOI: 10.1080/08927014.2010.489203

Ashelby, C. (2011). Palaemon macrodactylus. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Ashton, G.V. (2006). Distribution and dispersal of the non-native caprellid amphipod, Caprella mutica Schurin 1935. Ph.D. Thesis, University of Aberdeen, 180pp.

Avant, P. (2007). Haliotis tuberculata Green ormer. In Tyler-Walters H. and Hiscock K. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 05-05-2022]. Available from: https://www.marlin.ac.uk/species/detail/1692

Avendaño, M., & Cantillánez, M. (2013). Reproductive cycle, collection and early growth of Aulacomya ater, Molina 1782 (Bivalvia: Mytilidae) in northern Chile. *Aquaculture Research*, 44(9),1327-1338.

Bamber, R. (2012). Anthropogenic spread of the immigrant sea-spider Ammothea hilgendorfii (Arthropoda: Pycnogonida: Ammotheidae) in UK waters. Marine Biodiversity Records, 5. e78 DOI: https://doi.org/10.1017/S1755267212000668

Barnes, H., Barnes, M. (1965). Egg size, and their variation with local, geographical, and specific factors in some common cirripedes. *Journal of Animal Ecology*, 34(2), 391-402.

Barnes, H., Barnes, M. (1968). Egg numbers, metabolic efficiency of egg production and fecundity; local and regional variations in a number of common cirripedes. *Journal of Experimental Marine Biology and Ecology*, 2, 135-153.

Barreto, F., Avise, J. (2008). Polygynandry and sexual size dimorphism in the sea spider Ammothea hilgendorfi (Pycnogonida: Ammotheidae), a marine arthropod with brood-carrying males. *Molecular Ecology*, 17 (18) https://doi.org/10.1111/j.1365-294X.2008.03895.x

Bellan, G. (2001). Polychaeta, in: Costello, M.J. et al. (Ed.) (2001). European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification. *Collection Patrimoines Naturels*, 50, 214-231.

Bilewitch, J. (2009). Corella eumyota Orange-tipped sea squirt. In Tyler-Walters H. and Hiscock K. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 03-05-2022]. Available from: https://www.marlin.ac.uk/species/detail/2224

Bisby, F.A., Ruggiero, M.A., Soulier-Perkins, A., J. van Hertum, J. (2005). Species 2000 & ITIS Catalogue of Life: 2005 Annual Checklist. CD-ROM; Species 2000: Reading, U.K

Blanchard, M. (2009). Crepidula fornicata. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Blanchard, M., Pechenik, J.A., Giudicelli, E., Connan, J.P., Robert, R. (2008). Competition for food in the larvae of two marine molluscs, Crepidula fornicata and Crassostrea gigas. *Aquatic Living Resources*, 21, 197-205.

Bodden, S. (2011). "Callinectes sapidus" (On-line), Animal Diversity Web. Accessed May 03, 2022 at https://animaldiversity.org/accounts/Callinectes_sapidus/

Bonham, V. (2017). Magallana gigas (Pacific oyster). In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Boos, K. (2009). Mechanisms of a successful immigration from north-east Asia: population dynamics, life history traits and interspecific interactions in the caprellid amphipod Caprella mutica Schurin, 1935 (Crustacea, Amphipoda) in European coastal waters. Dr. rer. nat. thesis, Freie Univertität, Berlin, 158pp.

Bottom, M. L., Ropes, J. W. (1988). An indirect method for estimating longevity of the horseshoe crab (Limulus polyphemus) based on epifaunal slipper limpet Crepidula fornicata. *Journal of Shellfish Research*, 7 (3), 407-712.

Bower, S.M. (2009): Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish: Mytilicola intestinalis (Red Worm Disease) of Mussels.

Brink AM van den; Godschalk, M., Smaal, A., Lindeboom, H., McLay, C. (2013). Some like it hot: the effect of temperature on brood development in the invasive crab Hemigrapsus takanoi (Decapoda: Brachyura: Varunidae). *Journal of the Marine Biological Association of the United Kingdom*, 93(1), 189-196.

Brunel, P., L. Bosse & G. Lamarche. (1998). Catalogue of the marine invertebrates of the estuary and Gulf of St. Lawrence. Canadian Special Publication of Fisheries and Aquatic Sciences, 126. 405 pp

Cairns, S.D., D.R. Calder, A., Brinckmann-Voss, C.B., Castro, D.G., Fautin, P.R., Pugh, C.E., Mills, W.C., Jaap, M.N., Arai, S.H.D., Haddock, D.M. Opresko (2003). Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Cnidaria and Ctenophore, Second Edition. American Fisheries Society Special Publication, no,28. XI+115.

Carlton, J.T. (1979). History, Biogeography, and Ecology of the Introduced Marine and Estuarine Invertebrates of the Pacific Coast of North America. Ph.D. thesis, University of California, Davis, CA (pp. 384-394).

Carter, M.C., Jackson, A. (2007). Victorella pavida Trembling sea mat. In Tyler-Walters H. and Hiscock K. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 12-05-2022]. Available from: https://www.marlin.ac.uk/species/detail/1302

Carver, C., Mallet, A., Vercaemer, B. (2005). Biological Synopsis of the colonial tunicates, Botryllus schlosseri and Botrylloides violaceus. Canadian Manuscript Report of Fisheries and Aquaculture Science. No. 2724.

Castro, N.F., Lucas, A. (1987). Variability of the frequency of male neoteny in Ostrea puelchana (Mollusca: Bivalvia). *Mar. Biol*, 96, 359–365. https://doi.org/10.1007/BF00412518

Clench, W.J., R.D. Turner. (1946). The genus Bankia in the Western Atlantic. *Johnstonia,* 2(19).

Clifford, H., Thorp, S., West, S. (1987). Hydroides ezoensis Okuda, a fouling serpulid new to British coastal waters. *Journal of Natural History,* 21(4), 863-877, DOI: 10.1080/00222938700770521

Cochennec, N., Renault, R., Boudry, P., Chollet, B., Gerard, A. (1998). Bonamia-like parasite found in the Suminoe oyster Crassostrea rivularis reared in France. *Diseases of Aquatic Organisms*, 34, 193-197.

Cohen, A. (2016). Styela clava. In. Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Cohen, A. (2011). The Exotics Guide: Non-native Marine Species of the North American Pacific Coast. Center for Research on Aquatic Bioinvasions, Richmond, CA, and San Francisco Estuary Institute, Oakland, CA. Revised September 2011. http://www.exoticsguide.org

Cohen, A.N.., J.T. Carlton. (1995). Nonindigenous Aquatic Species in a United States Estuary: A Case Study of the Biological Invasions of the San Francisco Bay and Delta. U.S. Fish and Wildlife Service, Washington, DC (pp. 111-112).

Cook, E. (2005). Japanese skeleton shrimp Caprella muticum. Marine Aliens project. [On-line] http://www.marlin.ac.uk/marine_aliens/marine_aliens.htm

Cook, E. (2007). Caprella mutica. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Cook, E.J., Willis, K.J.., Lozano-Fernandez, M. (2007). Survivorship, growth and reproduction of the non-native Captrlla mutica Schurin, 1935 (Crustacea: Amphipoda). *Hydobiologia*, 590, 55-64.

Costlow, J., Bookhout, C. G. (1957). Larval development of Balanus eburneus in the laboratory. *Biological Bulletin*, 112(3), 313-324

Craeymeersch, J & Goudswaard, K. (2010). Ensis leei. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Crisp, D.J., Davies, P.A. (1955). Observations in vivo on the breeding of Elminius modestus grown on glass slides. *Journal of the Marine Biological Association of the United Kingdom*, 34, 357-380.

Crisp, D.J., Patel, B. (1961). The interaction between breeding and growth rate in the barnacle Elminius modestus Darwin. *Limnology and Oceanography*, 6(2), 105-115.

Czerniejewski, P. (2013). Realized Fecundity in the First Brood and size of Eggs of Chinese Mitten crab (Eriocheir sinensis)- Laboratory Studies. *International Journal of Biological Sciences*, 2(2), 1-6.

da Costa Fernando's, F. (2010). Brachidontes pharaonis. In: Invasive Species Compendium. Wallingford, UK: CAB International.

DAISIE (2009). Ficopomatus enigmaticus. In: European Invasive Alien Species Gateway, http://www.europe-aliens.org/index.jsp

Darbyson, E.A., Hanson, J.M., Locke, A., Willison, J.H.M. (2009). Settlement and potential for transport of clubbed tunicate (Styela clava) on boat hulls. Aquatic Invasions [Proceedings of the 2nd International Invasive Sea Squirt Conference, Prince Edward Island, Canada, 2-4 October 2007.], 4(1), 95-103.

Davis, M., Davis, M. (2008). First record of Styela clava (Tunicata, Ascidiacea) in the Mediterranean region. *Aquatic Invasions*, 3(1), 125-132.

Davis, M., Lützen, J., Davis, M. (2009). The spread of Styela clava Herdman, 1882 (Tunicata, Ascidiacea) in European waters. *Aquatic Invasions*, 2(4), 378-390.

Denitto, F., Miglietta, M., Boero, F. (2007). Life cycle of Bougainvillia nana (Cnidaria: Hydrozoa: Bougainvilliidae) from Italy, including a discussion of Bougainvillia muscus in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 87(4), 853-857. doi:10.1017/S0025315407054574

Desai, D., Khandeparker, L., Shirayama, Y. (2006). Larval development and metamorphosis ofBalanus albicostatus (Cirripedia: Thoracica); implications of temperature, food concentration and energetics, *Journal of the Marine Biological Association of the United Kingdom*, 86, 335-343.

Deslou-Paoli, J.M., Heral, M., (1986). Crepidula fornicata (L.) (Gastropoda, Calyptraeidae) in the bay of Marennes-Oleron: Biochemical composition and energy value of individuals and spawning. *Oceanologica Acta*, 9, 305-311.

Didžiulis, V. (2006): NOBANIS – Invasive Alien Species Fact Sheet – Marenzelleria neglecta. – From: Online Database of the North European and Baltic Network on Invasive Alien Species - NOBANIS www.nobanis.org,

Didžiulis, V. (2011): NOBANIS – Invasive Alien Species Fact Sheet – Teredo navalis. – From: Online Database of the

Didžiulis, V., Żurek, R. (2013): NOBANIS – Invasive Alien Species Fact Sheet – Craspedacusta sowerbii. – From: Online Database of the European Network on Invasive Alien Species – NOBANIS www.nobanis.org, Date of access 05/05/2022

Dineen, J., Hines, A. (1994). Larval settlement of the polyhaline barnacle Balanus eburneus: cue interactions and comparisons with two estuarine congeners. *Journal of Experimental Marine Biology and Ecology*, 179, 223-234.

Dobbs, F., Whitlatch, R. (1982). Aspects of deposit feeding by the polychaete Clymenella torquata, *Journal of Marine Research*, 21(2), 159-162.

Droual, G., Le Garrec, V., Cabelguen, J., Gélinaud, G., Grall, J. (2017). The spread goes on: the non-indigenous species Grandidierella japonica Stephensen, 1938 (Amphipoda: Aoridae) has reached Brittany (Gulf of Morbihan). *Biology*, 1, 21-29.

Duchêne, J.C. (1984). Reproductive biology of Boccardia polybranchia (Carazzi) in Kerguelen (Subantarctic Province). *Polar Biology*, 2, 251–257. https://doi.org/10.1007/BF00263632

D'Udekem d'Acoz, C., Sorbe, J. (2004). First record of Bythocaris cosmetops (Crustacea: Decapoda: Hippolytidae) in European waters. *Journal of the Marine Biological Association of the United Kingdom*, 84(5), 1039-1040. doi:10.1017/S0025315404010380h

Duenas, M. (2013). Hemigrapsus takanoi. In Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Eastern Oyster Biological Review Team. (2007). Status review of the eastern oyster (Crassostrea virginica). Report to the National Marine Fisheries Service, Northeast Regional Office. February 16, 2007. NOAA Tech. Memo. NMFS F/SPO-88, 105 p.

Edwards, C. (1966). The hydroid and the medusa Bougainvillia principis, and a review of the British species of Bougainvillia. *Journal of the Marine Biological Association of the United Kingdom*, 46(1), 129-152. doi:10.1017/S0025315400017604

Elhasni, K., Ghorbel, M., Vasconcelos, P., Jarboui, O. (2010). Reproductive cycle and size at first sexual maturity of Hexaplex trunculus (Gastropoda: Muricidae) in the Gulf of Gabès (southern Tunisia). *Invertebrate Reproduction & Development*, 54(4), 213-225, DOI: 10.1080/07924259.2010.9652335

Encyclopedia of Life. (2022) Available from https://eol.org/pages/1020212.

Eno, N.C., Clark, R.A., Sanderson, W.G. (1997). Non-native marine species in British waters: a review and directory, JNCC, Peterborough.

Estrella, B., Cadrin, S. (1995). Fecundity of the American lobster (Homarus americanus) in Massachusetts coastal waters. *ICES mar. Sei. Symp.*, 199, 61-72.

European Network on Invasive Alien Species - NOBANIS www.nobanis.org, Date of access 11/05/2022

Faasse, M. (2009). Urosalpinx cinereal. In. Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Faassee, M. (2013). Further dispersal of the sea-spider Ammothea hilgendorfi (Böhm, 1879) in the North Sea to The Netherlands. *BioInvasions Records*, 2(4), 287-289.

Faulwetter, S., Markantonatou, V., Pavloudi, C., Papageorgiou, N., Keklikoglou, K., Chatzinikolaou, E., Pafilis, E., Chatzigeorgiou, G., Vasileiadou, K., Dailianis, T., Fanini, L., Koulouri, P., Arvanitidis, C. (2014). Polytraits: A database on biological traits of marine polychaetes. *Biodiversity Data Journal*, 2: e1024. doi:10.3897/BDJ.2.e1024

Fedotov, P.A. (1991). Population and production biology of amphipod Caprella mutica in Posyet Bay, Sea of Japan. *Biologiya Morya*, 4, 53-60.

Fishelson, L. (1971). Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea. *Marine Biology*, 10, 113-133.

Fofonoff, P. W., Ruiz, G. M., Steves, B., Hines, A. H., Carlton, J. T. (2003). In: National Exotic Marine and Estuarine Species Information System: Chesapeake Bay Introduced Species Database, http://invasions.si.edu/nemesis/chesapeake.html

Frost, J.R., Jacoby, C.A., Youngbluth, M.J. (2010). Behavior of Nemopsis bachei L. Agassiz, 1849 medusae in the presence of physical gradients and biological thin layers. In: Purcell, J.E., Angel, D.L. (eds) Jellyfish Blooms: New Problems and Solutions. Developments in Hydrobiology 212, vol 212. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-9541-1_8

Fukui, Y. (1991). Embryonic and larval development of the sea anemone Haliplanella lineata from Japan. *Hydrobiologia*. 216, 137-142.

Fukui, Y. (1995). Seasonal changes in testicular structure of the sea anemone Haliplanella lineata (Coelenterata: Actiniaria). *Invertebrate Reproduction & Development*, 27(3), 197-204, DOI: 10.1080/07924259.1995.9672449

Gaffney, P. N., McGee, B. (1992). Multiple paternity in Crepidula fornicata (L). *Veliger*, 35 (1), 12-15.

Gallagher, M., Davenport, J., Gregory, S., McAllen, R & O'Riordan, R. (2015). The invasive barnacle species, Austrominius modestus: Its status and competition with indigenous barnacles on the Isle of Cumbrae, Scotland. *Estuarine, Coastal and Shelf Science*, 152, 134-141.

Ghotbeddin, N., Naderloo, R. (2014). Confirming of the occurrence of three intertidal xanthid crabs (Crustacea: Decapoda: Brachyura: Xanthidae) in the Gulf of Oman. *Marine Biodiversity Records*, 7, E98. doi:10.1017/S1755267214000712

Gibson, N. R. (2001). Oceanography and Marine Biology, An Annual Review, Volume 39.

Gittenberger, A., Moons, J. (2011). Settlement and possible competition for space between the invasive violet tunicate Botrylloides violaceus and the native star tunicate Botryllus schlosseri in The Netherlands. *Aquatic Invasions*, 6(4), 435-440.

Global Invasive Species Database (2022) Species profile: Ficopomatus enigmaticus. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1382 on 04-05-2022.

Global Invasive Species Database. (2022). Species profile: Mytilopsis leucophaeata. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=707 on 11-05-2022.

Global Invasive Species Database. (2022). Species profile: Rapana venosa. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=691 on 12-05-2022.

Global Invasive Species Database. (2022). Species profile: Rhithropanopeus harrisii. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1217 on 12-05-2022

Glon, H., Daly, M., Carlton, J.T., Flenniken, M.M., Currimjee, Z. (2020). Mediators of invasions in the sea: life history strategies and dispersal vectors facilitating global sea anemone introductions. *Biological Invasions*, 16, 1-28. doi: 10.1007/s10530-020-02321-6.

Gollasch S. (2006). Eriocheir sinensis. DAISIE Fact Sheet. Delivering Alien Invasive Species Inventories for Europe (DAISIE). http://www.europe-aliens.org/pdf/Eriocheir_sinensis

Gollasch, S., Kerckhof, F., Craeymeersch, J., Goulletquer, P., Jensen, K., Jelmert, A. and Minchin, D. (2015). Alien Species Alert: Ensis directus. Current status of invasions by the marine bivalve Ensis directus. ICES Cooperative Research Report No. 323. 32 pp.

Gollasch, S., Yang, N. (2014). Eriocheir sinensis. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Gonzalez, G. (2013). "Acartia tonsa" (On-line), Animal Diversity Web. Accessed April 29, 2022 at https://animaldiversity.org/accounts/Acartia_tonsa/

Goumri, M., Gillet, P., Chaouti, A., Maarouf, A., Cheggour, M., Mouabad, A. (2017). First record of Boccardia polybranchia (Haswell, 1885) (Polychaeta: Grave, B. H. “Natural History of Shipworm, Teredo Navalis, at Woods Hole, Massachusetts.” *Biological Bulletin*, vol. 55, no. 4, 1928, pp. 260–82, https://doi.org/10.2307/1537080.

Griffiths, C.L., King, J.A. (1979). Energy expended on growth and gonad output in the ribbed mussel Aulacomya ater. *Marine Biology*, 53, 217-222.

GSMFC. (2003). Fact sheet for Eriocheir sinensis – Gulf States Marine Fisheries Commission. Online at http://nis.gsmfc.org/nis_factsheet.php?toc_id=132. Accessed 03 June, 2004.

Harris, J. (2008). Pacific oyster, Crassostrea gigas (Thunberg, 1793). Aquatic Invasive Species Profile. 1-12.

Hassan, M., Li, X., Liu, Y., Qin, J. (2017). Sperm cryopreservation in the spermcasting Australian flat oyster Ostrea angasi by a programmable freezing method. *Cryobiology*, 76, 119-224.

Hayashi, R. (2016). First documentation of the barnacle Fistulobalanus albicostatus (Cirripedia: Balanomorpha) as an epibiont of loggerhead sea turtle Caretta caretta. *Oceanarium*, 47, 157-158.

Hayward, P.J., Ryland, J.S. (1990). The marine fauna of the British Isles and North-West Europe: 1. Introduction and protozoans to arthropods. Clarendon Press: Oxford, UK. ISBN 0-19-857356-1. 627 pp

Herbert, R.J.H., Roberts, C., Humphreys, J. and Fletcher, S. (2012). The Pacific Oyster (Crassostrea gigas) in the UK: Economic, Legal and Environmental Issues Associated with its Cultivation, Wild Establishment and Exploitation. Report for the Shellfish Association of Great Britain.

Hiebert, T.C. (2015). Grandidierella japonica. In: Oregon Estuarine Invertebrates: Rudys' Illustrated Guide to Common Species, 3rd ed. T.C. Hiebert, B.A. Butler and A.L. Shanks (eds.). University of Oregon Libraries and Oregon Institute of Marine Biology, Charleston, OR.

Hill, J.M. (2007). Polydora ciliata A bristleworm. In Tyler-Walters H. and Hiscock K. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 12-05-2022]. Available from: https://www.marlin.ac.uk/species/detail/1410

Hill, M., R. Baker, G. Broad, P.J. Chandler, G.H. Coop, J. Ellis, D. Jones, C. Hoyland, I. Laing, M. Longshaw, N. Moore, D. Parrott, D. Pearman, C. Preston., R. Waters. (2005). Audit of Non-native Species in England. English Nature Research Reports Number 662. 82 p.

Ho, M. (2013). "Teredo navalis" (On-line), Animal Diversity Web. Accessed May 12, 2022 at https://animaldiversity.org/accounts/Teredo_navalis/

Hockley, A.R. (1951). On the biology of Mytilicola intestinalis (Steuer). Journal of the Marine Biological Association of the United Kingdom 30: 223-232.

Holthuis, L.B. (1980). FAO Species Catalogue. Vol. 1. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. FAO Fish. Synop. 125(1):271 p. Rome: FAO.

Honma, Y.; Nakajima, J. (1973). Studies on gonad maturity in some marine invertebrates - 8.Structure of reproductive and related organs of a foreign barnacle, Balanus eburneus, that appears in Lake Kamo-ko, Sado Island., *Bulletin of the Japanese Society of Scientific Fisheries*, 39(4), 357-365.

Houghton, J (2018). Gonionemus vertens. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Huber, M. (2010). Compendium of bivalves. A full-color guide to 3,300 of the world's marine bivalves. A status on Bivalvia after 250 years of research. Hackenheim: ConchBooks. 901 pp

ICES. (2004). Alien Species Alert: Rapana venosa (veined whelk). Edited by Roger Mann, Anna Occhipinti, and Juliana M. Harding. ICES Cooperative Research Report No. 264. 14 pp.

ISSG. (2016.) Global Invasive Species Database (GISD). Invasive Species Specialist Group of the IUCN Species Survival Commission. http://www.issg.org/database/welcome/

ISSG. (2004). Global invasive species database entry for Eriocheir sinensis. Online at www.issg.org. Accessed 26 May, 2004.

James, T., Carlton, J., Chapman, Jonathan., Miller, A., Carlton, D., McCuller, M., Treneman, N., Steves,B., Ruiz, G. (2017). Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography. *Science*, 1402-1406.

Jaramillo, R & Navarro, J. (1995). Reproductive cycle of the Chilean ribbed mussel, Aulacomya ater (Molina, 1782). *Journal of Shellfish Research*, 14(1), 165-171.

Jeff's A. G., Hooker, S. H. & Creese, R. G. (1997). Variability in life history characters of the Chilean oyster Tiostrea chilensis (Philippi, 1845). *New Zealand Journal of Marine and Freshwater Research*, 31(4), 487-495, DOI: 10.1080/00288330.1997.9516782

Jensen, K., Knudsen, J. (2005). A summary of alien marine benthic invertebrates in Danish water. *Oceanological and Hydrobiological Studies*, 34 (1), 137-161.

Jensen, Kathe R. (2010): NOBANIS – Invasive Alien Species Fact Sheet – Elminius modestus – From: Identification key to marine invasive species in Nordic waters – NOBANIS www.nobanis.org,

Jensen, Kathe R. (2010): NOBANIS – Invasive Alien Species Fact Sheet – Caprella mutica – From: Identification key to marine invasive species in Nordic waters – NOBANIS www.nobanis.org, Date of access 03/06/2022.

Jensen, Kathe R. (2010): NOBANIS – Invasive Alien Species Fact Sheet – Crepidula fornicata – From: Identification key to marine invasive species in Nordic waters – NOBANIS www.nobanis.org, Date of access 03/05/2022

Jensen, Kathe R. (2010): NOBANIS – Invasive Alien Species Fact Sheet – Molgula manhattensis – From: Identification key to marine invasive species in Nordic waters – NOBANIS www.nobanis.org

Jensen, Kathe R. (2015): NOBANIS – Invasive Alien Species Fact Sheet – Amphibalanus improvisus – From:

Jivoff, P., A. Hines. (2003). "Reproductive biology of blue crabs" (On-line). Smithsonian Environmental Research Center.

Jonsson, P., Wrange, A., Lind, U., Abramova, A., Ogemark, M., & Blomberg, A. (2018). The Barnacle Balanus improvisus as a Marine Model - Culturing and Gene Expression. J*ournal of Vizualized Experiments*, 138. DOI: 10.3791/57825.

Jutting, B. (1952). On Bankia fimbriatula Moll & Roch in driftwood washed ashore on the Dutch Coast. *Basteria*, 16(3), 37-39.

Kajihara, T., Nakamura, K. (1985). Lifespan and oviposition of the parasitic copepod Pseudomyicola spinosus under rearing conditions. *Marine Biology*, 87, 55–60. https://doi.org/10.1007/BF00397005

Katsanevakis, S., Bogucarskis, K., Gatto, F., Vandekerkhove, J., Deriu, I., Cardoso A.S. (2012). Building the European Alien Species Information Network (EASIN): a novel approach for the exploration of distributed alien species data. *BioInvasions Records*, 1, 235-245., available online at http://easin.jrc.ec.europa.eu

Kennedy, V. (2010). The invasive dark falsemussel Mytilopsis leucophaeata (Bivalvia: Dreissenidae): a literature review. *Aquatic Ecology*, 45, 163-183.

Kimoto, K., Uye, S., & Onbe, T. (1986). Egv production of a Brackish-water Calanoida Copepod Sinocalanus tenellus in Relation to Food Abundance and Temperature. *Bulletin of Plankton Society Japan*, 33 (2), 133-145.

Koshio, S., Teshima, S.I., Kanazawa, A., Watase, T. (1993). The effect of dietary protein content on growth, digestion efficiency and nitrogen excretion of juvenile kuruma prawns, Penaeus japonicus. *Aquaculture*, 113(1/2), 101-114

Krupa, E.G., S. Barinova & M. Alyimov. (2015). Redescription of Acartia (Acanthacartia) tonsa Dana, 1849 (Copepoda: Calanoida) from the Caspian Sea. *Advanced Studies in Biology*, 7(9-11), 393-402. https://doi.org/10.12988/asb.2015.5530

Lahbib, Y., Abidli, S., Menif, N. (2010). Laboratory Study of the Intracapsular Development and Juvenile Growth of the Banded Murex, Hexaplex trunculus. *Journal of World Aquaculture Society*, 41(1), 18-34.

Lambert, C.C., Lambert, G. (1998). Non-indigenous ascidians in Southern California harbors and marinas. *Marine Biology*, 130, 675-688.

Lambert, C.C., Lambert, G. (2003). Persistence and differential distribution of nonindigenous ascidians in harbors of the Southern California Bight. *Marine Ecology Progress Series*, 259, 145-161.

Lambert, C.C., Lambert, I.M., Lambert, G. (1995). Brooding strategies in solitary ascidians: Corella species from north and south temperate waters. *Canadian Journal of Zoology*, 73, 1666-1671.

Lambert, G. (2002). "Nonindigenous Ascidians in Tropical Waters." Pacific Science, vol. 56 no. 3, 2002, p. 291-298. Project MUSE, doi:10.1353/psc.2002.0026.

Lango-Reynoso, F., Chavez-Villaba, J., Le Pennec, M. (2006). Reproductive patterns of the Pacific oyster Crassostrea gigas in France. *Invertebrate Reproduction & Development*, 49(1-2), 41-50, DOI: 10.1080/07924259.2006.9652192

Lee, C., Kim, C. (1991). Larval development of Balanus albicostatus Pilsby (Cirripedia, Thoracica) reared in the laboratory. *Journal of Experimental Marine Biology and Ecology*, 147, 231-144

Leone, D. (1970). "The Maturation of Hydroides Dianthus." *Biological Bulletin*, 138 (3), 306–15, https://doi.org/10.2307/1540214. Accessed 5 May 2022.

Li, S.J., Fang, J.C. (1990). Larval stages of marine planktonic copepods of China. *China Ocean Press*, Beijing 141 pp

Lucas, J.S., Costlow J.D., (1979). Effects of various temperature cycles on the larval development of the gastropod mollusc Crepidula fornicata. *Marine Biology*, 51, 111-117.

Lützen, J., Faasse, M., Gittenberger, A., Glenner, H., Hoffmann, E. (2012). The Japanese oyster drill Ocinebrellus inornatus (Récluz, 1851) (Mollusca, Gastropoda, Muricidae), introduced to the Limfjord, Denmark. *Aquatic Invasions*, 7 (2), 181-191.

Lydon, D. (2003). "Homarus americanus" (On-line), Animal Diversity Web. Accessed May 05, 2022 at https://animaldiversity.org/accounts/Homarus_americanus/

Macleod, A., Cottier-Cook, E., Hughes, D., Allen, C. (2016). Investigating the Impacts of Marine Invasive Non-Native Species. Environmental Science.

Marchessaux, G., Gadreaud, J., Martin-Gain, B., Thiéry, A., Ourgaud, M., Belloni, B., Thibaul, D. (2017). First report of the invasive jellyfish Gonionemus vertens A. Agassiz, 1862 in the Berre Lagoon, southeast France. *Bioinvasion Records*, 6(4), 339-344.

Marchini, A., Ferrario, J., Sfriso, A., Occhipinti-Ambrogi, A. (2015). Current status and trends of biological invasions in the Lagoon of Venice, a hotspot of marine NIS introductions in the Mediterranean Sea. *Biological Invasions*. https://doi.org/10.1007/s10530-015-0922-3

MarLIN. (2006). BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. [03-05-2022] Available from http://www.marlin.ac.uk/biotic/browse.php?sp=4316

Martin, D. & Gil, J. (2010). Checklist of class Polychaeta (Phylum Annelida). pp. 199-236 In Coll, M., et al., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE*, 5(8), 36

McGee, B. L., Targett, N. M. (1989). Larval habitat selection in Crepidula (L.) and its effect on adult distribution patterns. *Journal of Experimental Marine Biology and Ecology*, 131 (3), 195-214.

McHugh, D., Peter P. F. (2002). Do Life History Traits Account for Diversity of Polychaete Annelids? *Invertebrate Biology*, 121(4), 325–38, http://www.jstor.org/stable/3227165.

Meek, M., Wintzer, A., Shepherd, N., May, B. (2012). Genetic diversity and reproductive mode in two non-native hydromedusae, Maeotias marginata and Moerisia sp., in the upper San Francisco Estuary, California. *Biological Invasions*, 15(1), 199-212.

Meng, Y., Guo, Z., Fitzer, S. C., Upadhyay, A., Chan, V. B. S., Li, C., Cusack, M., Yao, H., Yeung, K. W. K., and Thiyagarajan, V. (2018). Ocean acidification reduces hardness and stiffness of the Portuguese oyster shell with impaired microstructure: a hierarchical analysis, *Biogeosciences*, 15, 6833–6846, https://doi.org/10.5194/bg-15-6833-2018.

Menzel, W. (2018). Estuarine and marine bivalve mollusk culture. Boca Raton: CRC Press, Taylor & Francis Group.

Mgaya, Y. D. (1995). Synopsis of biological data on the european abalone (Ormer), Haliotis tuberculata Linnaeus, 1758 (Gastropoda: Haliotidae). FAO fisheries synopsis., Food and Agriculture Organization.

Minchin, D., Nunn, J. (2006). Further Range Extensions of the Marine Gastropod Calyptraea Chinensis (L.) in Ireland. *The Irish Naturalists' Journal*, 28(5), 200–203, http://www.jstor.org/stable/25536712. Accessed 3 May 2022.

Monniot, C. (2001). Ascidiacea & Sorberacea. In: Costello, M.J. et al. (Ed.) (2001). European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification. *Collection Patrimoines Naturels*, 50, 352-355.

Moore, H. B., Frue, A. C. (1959). The settlement and growth of Balanus improvisus, B. eburneus, and B. amphitrite in the Miami area., *Bulletin of Marine Science of the Gulf and Caribbean*, 9(4), 421-440.

Morton, B. (1988). The population dynamics and reproductive cycle of Brachidontes variabilis (Bivalvia: Mytilidae) in a Hong Kong mangrove. *Malacological Review*, 21, 109-117.

Moura, P., Vasconcelos, P., Pereira, F., Chainho, P., Costa, J., & Gaspar, M. (2018). Reproductive cycle of the Manila clam (Ruditapes philippinarum): An intensively harvested invasive species in the Tagus Estuary (Portugal). *Journal of the Marine Biological Association of the United Kingdom*, 98(7), 1645-1657. doi:10.1017/S0025315417001382

Mukai, H. (1983). “Studies on the Reproduction of Three Species of Perophora (Ascidiacea).” *Biological Bulletin*, 164 (2), 251–66, https://doi.org/10.2307/1541143. Accessed 12 May 2022.

Naser,D., Rainbow, P., Clark, P., Yasser, A., Jones, D. (2015). The barnacle Amphibalanus improvisus (Darwin, 1854), and the mitten crab Eriocheir: one invasive species getting off on another!, *BioInvasions Records*, 4(3), 205-209.

Nasrolahi, A. (2007). Larval settlement of the barnacle, Balanus improvisus Darwin (1854) under different food concentration, substratum, light period, salinity, cyprid density and cyprid age. *Pakistan Journal of Biological Sciences*, 10(13), 2231-2236.

Neish, A.H. (2007). Styela clava Leathery sea squirt. In Tyler-Walters H. and Hiscock K. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 12-05-2022]. Available from: https://www.marlin.ac.uk/species/detail/188

Nestlerode, M. (2009). "Geukensia demissa" (On-line), Animal Diversity Web. Accessed April 29, 2022 at https://animaldiversity.org/accounts/Geukensia_demissa/

Newell, C.R., Hidu, H. (1986). Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (North Atlantic)—Softshell Clam. U.S. Fish and Wildlife Service, Washington DC (Biological Report 82(11.53)); and U.S. Army Corps of Engineers, Vicksburg, MS (TR EL-82-4). http://www.nwrc.usgs.gov/wdb/pub/0168.pdf

Newell, G. E. (1951). The life history of Clymenella torquata (Leidy). (Polychaeta), *Proceedings of the Zoological Society of London*, 121(3), 561-586.

Nishikawa, T., Bishop, J., Sommerfeldt, A. D. (2000). Occurrence of the alien ascidian, Perophora japonica at Plymouth., *Journal of the Marine Biological Association*, 80(5), 955-956

NOBANIS. (2022). Available from http://www.NOBANIS.org. Data of access 11/95/2022.

Noseworthy, R., Lee H., Choi, S., Choi, K. (2016). Unique substrate preference of Ostrea denselamellosa Lischke, 1869 (Mollusca: Ostreidae) at Haechang Bay, on the south coast of Korea. *Korean J of Malacol*, 32 (1), 31-36.

Oakley, J.A. (2006). Urosalpinx cinerea. American oyster drill. Marine life information network: biology and sensitivity key information sub-programme [on-line]. Plymouth, UK: Marine Biological Association of the United Kingdom, unpaginated. http://www.marlin.ac.uk/species/Urosalpinxcinerea.htm

Obenat, S.M., Pezzani, S.E. (1994). Life cycle and population structure of the polychaete Ficopomatus enigmaticus (Serpulidae) in Mar Chiquita Coastal Lagoon, Argentina. Estuaries, 17, 263-270.

Obenat, S.M., Spivak, E., Orensanz, J.M. (2006). Reproductive biology of the invasive reef-forming serpulid, Ficopomatus enigmaticus, in the Mar Chiquita coastal lagoon, Argentina. *Invertebrate Reproduction and Development*, 49(4), 263-271.

Occhipinti, A. (2009). Tricellaria inopinata. In. Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Occhipinti-Ambrogi, A., Marchini, A., Cantone, G., Castelli, A., Chimenz, C., Cormaci, M., Froglia, C., Furnari, G., Gambi, M. C., Giaccone, G., Giangrande, A., Gravili, C., Mastrototaro, F., Mazziotti, C., Orsi-Relini, L., Piraino, S. (2010). Alien species along the Italian coasts: an overview. *Biological Invasions*, 13(1), 215-237.

O'Connor, S.J. (2016). 'Factors effecting reproduction and larval development of Ostrea angasi (Sowerby 1871): advancing hatchery production', PhD thesis, University of Tasmania.

O'Riordan, R. (2009). Austrominius modestus. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Osborne, P. (1999). "Crassostrea virginica" (On-line), Animal Diversity Web. Accessed May 03, 2022 at https://animaldiversity.org/accounts/Crassostrea_virginica/

Ostrovsky, A. (2013). Evolution of Sexual Reproduction in Marine Invertebrates. Example of gymnolaemate bryozoans. Springer Dordrecht. First edition. https://doi.org/10.1007/978-94-007-7146-8

Palomares, M.L.D., Pauly, D. (2022). In: SeaLifeBase. World Wide Web electronic publication. www.sealifebase.org, version (04/2022).

Pärnoja, M., Kotta, J. (2009). Marenzelleria neglecta. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Parr, C. S., N. Wilson, P. Leary, K. S. Schulz, K. Lans, L. Walley, J. A. Hammock, A. Goddard, J. Rice, M. Studer, J. T. G. Holmes., R. J. Corrigan, Jr. (2014). The Encyclopedia of Life v2: Providing Global Access to Knowledge About Life on Earth. Biodiversity Data Journal 2: e1079, doi:10.3897/BDJ.2.e1079

Pechenik, J.A., Hilbish, T.J., Eyster, L.S., Marshall, D. (1996). Relationship between larval and juvenile growth rates in two marine gastropods, Crepidula plana and C. fornicata. *Marine Biology*, 125, 119-127.

Pernet, B., McArthur, L. (2006). Feeding by larvae of two different developmental modes in Streblospio benedicti (Polychaeta: Spionidae), *Marine Biology*, 149, 803-811.

Perron, F., Turner, R. (1977). Development, metamorphosis, and natural history of the nudibranch Doridella obscura Verrill (Corambidae: Opisthobranchia). *Journal of Experimental Marine Biology and Ecology*, 27(2),171-185.

Perry, A. (2007). Rhithropanopeous harrisii. USGS Nonindigenous Aquatic Species Database.

Picton, B.E., Morrow, C.C. (2016). Diadumene lineata (Verrill, 1869). [In] Encyclopedia of Marine Life of Britain and Ireland.

Pinney, E. (2009). Japanese Skeleton Shrimp Caprella Mutica. Fish 423: Invasion Ecology.

Ponurovsky, S.K., Selin, N.I, (1988). Distribution, population structure, and growth of the bivalve molusk Ruditapes philippinarum in Vostok Bay, Sea of Japan. *Sov. J. Mar. Biol*, 1, 11-15.

Raso, J., Marina, P & Baro, J. (2011). Bythocaris cosmetops (Decapoda: Caridea: Hippolytidae) in the western Mediterranean Sea. Marine Biodiversity Records. DOI: 10.1017/S1755267211000467

Rawlinson, K., Bolaños, M, Liana, M., Litvaitis, M. (2008). Reproduction, development and parental care in two direct-developing flatworms (Platyhelminthes: Polycladida: Acotylea), *Journal of Natural History*, 42(33-34), 2173-2192, DOI: 10.1080/00222930802262758

Rayment, W.J. (2008). Crepidula fornicata Slipper limpet. In Tyler-Walters H. and Hiscock K. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 03-05-2022]. Available from: https://www.marlin.ac.uk/species/detail/1554

Razouls C., Desreumaux N., Kouwenberg J., de Bovée F. (2005-2022). - Biodiversity of Marine Planktonic Copepods (morphology, geographical distribution and biological data). Sorbonne University, CNRS. Available at http://copepodes.obs-banyuls.fr/en

Reeve, L. A. (1846). Monograph of the genus Haliotis. In: Conchologia Iconica, or, illustrations of the shells of molluscous animals, vol. 3, pls 1-17 and unpaginated text. L. Reeve & Co., London. [stated dates: pls 1-4, April 1846; pls 5-8, May 1846; pls 9-12, June 1846; pl. 13-17

Richards, S. (2008). Ficopomatus enigmaticus A fanworm. In Tyler-Walters H. and Hiscock K. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 04-05-2022]. Available from: https://www.marlin.ac.uk/species/detail/19

Roche, D., Torchin, M. (2007) Established population of the North American Harris mud crab, Rhithropanopeus harrisii (Gould 1841) (Crustacea: Brachyura: Xanthidae) in the Panama Canal. *Aquatic Invasions*, 2(3), 155-161.

Roche, D., Torchin, M., Leung, B., Binning, S. (2009). Localized invasion of the North American Harris mud crab, Rhithropanopeus harrisii, in the Panama Canal: implications for eradication and spread. *Biological Invasions,* 11, 983-993.

Roegner, G. C., Mann, R. L. (1991). "Hard Clam Mercenaria mercenaria". VIMS Books and Book, Chapters. 20. https://scholarworks.wm.edu/vimsbooks/20

Rosenberg, G. (2009). Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca. [WWW database (version 4.1.1)] URL http://www.malacolog.org/.

Rossi, F. (2013). Dynamics of the Polychaetes Desdemona ornata and Perinereis cultrifera and Their Resources of Food in a Mediterranean Mudflat. *Marine Ecology*, 23(4), 285-296.

Rowley, S.J. (2005). Teredo navalis Great shipworm. In Tyler-Walters H. and Hiscock K. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 12-05-2022]. Available from: https://www.marlin.ac.uk/species/detail/2117

Rudnick, D. (2005). "Morphology and Impacts of the Burrows of the Chinese Mitten Crab, Eriocheir Sinensis H. Milne Edwards (Decapoda, Grapsoidea), in South San Francisco Bay, California, U.S.A." *Crustaceana*, 78(8), 787–807, http://www.jstor.org/stable/20107549.

Rudnick, D., Veldhuizen, T., Tullis, R. (2005). A life history model for the San Francisco Estuary population of the Chinese mitten crab, Eriocheir sinensis (Decapoda: Grapsoidea). *Biological Invasions*, 7, 333. https://doi.org/10.1007/s10530-004-2286-y

Sardá, R., Martin, D. (1993). Populations of Streblospio (Polychaeta: Spionidae) in temperate zones: Demography and production. *Journal of the Marine Biological Association of the United Kingdom,* 73(4), 769-784. doi:10.1017/S0025315400034718.

Satheesh, S., Wesley, S. (2009). Breeding biology of the barnacle Amphibalanus amphitrite (Crustacea: Cirripedia): Influence of environmental factors in a tropical coast. *Journal of the Marine Biological Association of the United Kingdom,* 89(6), 1203-1208. doi:10.1017/S0025315409000228.

Scheltema, R, S., Williams, I, P. (1982). Significance of temperature to larval survival and length of development in Balanus eburneus (Crustacea: Cirripedia). *Marine Ecology Progress Series*, 9, 43-49

Scheltema, R., Williams, I., Shaw, M., Loudon, C. (1981). Gregarious Settlement by the Larvae of Hydroides dianthus (Polychaeta: Serpulidae). *Marine Ecology Progress Series*, 5, 69-74.

Schotte, M., B.F. Kensley and S. Shilling (1995) World list of marine, freshwater and terrestrial crustacea isopoda. National Museum of Natural History Smithsonian Institution: Washington D.C., USA. Http://www.nmnh.si.edu/iz/isopod/ [Accessed 07/03/01].

Schwindt, E. (2014). Ficopomatus enigmaticus. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Sebesvari, Z., Esser, F., Harder, T. (2006). Sediment-associated cues for larval settlement of the infaunal spionid polychaetes Polydora cornuta and Streblospio benedicti, *Journal of Experimental Marine Biology and Ecology*, 337, 109-120.

Shalaeva, E. (2014). Corella eumyota. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Solovyeva, A., Bailey, K (2008). "Eriocheir sinensis" (On-line), Animal Diversity Web. Accessed May 04, 2022 at https://animaldiversity.org/accounts/Eriocheir_sinensis/

Southward, A.J. (2001). Cirripedia - non-parasitic Thoracica, in: Costello, M.J. et al. (Ed.) (2001). European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification. *Collection Patrimoines Naturels*, 50: pp. 280-283

Stebbing, P., Johnson, P., Delahunty, A., Clark, P., McCollin, T., Hale, C., Clark, S. (2012). Reports of American lobsters, Homarus americanus (H. Milne Edwards, 1837), in British waters. *BioInvasion Records*, 1(1),17-23.

Steele, P. (1979). "A synopsis of the biology of the blue crab Callinectes sapidus Rathbun in Florida" (On-line pdf). Florida Fish and Wildlife Conservation Commission. http://research.myfwc.com/engine/download_redirection_process.asp?file=79steele_1436.pdf&objid=20754&dltype=publication.

Stephenson, T. (1924). Notes on Haliotis tuberculata. Volume 1, London. 480-495.

Streftaris, N., Zenetos, A., Papathanassiou, E. (2005). Globalisation in marine ecosystems: the story of non-indigenous marine species across European seas. *Oceanogr. Mar. Biol. Ann. Rev*. 43, 419-453.

Sutton, M. (2009). The feeding mechanism, functional morphology and histology of the alimentary canal of Terebella lapidaria L. (Polychaeta). *Journal of Zoology*, 129(4),487-523.

Taheri, M., Seyfabadi, J., Abtahi, B., Foshtomi, M.Y. (2009). Population changes and reproduction of an alien spionid polychaete, Streblospio gynobranchiata, in shallow waters of the south Caspian Sea., JMBA2- Biodiversity Records (online)

Tamarin, A., Carriker, M.R. (1968). The egg capsule of the muricid gastropod Urosalpinx cinerea: an integrated study of the wall by ordinary light, polarized light and electron microscopy. *Journal of Ultrastructure Research*, 21, 26-40.

Templado, J., Villanueva, R. (2010). Checklist of Phylum Mollusca. pp. 148-198 In Coll, M., et al., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE*, 5(8), 36.

Terlizzi, A., Conte, E., Giangrande, A. (2000). Settlement patterns of two Spirorbidae (Annelida, Polychaeta) species in the harbour of Ischia (Gulf of Naples, Mediterranean Sea), *Italian Journal of Zoology*, 67(3), 303-306, DOI: 10.1080/11250000009356328

Therriault, T.W. (2004). Molecular resolution of the family Dreissenidae (Mollusca: Bivalvia) with emphasis on Ponto-Caspian species, including first report of Mytilopsis leucophaeata in the Black Sea basin. *Molecular Phylogenetics and Evolution*, 30(3), 479-489.

Thiyagarajan, V. (1997). “Description of the Naupliar Stages of Megabalanus Tintinnabulum (Cirripedia: Balanidae).” *Journal of Crustacean Biology*, 17 (2), 332–42. https://doi.org/10.2307/1549282.

Tompa, A.S., Verdonk, N.H., van den Biggelaar, J. (1984). The Mollusca. Volume 7: Reproduction. Florida, USA: Academic Press, Inc., 486 p.

Torres, A., Santos, A., Cuesta, J., Carbonell, A., Massuti, E., Alemany, F., Reglero, P. (2012). First record of Palaemon macrodactylus Rathbun, 1902 (Decapoda, Palaemonidae) in the western Mediterranean. *Mediterranean Marine Science*, 13 (2), 278-282.

Turgeon, D.D., J.F. Quinn Jr., A.E. Bogan, E.V. Coan, F.G. Hochberg, W.G. Lyons, P.M. Mikkelsen, R.J. Neves, C.F.E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F.G. Thompson, M. Vecchione., Willams, J.D. (1998). Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks, 2nd ed. American Fisheries Society (Special publication 26), Bethesda, Maryland. 526 p.

Turoboyski, K. (1973). Biology and ecology of the crab Rhithropanopeus harrisii ssp. tridentatus. *Marine Biology*, 23, 303-313.

Tyler-Walters, H., Hiscock, K. (eds), Tillin, H.M., Stamp, T., Readman, J.A.J., Perry, F., Ashley, M., De-Bastos, E.S.R., D'Avack, E.A.S., Jasper, C., Gibb, N., Mainwaring, K., McQuillan, R.M., Wilson, C.M., Gibson-Hall, E., Last, E.K., Robson, L.M., Garrard, S.L., Williams, E., Graves, K.P., Lloyd, K.A., Mardle, M.J., Granö, E., Nash, R.A., Roche, C., Budd, G.C., Hill, J.M., Jackson, A., White, N., Rayment, W.J., Wilding, C.M., Marshall, C.E., Wilson, E., Riley, K., Neal, K.J. Sabatini, M., Durkin, O.C., Ager, O.E.D., Bilewitch, J., Carter, M., Hosie, A.M., Mieszkowska, N. & Lear, D.B. (2022). Marine Life Information Network: Biology and Sensitivity Key Information Review Database [on-line]. Plymouth: Marine Biological Association of the United Kingdom. Available from: www.marlin.ac.uk

Tynana, S., Dutton, A., Eggins, S., Opdykea, B. (2014). Oxygen isotope records of the Australian flat oyster (Ostrea angasi) as a potential temperature. *Marine Geology*, 357, 195-209.

Uddin, J., Jeung, H., Yang, H., Kim, B., Ju, S., Choi, K. (2013). Quantitative assessment of reproductive effort of the Manila clam Ruditapes philippinarum in a lagoon on Jeju Island (Korea) using enzyme-linked immunosorbent assay, Invertebrate *Reproduction & Development*, 57(4), 316-324, DOI: 10.1080/07924259.2013.793219

Utting, S.D., Millican, P.F., Laing. I. (1996). The breeding potential and biochemical composition of triploid Manila clams, Tapes philippinarum Adams and Reeve. *Aquaculture Research*, 27(8), 573-580.

Uye, S. (1981). Fecundity studies of neritic calanoid copepods Acartia clause Giesbrecht and A. steuri Smirnov: a simple empirical model of daily egg production. *Journal of Experimental Marine Biology and Ecology*, 50, 255–271. doi.org/10.1016/0022-0981(81)90053-8.

Van den Biggelaar, J. A. M. (1993). Cleavage pattern in embryos of Haliotis tuberculata (Archaeogastropoda) and gastropod phylogeny. *Journal of Morphology*, 216, 121-139.

Verween, A., Vincx, M., Degraer, D. (2009). Seasonal variation in gametogenesis and spawning of Mytilopsis leucophaeata, an invasive bivalve in Europe. *Journal of Molluscan Studies*, 75 (3), 307–310, https://doi.org/10.1093/mollus/eyp015

Voight, J. (2015). Xylotrophic bivalves: aspects of their biology and the impacts of humans, *Journal of Molluscan Studies*, 81 (2), 175–186, https://doi.org/10.1093/mollus/eyv008

Wagstaff, M. (2017). Life history variation of an invasive species Botrylloides violaceus (Oka, 1927) between novel coastal habitats in the Gulf of Maine. *Aquatic Invasions*, 12(1), 43-51.

Wang, J., Cheng, X., Gao, Z.,, Chi, W.,, Wang, N. (2008). Primary results of polyculture of juvenile sea cucumber (Apostichopus japonicus Selenka) with juvenile sea urchin (Strongylocentrotus intermedius) and manila clam (Ruditapes philippinarum). *Journal of Fisheries of China*, 32(5), 740-748. http://www.scxuebao.cn

Webber, D. (2010). Demography and Population Projections of the Invasive Tunicate Styela clava in southern New Zealand. Thesis.

Williams, A. (1984). Shrimps, lobsters, and crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.

WoRMS Editorial Board (2022). World Register of Marine Species. Available from https://www.marinespecies.org at VLIZ. Accessed 2022-04-29. doi:10.14284/170

Wu, R.S.S., Shin, P.K.S. (1997). Sediment characteristics and colonization of soft-bottom benthos: a field manipulation experiment. *Marine Biology*, 128, 475-487.

Wyatt, H. V. (1961). The Reproduction, Growth and Distribution of Calyptraea Chinensis (L.). *Journal of Animal Ecology*, 30(2), 283–302, https://doi.org/10.2307/2299.

Xu, X., Yang, F., Zhao, L., Yan, X. (2016). Seawater acidification affects the physiological energetics and spawning capacity of the Manila clam Ruditapes philippinarum during gonadal maturation. *Comparative Biochemistry and Physiology. A, Molecular & Integrative Physiology,* 196, 20-29.

Yamaguchi, K. (1998). Cementation vs mobility: development of a cemented byssus and flexible mobility in Anomia chinensis. *Marine Biology,* 132, 651-661

Yano, I. (1988). Oocyte development in the kuruma prawn Penaeus japonicus. *Marine Biology,* 99, 547–553.

Zakas, C., Wares, J. (2012). Consequences of a poecilogonous life history for genetic structure in coastal populations of the polychaete Streblospio benedicti, *Molecular Ecology,* 21, 5447-5460.

Zalota, A., Spiridonov, V., Kolyuchkina, G. (2016). In situ observations and census of invasive mud crab Rhithropanopeus harrisii (Crustacea: Decapoda: Panopeidae) applied in the Black Sea and the Sea of Azov. *Arthropoda Selecta*, 25(1), 39-62.

Zaniolo, G., Manni, L., Brunetti, R., Burighel, P. (1998). Brood pouch differentiation in Botrylloides violaceus, a viviparous ascidian (Tunicata). *Invertebrate Reproduction and Development*, 33, 11-23.

Zenetos, A. (2016). Petricolaria pholadiformis. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Zenetos, A., Çinar, M.E., Pancucci-Papadopoulou, M.A., Harmelin, J., Furnari, G., Andaloro, F., Bellou, N., Streftaris, N., Zibrowius, H. (2005). Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. *Mediterranean Marine Science,* 6 (2), 63-118.

Zenetos, A., Gofas, S., Verlaque, M., Cinar, M., Garcia Raso, J., Bianchi, C., Morri, C., Azzurro, E., Bilecenoglu, M., Froglia, C., Siokou, I., Violanti, D., Sfriso, A., San Martin, G., Giangrande, A., Katagan, T., Ballesteros, E., Ramos-Espla, A., Mastrototaro, F., Ocana, O., Zingone, A., Gambi, M., Streftaris, N. (2010). Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive

(MSFD). Part I. Spatial distribution. *Mediterranean Marine Science*, 11(2), 381-493., available online at https://doi.org/10.12681/mms.87

Zenetos, A., Ovalis, P., Vardala-Theodorou, E. (2009). The American piddock Petricola pholadiformis Lamarck, 1818 spreading in the Mediterranean Sea. *Aquatic Invasions*, 4(2), 385-387.

Appendix S2: Reference list for the trait data of native species used in Chapter 2.

Link available from ORDA: https://doi.org/10.15131/shef.data.21185953

Figure S1: Fuzzy Correspondence Analysis bidimensional plots representing the 12 biological traits investigated. Each plot represents the distribution of trait modalities across the first two axes, with points (dots) corresponding to non-indigenous species listed in Table 1. Eigenvalue bars informs on the dimensionality of the cloud of species, i.e., how much variance is explained by each axes or dimension, with each bar representing an axis from 1 to 10 (left to right).

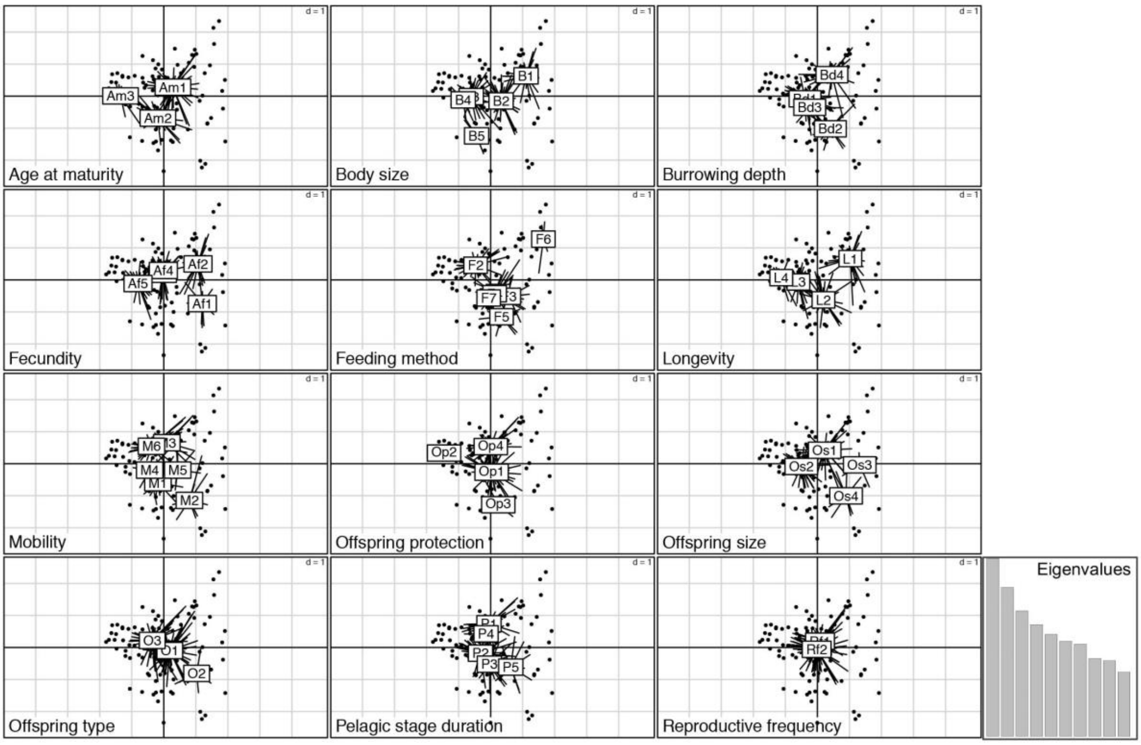


Figure S2: Fuzzy Correspondence Analysis bidimensional plot representing the 12 biological traits investigated. Each plot represents the distribution of trait modalities across axes 1 and 3, with points (dots) corresponding the non-indigenous species listed in Table 1.

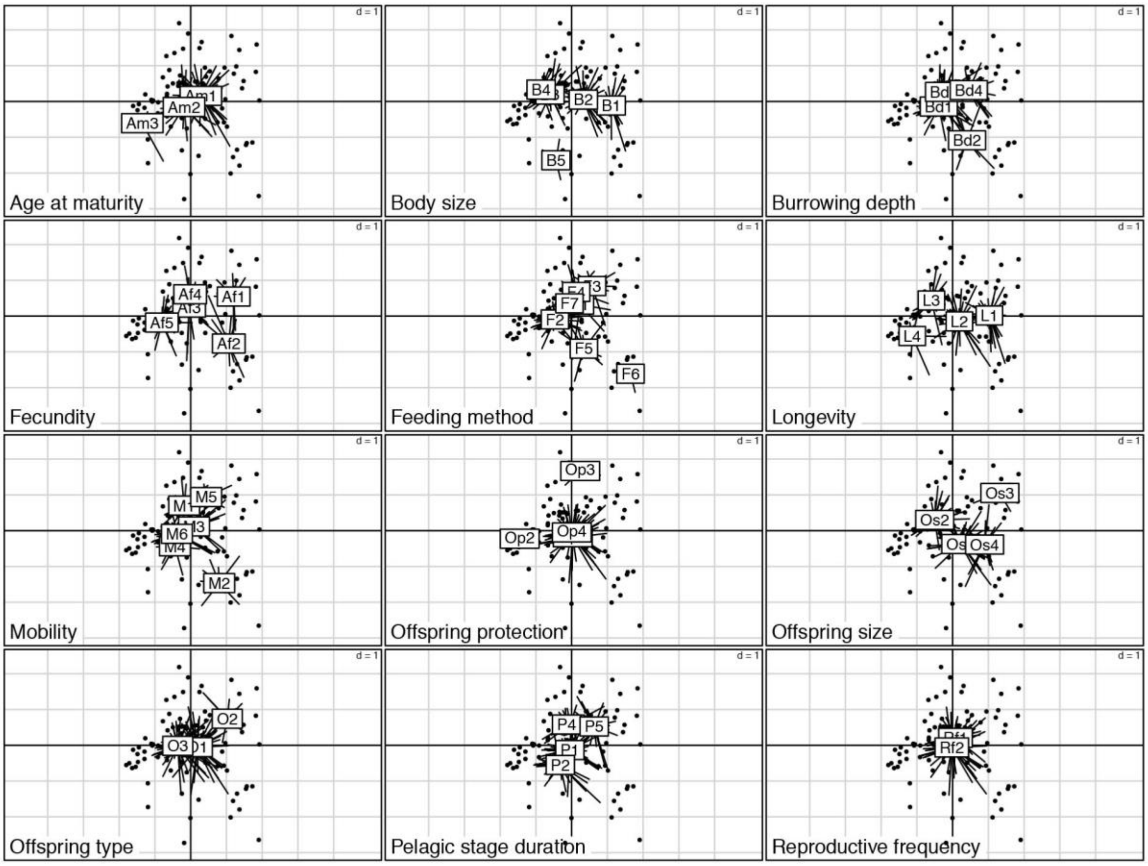
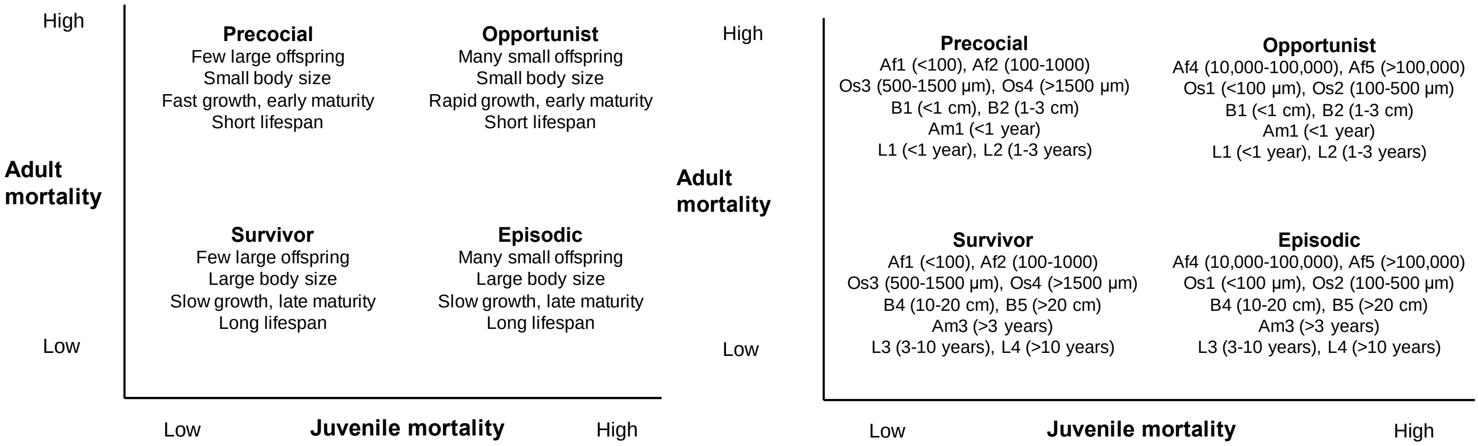


Figure S3: Adapted from Kindsvater et al (2016). Life history traits typical for each category of the POSE framework (Precocial-Opportunist-Survivor-Episodic) as dictated by differences in adult and juvenile mortality, shown on the left. Trait modalities considered in this investigation are also placed within this framework, shown on the right.



Appendix S3: Complete biological trait dataset of 1935 species used in Chapter 3.

Link available from ORDA: https://doi.org/10.15131/shef.data.21185953

Appendix S4: Biological trait dataset of 689 IUCN Red List Species used in Chapter 3.

Link available from ORDA: https://doi.org/10.15131/shef.data.21185953

Figure S4: The minimum depth of species using depth data collected from various online sources including SeaLifeBase, BIOTIC, published, and unpublished literature, against minimum depth calculated using depth summaries from OBIS. Points are scaled to the number of OBIS records per species and split according to each risk category.

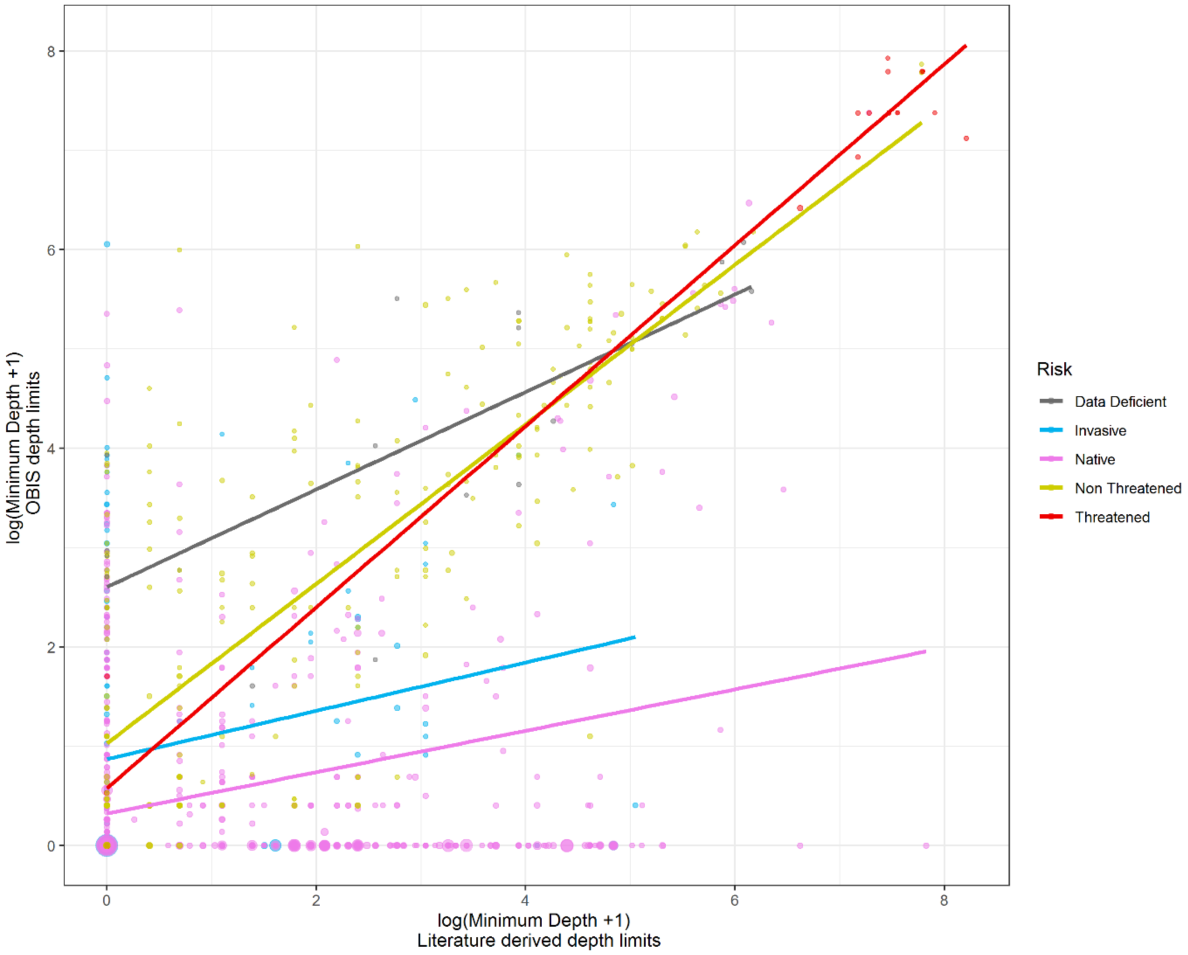


Figure S5: Number of OBIS occurrence records (log transformed) against A) thermal breadth (calculated using the maximum mean temperature at mean depth minus the minimum mean temperature at mean depth) and B) maximum temperature. Colour coded for each risk category.

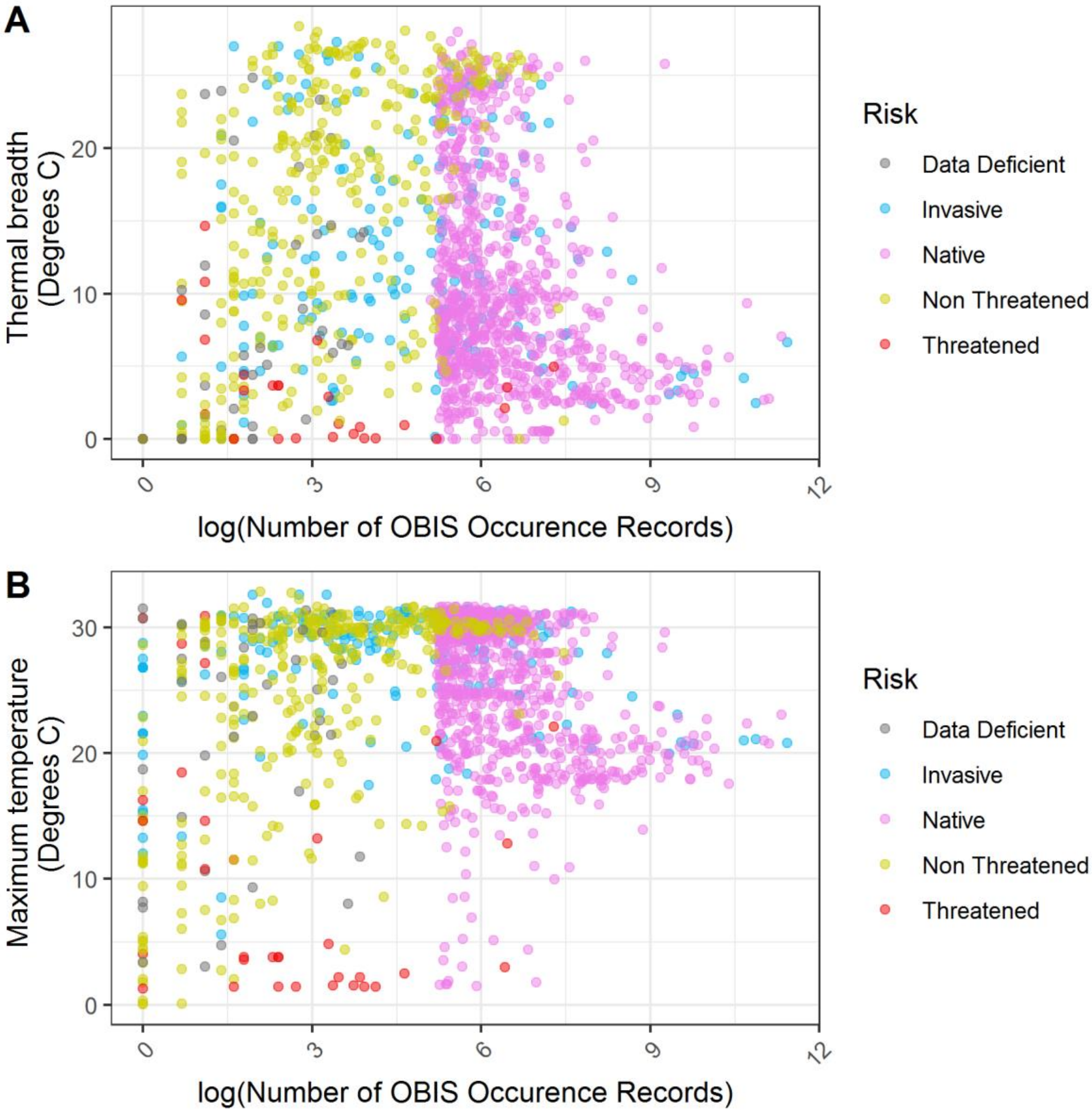


Figure S6: A) Principal Component Analysis (PCA) of 1530 marine molluscs split by five risk categories (Data deficient (n = 43), Invasive (n = 212), Native (n = 882), Non-threatened (n = 357), and Threatened (n = 36)) defined by the first two principal components (PC1 and PC2). PCA is a form of multivariate data analysis which is used to reduce the dimensionality of the data in order to provide a set of summary indices. Arrows indicate mean loadings (directions and weighing) of each life history in the PCA. Each point represents the position of a species within two-dimensional space. B) Boxplot of each risk category against PC1. C) Boxplot of each risk category against PC2. Width of the boxplots are scaled to the number of observations.

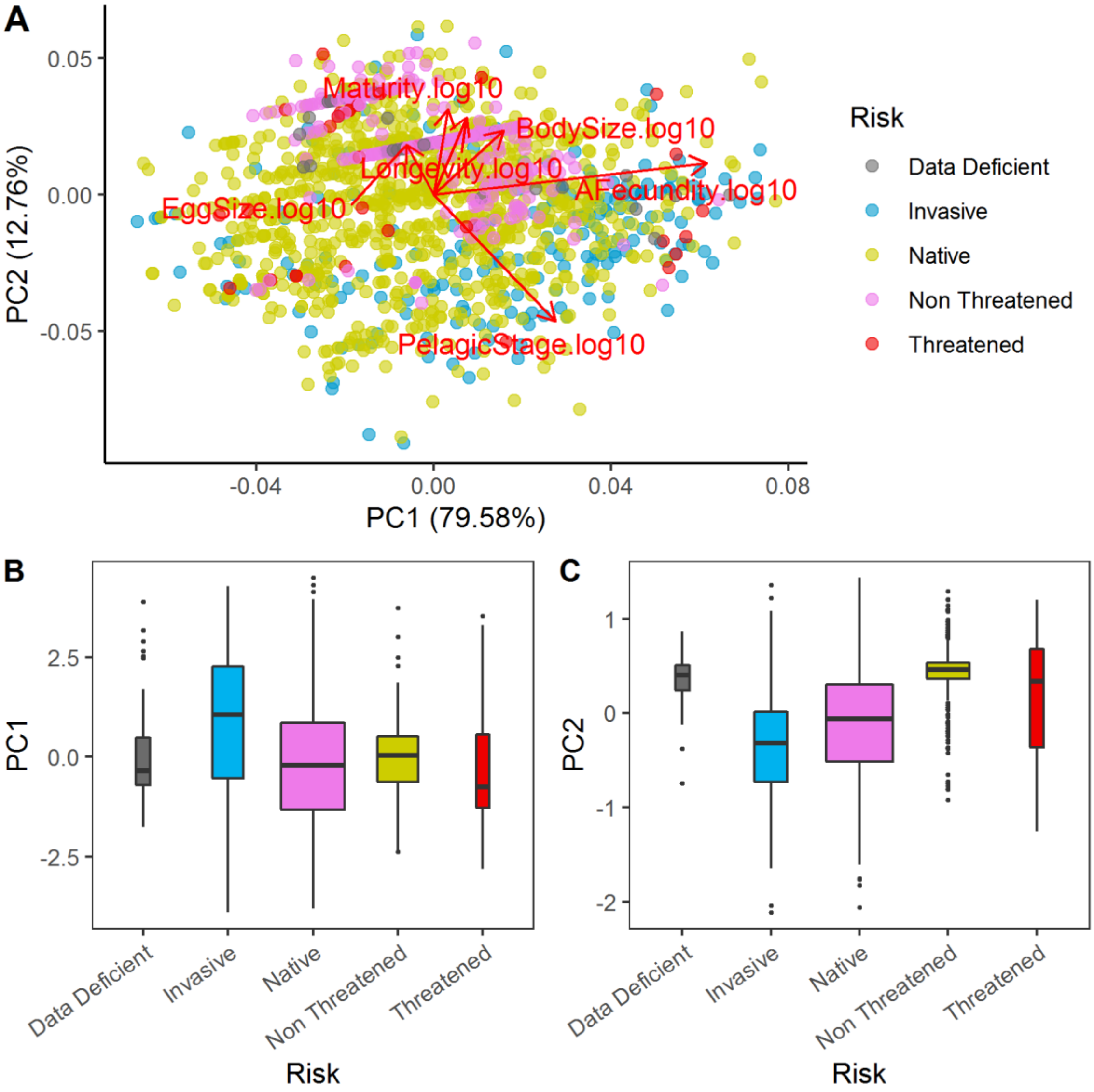


Table S8: Summary of the Principal Component Analysis (PCA) of trait data for marine molluscs (n = 1530).

	PC1	**PC2**
Variation explained (%)	79.6	12.8
Trait loadings		
Body Size	5.0	11.1
Longevity	1.1	16.2
Age at Maturity	0.2	19.8
Annual Fecundity	77.4	2.7
Pelagic Stage Duration	15.5	43.5
Egg Size	0.8	6.8

In marine molluscs, 92.4% of variation in life history traits is explained by the first two principal components (PC1 = 79.6% and PC2 = 12.8%) (Figure S3, Table S1). Axis one of the PCA was effective in separating species with varying annual fecundities while axis 2 of the PCA was effective in separating species with varying pelagic stage durations, ages of maturity, lifespans, and body sizes (Figure S6, Table S8). Annual fecundity was strongly positively correlated with PC1 (1.31), while egg size was negatively correlated with PC1 (-0.13). For PC2, maturity and longevity were positively correlated (0.27 and 0.24, respectively), while pelagic stage duration was negatively correlated (-0.39).

Appendix S5: Biological trait dataset of 1530 mollusc species used in Chapter 4

Link available from ORDA: https://doi.org/10.15131/shef.data.21185953