

# A global synthesis of predation on bivalves

Alexandra Meira<sup>1,\*</sup> , James E. Byers<sup>2</sup>  and Ronaldo Sousa<sup>1</sup> 

<sup>1</sup>CBMA – Centre of Molecular and Environmental Biology, Department of Biology, University of Minho, Campus Gualtar, Braga 4710-057, Portugal

<sup>2</sup>Odum School of Ecology, University of Georgia, 140 E. Green St, Athens, GA 30602, USA

## ABSTRACT

Predation is a dominant structuring force in ecological communities. In aquatic environments, predation on bivalves has long been an important focal interaction for ecological study because bivalves have central roles as ecosystem engineers, basal components of food webs, and commercial commodities. Studies of bivalves are common, not only because of bivalves' central roles, but also due to the relative ease of studying predatory effects on this taxonomic group. To understand patterns in the interactions of bivalves and their predators we synthesised data from 52 years of peer-reviewed studies on bivalve predation. Using a systematic search, we compiled 1334 studies from 75 countries, comprising 61 bivalve families ( $N = 2259$ ), dominated by Mytilidae (29% of bivalves), Veneridae (14%), Ostreidae (8%), Unionidae (7%), and Dreissenidae and Tellinidae (6% each). A total of 2036 predators were studied, with crustaceans the most studied predator group (34% of predators), followed by fishes (24%), molluscs (17%), echinoderms (10%) and birds (6%). The majority of studies (86%) were conducted in marine systems, in part driven by the high commercial value of marine bivalves. Studies in freshwater ecosystems were dominated by non-native bivalves and non-native predator species, which probably reflects the important role of biological invasions affecting freshwater biodiversity. In fact, while 81% of the studied marine bivalve species were native, only 50% of the freshwater species were native to the system.

In terms of approach, most studies used predation trials, visual analysis of digested contents and exclusion experiments to assess the effects of predation. These studies reflect that many factors influence bivalve predation depending on the species studied, including (i) species traits (e.g. behaviour, morphology, defence mechanisms), (ii) other biotic interactions (e.g. presence of competitors, parasites or diseases), and (iii) environmental context (e.g. temperature, current velocity, beach exposure, habitat complexity). There is a lack of research on the effects of bivalve predation at the population and community and ecosystem levels (only 7% and 0.5% of studies respectively examined impacts at these levels). At the population level, the available studies demonstrate that predation can decrease bivalve density through consumption or the reduction of recruitment. At the community and ecosystem level, predation can trigger effects that cascade through trophic levels or effects that alter the ecological functions bivalves perform. Given the conservation and commercial importance of many bivalve species, studies of predation should be pursued in the context of global change, particularly climate change, acidification and biological invasions.

*Key words:* ecology, marine, freshwater, defence mechanisms, literature review, population, community.

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\* Author for correspondence (Tel.: +351 253604317; E-mail: [alexandragmeira@gmail.com](mailto:alexandragmeira@gmail.com)).

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## I. INTRODUCTION

Predation is a primary selective agent on individuals, a key driver of ecological interactions, and an important structuring force of communities and ecosystems. Predators drive cryptic coloration in their prey (Kettlewell, 1955), differentially cull diseased prey (Gehman & Byers, 2017), and limit prey populations (Salo *et al.*, 2010). At the community level, effects of top predators can cascade down food chains, depressing or boosting different trophic levels (Molles, 2008; Estes *et al.*, 2011). For example, overfishing of sharks released several species of mesopredator rays and skates whose increased populations depressed those of their own prey – bay scallops *Argopecten irradians* – ending a century-long scallop fishery in the southeastern USA (Myers *et al.*, 2007).

Furthermore, predators may affect prey differently when the predator or prey are non-native, and thus lack a shared evolutionary history (Freeman & Byers, 2006; Pintor & Byers, 2015a). Effects of non-native predators may extend broadly, even affecting adjacent ecosystems. For example, the non-native rainbow trout *Oncorhynchus mykiss* in Japan indirectly increases algal biomass by monopolising terrestrial prey that fall into streams, a major feeding resource for native Dolly Varden charr *Salvelinus malma* (Baxter *et al.*, 2004). This forces the native charr to shift to foraging on invertebrate algae grazers. Not only does this shift affect the freshwater systems invaded by *O. mykiss*, but by feeding more on invertebrate grazers, the native fish decrease the biomass of adult insects and consequently the density of specialist spiders in the surrounding riparian forest.

Research during recent decades has demonstrated that predators affect prey populations through more than just depressing their density, but also by altering their prey's demography, energy allocation, and antipredator traits, including behaviour. Such behaviours can range from changes in habitat use, vigilance, foraging, aggregation, and movement, to preferences for various environmental conditions (reviewed in Creel & Christianson, 2008). The trade-offs of these antipredator behaviours can include costs of reduced survival, growth or reproduction. When multiple predators are present, prey often respond most strongly to the highest-risk predator, or develop a hybrid response to all predators (Freeman, Meszaros & Byers, 2009). Furthermore, multiple predators can also interfere with one another, reducing their cumulative effect below the sum of their values when foraging separately (e.g. Griffen & Byers, 2006).

One taxonomic group of prey that has received abundant attention is bivalves, in part because of the central ecological roles they hold. In fact, one of the most iconic experiments in

ecology addressed the importance of predation within marine rocky communities by examining the influence of sea-star predators on mussel prey (Paine, 1966). The mussel *Mytilus californianus* is competitively dominant for limited space in the rocky intertidal ecosystem. Paine (1966) demonstrated the importance of top-down effects in a food chain and how effect of the removal of a predatory starfish, *Pisaster ochraceus*, cascaded through the rocky intertidal community because of their preferential predation on the mussel. By preferentially consuming *M. californianus*, this sea star opened up space for inferior competitors, and thus boosted local diversity of species that would otherwise be competitively excluded. This process, known as keystone predation, became a cornerstone conceptual process canonised in ecological textbooks.

A heavy focus on bivalves as prey in predation studies is merited since bivalves play a major role in supporting ecosystems and their key functions and services (e.g. filtering water, nutrient cycling, bioturbation of sediments, provision of habitat for other organisms). They also have been an important resource (food, shells, pearls, etc.) for humans for millennia (Vaughn & Hakenkamp, 2001; Beck *et al.*, 2009; Zieritz *et al.*, 2022). Their filter feeding reduces eutrophication and turbidity, increasing water clarity and quality, and thus affecting biological communities (Soto & Mena, 1999; Nakamura & Kerciku, 2000). Deposit feeding by some bivalves decreases organic matter and bioturbates sediments (Vaughn & Hakenkamp, 2001; Vaughn & Hoellein, 2018). Bioturbation by bivalves can also result from their burrowing, which can release nutrients from the sediments into the water column and increase sediment porewater content and the depth of oxygen penetration (Vaughn & Hakenkamp, 2001; Vaughn & Hoellein, 2018). Moreover, bivalves can play a role in provisioning of habitats (e.g. oyster reefs, mussel beds) that provide shelter and protection to other species (Vaughn & Hakenkamp, 2001; Gutiérrez *et al.*, 2003; Beck *et al.*, 2009; Bódis *et al.*, 2014; Ilarri *et al.*, 2018). Bivalve shells can be used to stabilise acidic soils and improve soil chemical and biological properties, as absorbents in cleaning processes and filters for wastewater, in construction as a complement to sand for cement and concrete production, and as fertiliser and poultry grit in agriculture (Yao *et al.*, 2014; van der Schatte Olivier *et al.*, 2020). Bivalves are also a source of protein for humans. According to FAO (2020), the worldwide annual aquaculture production of bivalves was 15.82 million tonnes (\$27.32 billion) in 2018. Additionally, pearls or nacre derived from bivalves are used in the production of jewellery and buttons (van der Schatte Olivier *et al.*, 2020). Overall, the

ecosystem goods and services provided by bivalves and their by-products are estimated to be at least \$30.3 billion per year (van der Schatte Olivier *et al.*, 2020). Thus, any change in bivalve density and biomass due to biotic interactions such as predation could have large ecological and economic effects and deserves scientific attention.

In addition to their important ecological roles, bivalves are also appealing study taxa for logistical reasons. They are often sessile, their shells are easy to mark, and their shells often provide forensic evidence of specific predators (e.g. Byers, 2002; Freeman *et al.*, 2009). Such evidence can allow researchers to assess predatory impacts on bivalves in palaeontological studies. By comparing predation boreholes in fossil and modern scallop species, Jonkers (2000) found that the palaeospecies was likely preyed upon by a large gastropod that targeted mature individuals, in contrast to predation on a modern congeneric scallop where predation by similar predators was restricted to juveniles. The differences in estimated predator size could explain the differences found in their preferences.

Given the prominent role of predation and the key ecological and economic importance of bivalves in aquatic ecosystems, the purpose of this review is to synthesise the very large body of scientific research on predator–bivalve interactions. In so doing, we sought to understand better the effects of bivalve predation at the individual, population, community and ecosystem levels, and the factors that influence predation of bivalves and its outcomes. There is a rich literature on this topic; we evaluated 1334 peer-reviewed publications from across the globe that investigated many different predatory taxa that prey on bivalves. To assess the major drivers and possible gaps or biases on research on bivalve predation and to guide future studies we quantified: (i) temporal patterns in publication; (ii) the major focus of these studies; (iii) the different factors and interactions influencing bivalve predation and its impacts; and (iv) the organisational level at which effects were assessed (individual, population, community, ecosystem). Our analysis addresses factors influencing this biotic interaction to obtain ecological insights into an influential ecological process on a prominent, important, and well-studied taxonomic class.

## II. METHODS

### (1) Data collection

To quantify interactions of bivalves with their predators comprehensively, we searched the biological literature using Clarivate *Web of Science* (WoS). The search was based on an exhaustive compilation of search terms, including: ‘predation’ OR ‘predator’, common terms for bivalve groups (e.g. bivalve, mussel, clam), and bivalve genera (e.g. *Mytilus*, *Unio*, *Pisidium*, *Dreissena*) or species name (e.g. *Limnoperna fortunei*, *Pharella waltoni*) (see online Supporting Information, Appendix S1). Genera and species names were

generated using the Global Biodiversity Information Facility (GBIF) and used to ensure we captured studies on all bivalve species. There is a potential bias when using a single bibliographical data source. Older studies might not be present in the database, potentially creating artifacts (Singh *et al.*, 2021). However, WoS is very comprehensive and presents clear selection criteria and we captured thousands of studies which we consider a very comprehensive coverage of this topic. All publications were checked for relevance to our objectives (i.e. to synthesise global information and trends on bivalve predation) based on the title and abstract. Studies published in scientific journals up to June 2023 were considered. Only studies reporting explicit evidence of predation of bivalves (e.g. direct observation of predation or predation marks, and mortality linked to predation) or predator effects on bivalves were retained, while records from literature reviews or meta-analyses were excluded to avoid double counting.

To identify the motivations for each study we extracted information on the study focus (i.e. the main goal of the research) (Table 1). Categories of study focus included how predator–bivalve interactions influenced or were influenced by: production yield in fisheries/aquaculture, bivalve attributes (i.e. defence mechanisms and behaviour), predator attributes (i.e. predator behaviour and diet preferences), bivalve and predator attributes (i.e. studies that focused on both predator and prey), parasites and epibionts, environmental effects, trophic chains (i.e. studies assessing effects of top predators on mesopredators on bivalves), impacts on

Table 1. List of categories for the classification of the studies on predator–bivalve interactions by study focus and approach used.

Study focus	Approach used
Bivalve production <sup>1</sup>	Predation trials <sup>6</sup>
Bivalve attributes	Visual digested content analysis
Predator attributes	Exclusion experiments
Both bivalve and predator attributes	Video recording
Parasite and epibiont effects on predation	Visual observation
Environmental effects on predation	Molecular digested content analysis
Trophic chains <sup>2</sup>	Stable isotopes
Impacts on bivalves <sup>3</sup>	Predatory cues
Impacts on bivalves and other prey <sup>4</sup>	
Other <sup>5</sup>	

<sup>1</sup>Studies specifically based on increasing production yield for commerce.

<sup>2</sup>Studies assessing effects of top predators on mesopredators on bivalves.

<sup>3</sup>Impacts on bivalve fitness, survival, and/or abundance.

<sup>4</sup>Impacts on bivalve and other prey fitness, survival, and/or abundance recorded as part of a study that also studied other prey.

<sup>5</sup>Studies that did not directly focus on predation or predators but collected incidental data on predation on bivalves.

<sup>6</sup>All trials where predators were purposely added to experimental cages/tanks.

bivalves (i.e. effects on bivalve fitness, survival or abundance), and impacts on bivalves and other prey. The distinction between these two latter categories captures whether a study was purely focussed on bivalves or on the prey community, respectively. Finally, we included a category of ‘other’ for studies that did not focus on bivalve predation but collected incidental data on it.

We also recorded the approach used to observe bivalve predation or predation effects. All studies that investigated bivalve predation using trials where predators were added to experimental cages or tanks with prey were classified as ‘predation trials’. Visual digested content analysis included stomach, faecal, bolus and regurgitation contents. Exclusion experiments used cages or mesh to block predator access to bivalves. Other categories include video recording and visual observation of bivalve predation, molecular digested content analysis (i.e. DNA or protein analysis), stable isotopes analysis, and predatory cues, which focus on the use of isolated cues from predators, rather than the predators directly, to assess their effects on bivalves. It should be noted that in some studies prey were placed on tethers; however, we categorised the studies using this technique into the more general predation trials, exclusion experiments, and visual observation categories.

We also recorded the level of biological organisation (individual, population, community and ecosystem) at which bivalve predation effects were reported. Studies that showed changes in morphology, behaviour, and mortality were classified as predation effects assessed at the individual level. When bivalve predation effects on populations were evidenced (i.e. changes in recruitment and natural population abundances) these studies were classified at the population level. Studies demonstrating effects of bivalve predation on several species beyond the focal bivalves and/or in ecosystem functions were classified as community- and ecosystem-level effects, respectively.

Lastly, we extracted data on the geographic location (i.e. country and continent), ecosystem type (i.e. marine or freshwater), type of study (i.e. laboratory or field), and taxonomy (i.e. family, genus and species) of the studied predators and prey. The predator species were categorised by faunal group (i.e. annelids, birds, chelicerates, cnidarians, crustaceans, ctenophores, echinoderms, fish, insects, mammals, molluscs, nemertean, platyhelminths, and reptiles). Studies with specimens from estuaries were classified as marine because the majority of species in those studies were marine; however, one estuarine study (Boles & Lipcius, 1997) was classified as freshwater because salinity levels were low and it examined freshwater species (i.e. *Dreissena polymorpha*, *Lepomis auritus*, and *Lepomis gibbosus*).

Given changes in taxonomic classification over time, and differences found throughout the collected data, all taxonomic names were changed to the currently accepted names. Based on the information gathered, the taxa for each predator and bivalve record were categorised as native or non-native to the country of the study, using information on species distribution from CABI (2023) and the available

literature. We also assessed whether the bivalve species was of commercial interest to the country in which the study was performed through literature and technical reports.

Our search yielded an initial total of 5034 studies. After excluding studies that did not meet our criteria (i.e. studies not reporting explicit evidence of predation on bivalves, and review papers and books), the data set comprised 1334 studies. This corresponded to 2682 records of predation (i.e. predator–prey interactions recorded), because some studies reported interactions between more than one bivalve and/or predator species.

## (2) Data visualisation

To evaluate the temporal and geographic patterns of bivalve predation studies, the data were grouped by year at the country and the continent level. To visualise relations between combinations of study attributes, we conducted three main analyses of the linkages among various attributes captured in this review (i.e. ecosystem type, predator group and predator origin; ecosystem type, commercial interest, and bivalve and predator origin; and ecosystem type and approach used) using the function ‘sankeyNetwork’ from the R-package *networkD3* (Allaire *et al.*, 2017). First, we ran a network analysis to assess how ecosystem type, predator origin and predator group were related to each other by calculating the number of records of predators in each system, and how many of those were native or non-native and associated with each predator group. Second, the relationships between bivalve origin, bivalve commercial interest and predator origin were assessed using the same method by calculating the number of records of native and non-native bivalves, how many were of commercial interest, and how many native and non-native predators preyed upon them for each system. It is important to note that this network analysis takes into consideration the fact that each bivalve or predator can have multiple predator–prey relationships in the same study, thus multiplying the number of entries for each component compared to the number of bivalves and prey identified per study. Lastly, we assessed the relationship between the approaches used in freshwater and marine studies to assess how predation or predator effects on bivalves were used in combination or as isolated approaches, by using the function ‘forceNetwork’ from the same R package. R scripts used to generate all figures are available at zenodo (<https://doi.org/10.5281/zenodo.10041131>).

## (3) Statistical analysis

To evaluate effects of epifaunal *versus* infaunal life histories on vulnerability to predation, we looked at studies that conducted exclusion experiments that restricted predator access to bivalves. Within each study, we calculated the proportional change in bivalve densities between treatments with predator access (controls) and predator exclusion, and we tracked whether the study examined epifaunal (Ostreidae and Mytilidae;  $N = 8$  cases) or infaunal bivalve populations

(Myidae, Cardiidae, Veneridae;  $N = 10$ ). These sample sizes were small due to the disparate nature of the response variables and approaches used. To assess whether epifaunal and infaunal bivalves exhibited larger proportional change in abundance when protected from predators we used a non-parametric Mann–Whitney U test to test between the two groups. The statistical analysis was conducted in R version 4.2.2 (R Core Team, 2022) and RStudio version 2022.12.0.353 (Posit Team, 2022). No formal analysis was attempted to test the effects of other functional traits due to the variability of methods used and lack of data.

### III. RESULTS

The earliest research paper studying bivalve predation in our data set was conducted in the United Kingdom (UK, Europe) by Dunthorn (1971) and assessed the predation of *Mytilus edulis* by *Somateria mollissima*. This was followed by studies from Tanzania (Africa) (Smith, 1975), and the USA (North America) (Paine, 1976). Studies from other continents date back to 1981 (Asia, Malaysia; Broom, 1981), 1985 (Oceania, Republic of Palau; Perron, Heslinga & Fagolimul, 1985), and 1991 [South America, Argentina (Iribarne, Fernandez & Zucchini, 1991) and Brazil (Fernandes, 1991)]. After 1991 there was an increase in the number of studies (Fig. 1B), and subsequently the number of publications per year in Europe and North America has increased. However, on the other continents the numbers have remained low (Fig. 1A).

Most studies were conducted on marine/estuarine species (~86%;  $N = 1153$  studies; Fig. 1B), including the first record of bivalve predation in our data set (Dunthorn, 1971). The first study on a freshwater species in our data set was from North America assessing the predation of *Corbicula fluminea* by *Procambarus clarkii* (Covich, Dye & Mattice, 1981). Africa has very few studies, only one of which was on freshwater bivalve predation (Ethiopia; Eyayu & Getahun, 2022). Two studies were conducted with both marine and freshwater bivalve species (Prado *et al.*, 2020; Schmitt *et al.*, 2019).

Of the 2341 different records of predated bivalves in our data set a total of 298 genera and 478 species across 61 bivalve families were represented. Records of predated bivalves from identified families ( $N = 2259$ ) were dominated by Mytilidae (~29%), followed by Veneridae (~14%), Ostreidae (8%), Unionidae (~7%), Dreissenidae and Tellinidae (~6% each), Pectinidae and Cardiidae (~5% each), Myidae (~3%), Mactridae (~2%), and Arcidae, Cyrenidae, Donacidae and Lucinidae (~1% each); the remaining 47 families accounted for <1% each. Some bivalves were only identified to the genus level ( $N = 190$ ), or family level ( $N = 66$ ) or could be identified only as 'bivalves' ( $N = 82$ ) through shell fragments, visual observation, or analyses of stable isotopes.

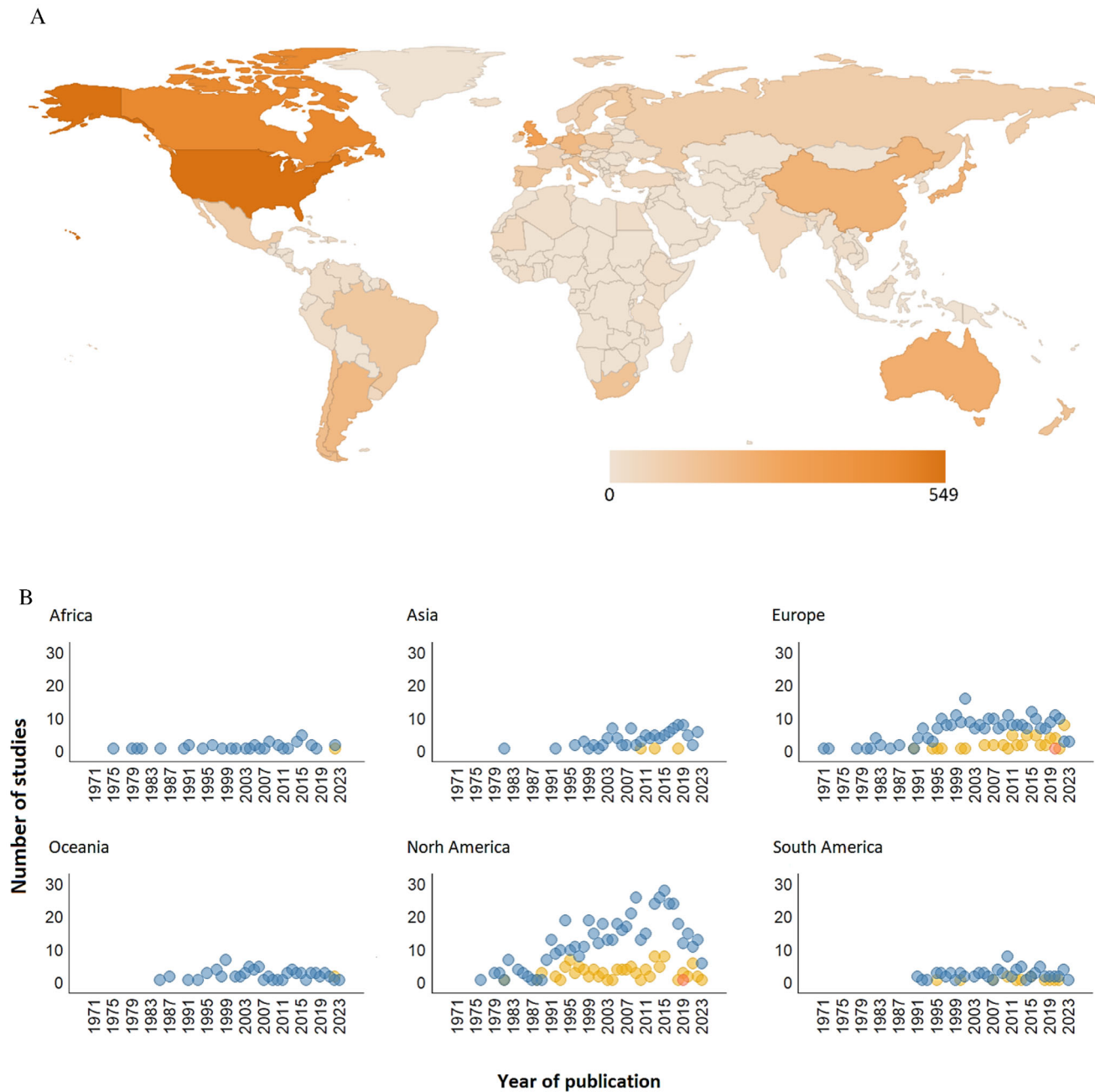
Records of freshwater bivalves from identified families ( $N = 331$ ) were dominated by Unionidae (~44%) and

Dreissenidae (~38%), with the zebra mussel *Dreissena polymorpha* the most studied species (~27%;  $N = 79$ ) of the bivalves identified to species level ( $N = 290$ ), followed by *D. rostriformis* (~8%;  $N = 23$ ) and *Corbicula fluminea* (~7%;  $N = 19$ ). Of all bivalves identified to species level in marine studies ( $N = 1667$ ), the most studied was *Mytilus edulis* (~13%;  $N = 216$ ; Fig. 2B), followed by *Crassostrea virginica* (~6%;  $N = 100$ ), and *Macoma balthica* and *Mya arenaria* (~4%;  $N = 62$  each) (see online Supporting Information, Tables S1 and S2).

The majority of bivalves recorded were native to the study area (~76%;  $N = 1775$ ), while only 274 (~12%) were non-native and 292 (~12%) did not have their origin identified due to a lack of information to species level. The percentage of non-native bivalves, however, was considerably different between ecosystem types, with ~81% of the marine bivalve records native to the study area (Fig. 3A), while only 50% of the freshwater species were native (Fig. 3B). Lastly, ~54% of the identified bivalve species were of commercial interest to the study country. Again, there is a large difference between ecosystems, with most marine records addressing species of commercial interest (~63%;  $N = 1042$  from 1667 identified marine bivalves), while only ~4% ( $N = 12$ ) of the freshwater records were from species with recognised commercial value (Fig. 3A, B). Overall, research on predation of freshwater species appears to be driven more by a conservation agenda and in assessment of possible impacts generated by the introduction of non-native predators, while marine research tends to incorporate more economically important species. However, this will reflect a generally higher number of marine bivalve species of commercial interest than freshwater species (FAO, 2023), and a larger number of documented invasions in freshwater compared to marine systems (Global Invasive Species Database, 2023), which could result in such skews. Studies were split evenly between epifaunal (49%) and infaunal (~47%) bivalves, while this could not be assessed in 4% of studies.

Crustaceans were the most predominant predator group, accounting for approximately 34% ( $N = 687$ ) of the predator records ( $N = 2036$ ), followed by fish (~24%;  $N = 480$ ), molluscs (~17%;  $N = 349$ ), echinoderms (~10%;  $N = 200$ ), birds (~6%;  $N = 126$ ), mammals (~2%;  $N = 31$ ), and cnidarians (~1%;  $N = 28$ ) (Fig. 3C). The other seven taxonomic groups (annelids, chelicerates, ctenophores, insects, nemertean, platyhelminthes and reptiles) accounted for less than 1% each. In ~5% ( $N = 97$ ) of predator records, the predators could not be identified nor assigned to a group due to the approach used (e.g. use of exclusion cages; observation of predation marks only). In total, 625 predator species ( $N = 1776$  predator records) were identified; 163 predators could only be identified to the genus ( $N = 40$ ), family ( $N = 6$ ), and order ( $N = 3$ ) level, or could only be associated to a group of predators ( $N = 114$ ).

Overall, and considering predators whose origin could be assessed ( $N = 1822$ ), ~87% ( $N = 1585$ ) were native to the study area (Fig. 3C). Regarding each ecosystem, native predators accounted for ~90% ( $N = 1329$ ) of predation records in marine systems (Fig. 3A), and ~77% ( $N = 264$ )



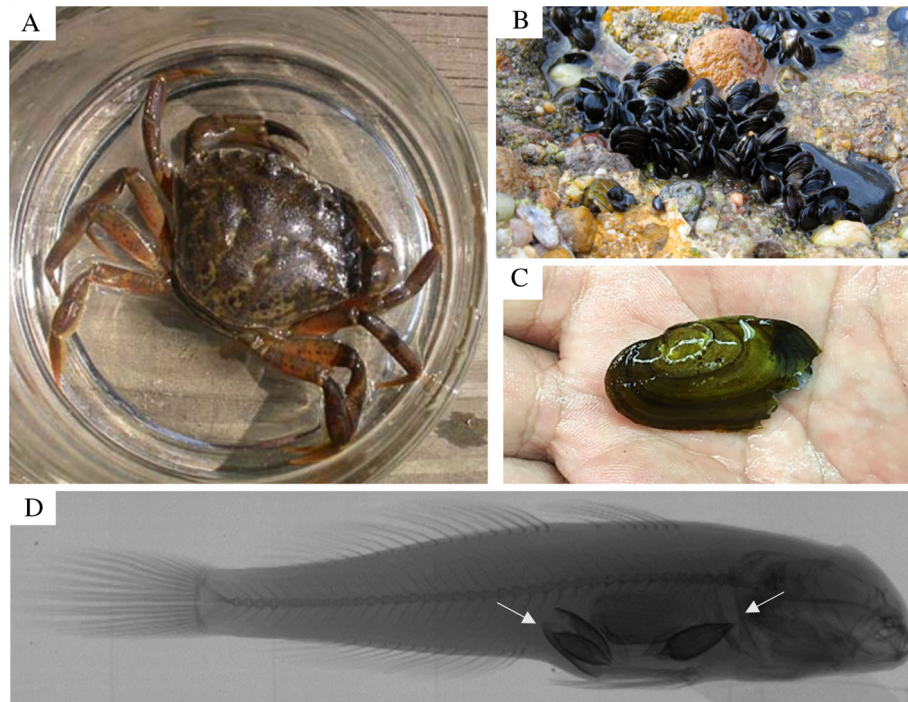
**Fig. 1.** Geographic and temporal patterns of published studies on bivalve predation. (A) Heat map of total number of studies per country. (B) Number of studies per year of publication per continent grouped by ecosystem studied: marine (blue) and freshwater (brown). Please note that the number of studies in 2023 only includes studies published until June.

in freshwater systems (Fig. 3B). Furthermore, research conducted in marine systems reported a higher percentage of unidentified predators ( $N = 150$ ;  $\sim 9\%$  of the total predators in this system) than freshwater studies ( $N = 18$ ;  $\sim 5\%$ ) (Fig. 3A, B).

*Carcinus maenas* was the most predominant predator species in marine studies, accounting for  $\sim 10\%$  of records ( $N = 148$ ) (excluding non-identified predators) (Fig. 2A and Table S2). More than half of the studies referring to *C. maenas* were

conducted in areas where this species is non-native ( $\sim 55\%$ ;  $N = 82$ ), making it also the most represented marine non-native predator species. It was followed by the blue crab *Callinectes sapidus* ( $N = 88$ ;  $6\%$ ), which has only been studied once outside its native range, and the sea star *Asterias rubens* ( $N = 69$ ;  $\sim 5\%$ ), which was native in all studies.

For freshwater studies, the most cited predator was the fish *Neogobius melanostomus* ( $N = 39$ ) (Fig. 2D), which accounted for  $\sim 12\%$  of records of predation excluding non-identified



**Fig. 2.** Four representatives of marine and freshwater species cited in bivalve predation records. (A) The most commonly studied marine predator of bivalves, the predatory crab *Carcinus maenas* (image credit: James Byers). (B) The most commonly studied marine bivalve prey, blue mussels *Mytilus edulis* (image credit: Andreas Trepte; [www.avi-fauna.info](http://www.avi-fauna.info)). (C) Freshwater pearl mussel *Margaritifera margaritifera* shell with predation marks from the invasive signal crayfish *Pacifastacus leniusculus* (image credit: Ronaldo Sousa). (D) X-ray image of the most commonly studied freshwater bivalve predator, the round goby *Neogobius melanostomus*, with whole juvenile unionid mussels ingested (marked by the arrows; image credit: Kyle Clark; Clark *et al.*, 2022).

predators. In ~90% of these records, this fish species was considered non-native. The next most studied freshwater predators were *Lepomis gibbosus* and *Rutilus rutilus* (~4% each;  $N = 12$ ), followed by *Ondatra zibethicus* (~3%;  $N = 11$ ). All three species were native to all but one study area.

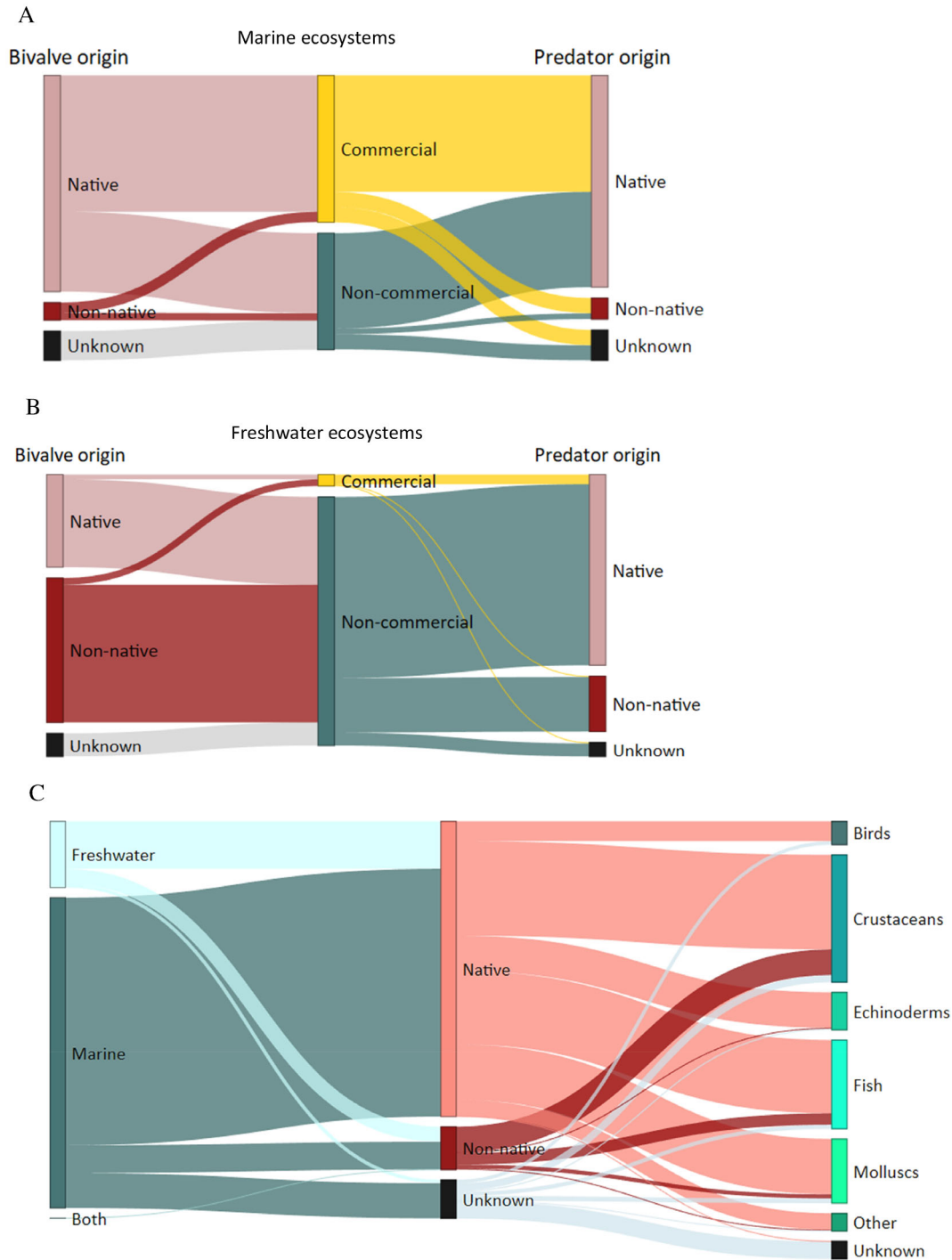
Studies were mostly conducted in the field (~49%;  $N = 649$ ), followed by the laboratory (~38%;  $N = 510$ ), and, in some cases, in both field and laboratory conditions (~13%;  $N = 175$ ). Marine studies were conducted almost equally in the laboratory (40%;  $N = 462$ ) and in the field (~46%;  $N = 531$ ), while ~14% ( $N = 160$ ) were conducted in both field and laboratory. Freshwater studies were conducted mostly in the field (~66%;  $N = 117$ ), followed by laboratory (~26%;  $N = 47$ ) and lastly in both field and laboratory (~8%;  $N = 15$ ).

The most common study focus (Table 2) was assessment of predator attributes (~50%;  $N = 661$ ), followed by studies classified as ‘other’ (~13%;  $N = 179$ ) (i.e. not directly focusing on predation, but incidentally reporting predation on bivalves) and studies on impacts of predation on bivalves (~10%;  $N = 138$ ). Bivalve attributes (i.e. defence mechanism and behaviour) were also studied (~8%;  $N = 104$ ). A smaller proportion of studies focused on the effects of the environment on predation (~8%;  $N = 101$ ) and the impacts of predation on bivalves and other prey (~6%;  $N = 73$ ). A few studies addressed both bivalve and predator attributes to understand the relationship between them (<1%;  $N = 3$ ), focused on trophic chains (~2%;  $N = 29$ ), bivalve production

(~2%;  $N = 24$ ), and the effect of parasites and epibiont infection on predation (~2%;  $N = 22$ ) (Table 2).

Most studies (~75%;  $N = 997$ ) used only one approach to achieve their objective, while 318 (~24%) used two approaches, and 18 (~1%) used three (Fig. 4). One study (Boles & Lipcius, 1997) used four approaches (video recording, visual observation, exclusion experiments and predation trials) to study the effects of predation on a bivalve species in natural conditions.

Overall, predation trials were the most frequently used approach (~50%;  $N = 669$ ), followed by visual analysis of digested contents (~22%;  $N = 289$ ), visual observation (~21%;  $N = 273$ ), exclusion experiments (~18%;  $N = 240$ ), the use of predatory cues (~8%;  $N = 104$ ), video recording (~5%;  $N = 71$ ), stable isotopes (~2%;  $N = 29$ ), and molecular analysis of digested content (~1%;  $N = 15$ ) (Table 3). Because marine studies composed the majority of studies, they followed the same patterns as the general analysis with a few exceptions (Table 3). By contrast, freshwater studies used visual analysis of digested contents most often (48%;  $N = 86$ ) (Table 3). Predation trials and exclusion experiments are the easiest ways to assess predation and can allow simultaneous study of numerous questions related to this biotic interaction (e.g. predator behaviour, prey behaviour, prey defence mechanisms, and impacts of predation at different trophic levels), perhaps explaining the popularity of these approaches. Note that tethering trials can generate some



**Fig. 3.** Linkages among published records of predation between bivalve origin (native and non-native), the commercial status of bivalves ('commercial' bivalves are species supporting an economy at local or global scale) and predator origin (native and non-native), (A) for marine systems, and (B) for freshwater systems. (C) Linkages between predator groups examined as a function of ecosystem type across all 1334 published studies and predator origin (native and non-native). The predator group 'Other' comprises annelids, chelicerates, cnidarians, ctenophores, insects, mammals, platyhelminths, nemerteans, and reptiles. Non-identified organisms and origins are represented by 'Unknown'.

artefacts; however, bivalves are one of the most suitable taxa for such studies because of their low mobility (Peterson & Black, 1994a).

Differences in preferred methodology between freshwater and marine studies could be explained by differences in the ability to sample and observe species. Freshwater systems



Table 2. Overall number and percentage of studies ( $N = 1334$ ) with different study focus.

Study focus	Number of studies	Percentage (%)
Predator attributes	661	49.6
Impacts on bivalves	138	10.3
Bivalve attributes	104	7.8
Environmental effects on predation	101	7.6
Impacts on bivalves and other prey	73	5.5
Trophic chains	29	2.2
Bivalve production	24	1.8
Parasite and epibiont effect on predation	22	1.6
Both bivalve and predator attributes	3	0.2
Other	179	13.4

are more easily accessed and easier to sample (at least compared to deep marine areas), which facilitates use of methods such as gut and faecal contents analysis, and stable isotopes. Ease of access may also explain why a greater proportion of freshwater studies was carried out in the field.

Studies mainly addressed the effects of bivalve predation at the individual level ( $\sim 93\%$ ;  $N = 1236$ ) while effects at the population level were reported 92 times ( $\sim 7\%$ ). Very few studies ( $0.5\%$ ;  $N = 6$ ) observed effects of bivalve predation at community levels. Note that all studies reporting effects at the population and community/ecosystem levels were conducted in natural environments.

#### IV. IMPACTS OF PREDATION ON BIVALVES

Predation of bivalves may have multiple effects, affecting organisms from the individual to the community and ecosystem levels. Lethal impacts of predators on bivalves are most commonly examined *via* consumption of the entire prey or records of lethal damage caused by predation. However, predator–prey interactions are complex and impacts can be sub-lethal or a combination of lethal and sub-lethal. In this section we synthesise information on the effects of predation on bivalves, from individuals to ecosystems, to understand this biotic interaction better in a key taxonomic group in aquatic ecosystems.

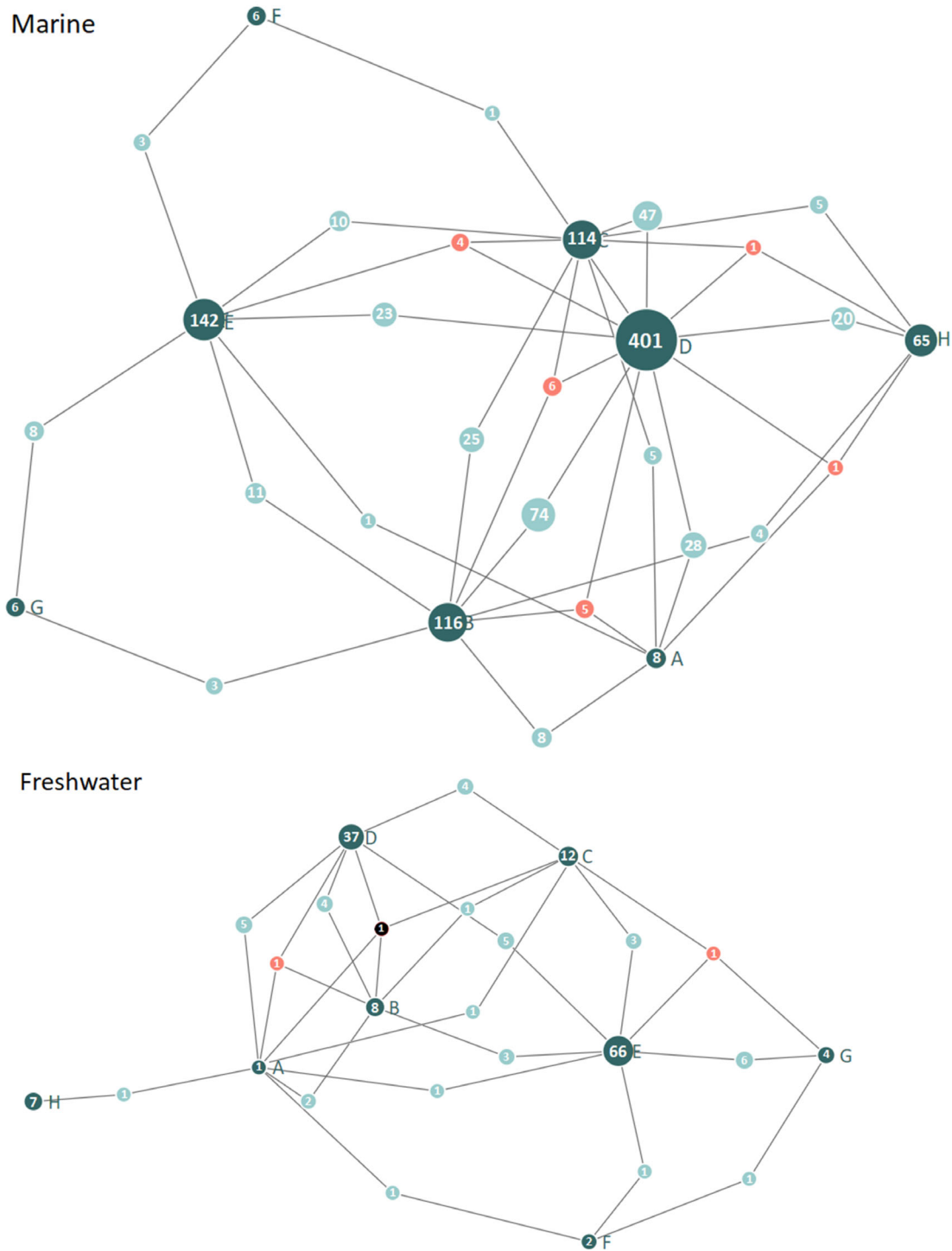
##### (1) Individual level

Numerous studies report a direct lethal effect of predation on bivalves at an individual level (e.g. Navarrete & Menge, 1996; Beal, 2006b; Brousseau, Goldberg & Garza, 2014; Dethier *et al.*, 2019a). Several factors can influence the rates of mortality/survival, including individual differences or temporal effects. Predation mortality could vary with time and be greater in seasons when predators are more abundant or active, bivalves are more vulnerable, and/or environmental conditions are less favourable (Sanchez-Salazar, Griffiths & Seed, 1987; Bishop *et al.*, 2005; Lewis, Esler & Boyd, 2007).

Migrating predators like *Melanitta perspicillata* and *M. fusca* can temporarily increase predation pressure on bivalves before moving to another area. These species were found to increase bivalve mortality during their stay in a given area (Lewis *et al.*, 2007). In temperate regions, predators may be more active in the summer months which can translate into greater feeding rates and bivalve mortality (Sanchez-Salazar *et al.*, 1987).

Predators can exert indirect effects *via* sub-lethal predation. For example, De Goeij *et al.* (2001) found that siphon nipping of *Macoma balthica* decreased its burial depth, making it more vulnerable to other predators; however, this effect and the speed of recovery varied with differences in initial burying depth. While this form of sub-lethal predation can facilitate lethal predation, the relationship may vary among ecologically similar bivalve species with different siphon lengths. Bivalves with longer siphons can remain buried at relatively safe depths, while species with shorter siphons are more prone to mortality after suffering sub-lethal siphon cropping (Meyer & Byers, 2005). This sub-lethal predation can also translate into energy costs to the bivalves, as energy needs to be allocated to siphon regeneration at the cost of available energy for bivalve growth and gonad development (Peterson & Quammen, 1982; Kamermans & Huitema, 1994). For example, growth of *Leukoma staminea* can be reduced in the presence of siphon-feeding predators, with this reduction not explained by the inhibition of bivalve feeding but possibly by a reduction in available energy as a result of the clams regenerating the lost tissues (Peterson & Quammen, 1982).

Effects on individual traits may also affect fitness. Bivalves can make behavioural changes to protect themselves from predation, such as retraction of the feeding siphon, which inevitably reduces feeding activity (Maire *et al.*, 2010). Similarly, predation risk can negatively affect the filtration rate and oxygen consumption of bivalves, leading to impacts on bivalve fitness and mortality by cumulative sub-lethal effects (Lopez *et al.*, 1995; Naddafi, Eklöv & Pettersson, 2007). This occurs because bivalves use valve closure as a defence mechanism when they recognise a predation threat either *via* chemical cues or physical contact with the predator (Irlandi & Mehlich, 1996; Naddafi *et al.*, 2007; Maire *et al.*, 2010). However, these physiological and behavioural changes, commonly referred to as the ‘ecology of fear’, do not always translate into decreased activity. For example, Byers *et al.* (2014) and Dodd *et al.* (2018) found that predation and predator cues did not alter filtration rates in the oyster *Crassostrea virginica*. Valve closure can increase the heart rate in bivalves due to limitation of the oxygen supply. However, this correlation is not linear, with more studies needed (Taylor, 1976; Rovero, Hughes & Chelazzi, 1999; Kholodkevich *et al.*, 2009). Some studies have shown an increased heart rate in bivalves due to predation and/or the presence of a predator, which implies an impact on their stress levels (Rovero *et al.*, 1999; Kamenos, Calosi & Moore, 2006). This effect was reduced when bivalves had access to refuges (Kamenos *et al.*, 2006).



**Methods used:**

- A Video recording
- B Visual observation
- C Exclusion experiments
- D Predation trials
- E Visual digested content analysis
- F Molecular digested content analysis
- G Stable isotopes
- H Predatory cues

**Fig. 4.** Linkage among approaches to show which tend to be used on their own and which tend to be paired with others for marine (top;  $N = 1464$ ) and freshwater (bottom;  $N = 225$ ) systems. Node size and number correspond to the relative number of studies using a single approach (dark blue) or set of two (light blue), three (pink), or four (black) methodologies in each system. Because multiple approaches could be used in a single study, the total number of approaches used is higher than the total number of studies ( $N = 1334$ ).

Table 3. The number and percentage of studies using different approaches across all studies ( $N = 1334$ ), in marine (1153 studies), and in freshwater (179 studies) systems. Two studies were conducted in both marine and freshwater systems that used predation trials and visual digested contents analysis, these are included in the ‘overall’ columns. Because studies can use multiple approaches the total of the percentages across all study approaches exceeds 100%.

Approach	Overall		Marine		Freshwater	
	Number of studies	Percentage (%)	Number of studies	Percentage (%)	Number of studies	Percentage (%)
Video recording	71	5.3	57	4.9	14	7.8
Visual observation	273	20.5	253	21.9	20	11.1
Exclusion experiments	240	18	217	18.8	23	12.9
Predation trials	669	50.2	611	53.1	57	31.7
Visual digested content analysis	289	21.7	202	17.5	86	48.1
Molecular digested content analysis	15	1.1	10	0.9	5	2.8
Stable isotopes	29	2.2	17	1.5	12	6.7
Predatory cues	104	7.8	96	8.3	8	4.5

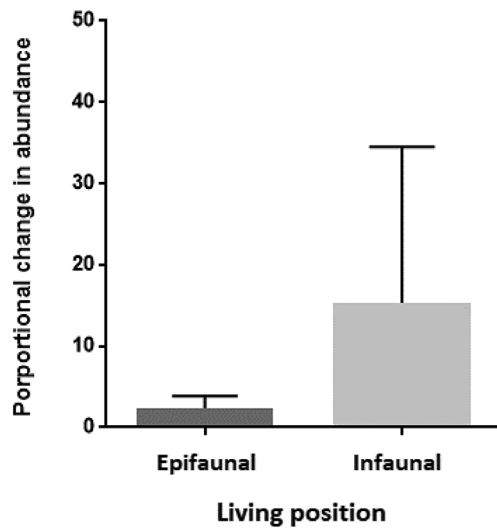
Bivalves have mechanisms of morphological defence; they may invest in increased shell growth or thickness/toughness to make them less vulnerable to predation (Newell, Kennedy & Shaw, 2007; Johnson & Smee, 2012). Freeman & Byers (2006) found that mussels formed thicker shells in response to chemical cues from predators (the non-native crabs *Carcinus maenas* and *Hemigrapsus sanguineus*); however, this response was dependent on their previous experience with the predators. Growth rates can vary among bivalve size classes, species and even with predator species. In response to the presence of a predator, bivalves may show higher shell growth and less soft-tissue growth, or less growth of both soft tissue and shell mass (Johnson & Smee, 2012). These differences may be due to changes in energy allocation or to reduced feeding time. Shell damage and siphon nipping not only requires energy for wound healing and recovery in the bivalve, which could translate into less energy available for growth, but also means greater exposure to predation at vulnerable sizes (Kamermans & Huitema, 1994; Ansell, Harvey & Günther, 1999).

## (2) Population level

Bivalve mortality due to predation has the potential to limit population density (Carroll & Highsmith, 1996; Hunt & Mullineaux, 2002; Barton *et al.*, 2005), biomass and size structure, although such effects will be dependent on the reproductive potential of the bivalves and the density of their predators (Magoulick & Lewis, 2002). Bishop *et al.* (2005) found that the mortality of scallop recruits was lower in late autumn and winter (when it was almost negligible) than in late spring and summer (when it could reach 100%) due to variation in predator species and abundance, and the presence of competitors. Recruitment success also can be affected by predation of particular life stages, such as greater consumption of larvae and juveniles (Flach, 2003; Beal, 2006b; Knights, Firth & Walters, 2012). Furthermore, populations can be affected by predators changing recruitment and larval production by adult bivalves. For example, recruitment can

be impacted by predation changing the time of release of offspring (Evans, Gasparini & Pilastro, 2007). Ehlers, Scrosati & Ellrich (2018) showed that the presence of dogwhelk predator *Nucella lapillus* can significantly inhibit mussel *Mytilus* spp. recruitment *via* chemical cues. Shell damage and defence mechanisms can have a fitness cost which may also reduce the reproductive output of bivalves by limiting the energy available to allocate to reproduction (Nakaoka, 2000; Kimbro *et al.*, 2020a), with a resulting effect on bivalve populations.

The effects of predation on bivalve populations will be dependent on multiple factors including antipredator defences, predator and prey behaviours, habitat complexity, and bivalve living position (i.e. epifaunal or infaunal) (Seitz *et al.*, 2001). By burrowing into the substratum, infaunal bivalves are protected to some extent, with reduced encounter rates with predators compared to their epifaunal counterparts. However, epifaunal bivalves may show adaptations such as heavier investment in defensive features such as thicker shells (Seitz *et al.*, 2001; Pickering & Quijón, 2011). We investigated whether epifaunal or infaunal bivalves appear more vulnerable to predators in the eight quantitative studies that compared bivalve densities in a predator-exclusion cage against a control with normal predator access (Petraitis, 1991; Peteiro *et al.*, 2010; Hidalgo *et al.*, 2011; Carroll, Marion & Finelli, 2015b; Beal *et al.*, 2016b, 2018, 2020a; de Fouw *et al.*, 2020). The proportional change in the number of individuals between control sites and exclusion cages was positive for both epifaunal and infaunal bivalve populations; however, the proportional increase showed a non-significant trend to be higher for infauna (Mann–Whitney U test,  $U = 22$ ,  $P > 0.122$ ) (Fig. 5). Thus infaunal bivalves may benefit more from the exclusion of predators than epifaunal bivalves, but clearly additional studies are needed, given the high degree of variability, especially in infaunal studies. This variability may be due to species-specific differences in burrowing depths, habitat characteristics, density, predator type, and study design (Hulscher & Ens, 1992; Seitz *et al.*, 2001; van der Heide *et al.*, 2014; Beal *et al.*, 2018).



**Fig. 5.** Proportional change per experiment in the abundance of bivalves between controls with access by predators and predator-exclusion plots. Data were categorised according to whether the bivalves in the study were epifaunal or infaunal. Values are means +SD. Data from Petraitis (1991), Peteiro *et al.* (2010), Hidalgo *et al.* (2011), Carroll *et al.* (2015b), Beal *et al.* (2016b, 2018, 2020a), and de Fouw *et al.* (2020).

Predators may exhibit size preferences or a lack of ability to consume particular bivalve size ranges. Studies generally report greater predation on smaller bivalve size classes (e.g. Brown & Haight, 1992; MacIsaac, 1994; Gosselin & Chia, 1996; Cordero & Seitz, 2014; Pickering *et al.*, 2017; Sousa *et al.*, 2019). Such size-biased predation can change a population's size structure, by reducing the abundance of smaller bivalves. Bijleveld *et al.* (2015) observed this in a cockle *Cerastoderma edule* population where birds preferentially preyed on smaller individuals, shifting the size distribution towards larger bivalves. By contrast, some studies addressing size-dependent predation have shown a preference of predators for medium and large bivalve prey, leading to a shift in size distribution towards smaller bivalves (e.g. Kvittek *et al.*, 1992; Anderson & Connell, 1999; Mitchell, Bailey & Knapton, 2000; Nakano, Kobayashi & Sakaguchi, 2010; Booth *et al.*, 2018).

Bivalves provide ecological goods and services, thus there will be direct economic effects of bivalve predation. Because monetary calculations seldom form the focus of most ecological studies, there are few direct assessment of this cost. In Hokkaido, Japan, the removal of predatory starfish, along with other practices intended to boost bivalve production (e.g. increasing the supply of larvae, and maintaining preferred habitat traits) increased the scallop harvest following a collapse in 1945 (Uki, 2006). These measures resulted in an increased scallop harvest from 70,000 tonnes (around \$102 million) in 1975 to 272,000 tonnes (around \$245 million) in 2002. Many fisheries have attempted to develop new sustainable ways to protect their stocks from predation, for example by using suspension cultures and deploying

protective nets (Quayle & Newkirk, 1989; Spencer, Edwards & Millican, 1992).

### (3) Community and ecosystem level

Many bivalve species function as ecosystem engineers (i.e. structural and/or chemical engineers and bioturbators; Gutiérrez *et al.*, 2003), and thereby regulate the availability of resources for other species. Bivalve predation can thus affect entire communities through changes in competition and other biotic interactions, habitat composition, and succession (Bonsdorff, Norkko & Sandberg, 1995; Navarrete, 1996; Hamilton, 2000; Needles *et al.*, 2015). For example, the biomass of species associated with *Mytilus californianus* mussel beds may be reduced by the presence of sea otters *Enhydra lutris* as a result of mussel predation and consequent limitation of suitable habitat available for mussel-associated species (Singh *et al.*, 2013). Comparisons between regions occupied and unoccupied by sea otters showed that selective predation of larger mussels led to changes in the secondary substrate and habitat available for other invertebrates. These changes caused population reductions in species dependent on the habitat provided by the mussels, and indirectly affected mussel-bed-associated communities (Berke, 2010; Singh *et al.*, 2013). Whelk predation on mussels is another example of impacts at the community level: it may negatively affect sea anemones by reducing the availability of mussel-bed refuges leading to higher mortality of juvenile anemones (Navarrete, 1996).

Consumption of mussels in the rocky intertidal zone can also benefit some species. Whelk predation of mussels reduces competition with barnacles, resulting in a net positive effect on the barnacles even though they are also preyed upon by the whelks (Navarrete, 1996). Needles *et al.* (2015) showed that the percentage cover of the exotic bryozoan *Watersipora subtorquata* was negatively correlated with mussel cover and the presence of mussel predators increased the rate of invasion of *W. subtorquata*, suggesting that reduced competition with mussels had a positive effect on this non-native species. Paine (1966) observed a similar effect following removal of the predator *P. ochraceus*, allowing its prey *M. californianus* to dominate the area to the detriment of other species.

Intensive bivalve predation can lead to the loss of important ecosystem functions such as water filtration, nutrient cycling, bioturbation, and habitat provision (Vaughn & Hakenkamp, 2001; Gutiérrez *et al.*, 2003). Myers *et al.* (2007) found that the decline of shark populations (apex predators) increased the abundance of rays (mesopredators) that prey upon bay scallops. The scallop populations declined severely due to increased predation pressure, with potential cascading effects on seagrass habitat because rays uproot seagrass as they forage, consequently affecting the availability of nursery habitat (Orth, 1975; Myers *et al.*, 2007).

Through filter feeding, bivalves reduce the abundance of phytoplankton. In a laboratory experiment, Naddafi & Rudstam (2013a) showed that the presence of fish and

crayfish predators can lead to increased abundance of phytoplankton *via* a trophic cascade. When these predators consumed non-native dreissenid mussels, phytoplankton abundance increased, potentially resulting in harmful algal blooms, low water transparency, and reduced oxygen levels that can affect the entire ecosystem (Hallegraeff, 2003; Rensel & Whyte, 2003). These effects depended on the number of predator species present, and decreased with increased predator diversity, possibly due to competitive interference. Extrapolation of these results to the natural world may be problematic and further research in natural settings is needed. Few studies examine community or ecosystem effects in a field setting. However, in the Hudson River (USA), invasion of the zebra mussel *D. polymorpha* initially decreased turbidity through reductions in phytoplankton and zooplankton abundance. This ecosystem has since begun to recover to pre-invasion conditions, likely due to higher mortality rates in zebra mussels partly caused by increased predation by the native blue crab *Callinectes sapidus* which has adapted to feeding on this novel prey (Carlsson *et al.*, 2011; Strayer, Cid & Malcom, 2011; Strayer *et al.*, 1999, 2014). Such examples highlight the complexity of the interactions and the difficulty of assessing effects at the community or ecosystem level.

## V. FACTORS INFLUENCING PREDATION

The severity and intensity of predation may vary according to predator and prey traits and behaviour, environmental factors, or other biotic interactions such as disease and parasites, among other factors. Predators generally have a preferred range of prey. Such preferences may result from proximity or familiarity (with predators preferring native prey over newly introduced prey or failing to recognise novel prey), higher energy payoffs, or a lower handling cost (Barbeau & Scheibling, 1994a; Saito *et al.*, 2004; Pintor & Byers, 2015a; Meira *et al.*, 2019). For example, the polychaete *Halla okudai* selects larger clams due to a higher net rate of energy intake (Saito *et al.*, 2004). However, because foraging time increases with clam size, it is not profitable for small polychaetes to select larger prey, resulting in their preference for smaller prey. Similarly, Aronhime & Brown (2009) found that *Callinectes sapidus* consistently selected smaller mussels, which they argued was due to the higher handling time and larger crushing force required to consume larger mussels which increases their own predation risk and can damage the crab's claws.

Predators have different strategies to obtain their prey: starfish pry open bivalve shells to consume the flesh inside; crustaceans will chip the shells, sometimes failing to reach the flesh inside; cownose ray *Rhinoptera bonasus* mash the bivalves completely (Zafriou, Whittle & Blumer, 1972; Fisher, Call & Grubbs, 2011; Meira *et al.*, 2019). The success of these mechanisms will be related to both prey and predator traits. For example, round gobies prey on bivalves by ingesting them whole or crushing them and thus prey

selectively on smaller individuals, with a strong negative correlation between prey size and consumption rate (Andraso, Ganger & Adamczyk, 2011). Klompmaker & Kelley (2015) examined the location of drill holes in four Cenozoic bivalve species. The results showed that the number of holes between ribs increased with rib strength, the number of incomplete holes was greater on top of the ribs, and the percentage of incomplete holes was lower in strongly ribbed (less-spaced ribs) species. This study showed that ornamented shells are likely to be an effective defence mechanism against predatory drilling by naticid and muricid gastropods.

Bivalves can perceive chemical signals (kairomones) released by predators, allowing them to detect predation risk and potentially to evade predation (Ferrari, Wisenden & Chivers, 2010). Castorani & Hovel (2016) found that the non-native Asian nest mussel *Arcuatula senhousia* not only recognised its native predators' kairomones but also differentiated between them, adopting different anti-predation behaviours according to which predator was present. *Arcuatula senhousia* reduced its feeding in the presence of predatory snails and stingrays, but in the presence of lobster the mussels burrowed deeper into the sediment; exposure to kairomones from snails increased mussel aggregation. Aggregation has been observed in other bivalve species (e.g. Reimer & Tedengren, 1997; Kobak & Kakareko, 2009) and may increase the chances of survival (Hamilton, 1971).

Environmental factors, such as wave exposure, current flow, oxygen and carbon dioxide levels, salinity, and temperature, can affect both prey and predators (Garton & Stickle, 1980; Tallqvist, Sandberg-Kilpi & Bonsdorff, 1999; Byers, 2005; Freeman *et al.*, 2009; Pruettt & Weissburg, 2021). For instance, acidification can reduce the growth and feeding rates of predators (Appelhans *et al.*, 2012) and/or reduce shell growth in bivalves (Sanford *et al.*, 2014; Glaspie, Longmire & Seitz, 2017). Currents affect the strength of chemical cues that a predator receives and can thus influence its efficiency in locating prey (Weissburg *et al.*, 2002). Higher temperatures increase metabolic rates, which can increase predator activity up to a threshold. For example, Sanchez-Salazar *et al.* (1987) found that the feeding rates of the shore crab *C. maenas* rose with increasing temperature, resulting in the consumption of a higher number of cockles while the size range of prey consumed remained unchanged.

Pollution can also alter predator and prey behaviour. For instance, clams showed shallower burial and slower reburrowing in oil-contaminated sediment compared to controls, allowing predatory crabs to consume more clams in oiled sediments (Pearson *et al.*, 1981). However, oil exposure can also disrupt predator foraging behaviour, affecting their ability to locate prey through chemoreception (Temara, Gulec & Holdway, 1999). Water turbidity can affect the ability of predators to locate their prey. Reustle & Smee (2020) showed that this applies to visual predators (e.g. fishes), whereas predators that forage by chemoreception (e.g. crabs) were unaffected by turbidity. In fact, predation on the oyster *Crassostrea virginica* by crabs increased with turbidity, as turbidity impacted the ability of fishes

to locate crabs and hence reduced top-down control of these oyster predators.

Lastly, habitat features and complexity, and the presence of other species may provide protection against predation (e.g. Seitz *et al.*, 2001; Talman *et al.*, 2004). Substrate type can influence encounter and predation rates between predator and prey: Wong & Barbeau (2003) found that sea stars encountered and preyed less on small scallops with increasing particle size in soft sediments. The presence of other species can both dilute predation pressure and also create refuges for bivalves. For instance, bivalve survivorship can be enhanced by the structure provided by other bivalve species, because they can use it as a refuge from predators (Skilleter, 1994). In addition, the presence of apex predators can reduce bivalve predation *via* trophic cascades or competition (Morissette & Himmelman, 2000a; Gaymer, Himmelman & Johnson, 2002; Ellis *et al.*, 2007; Byers, Holmes & Malek, 2017). Epibionts and parasites of bivalves may affect their susceptibility to predation. Epibionts can provide chemical, structural or visual protection against predators (e.g. Laudien & Wahl, 1999; Marin & López Belluga, 2005), but may also increase prey attractiveness (Enderlein *et al.*, 2003). Parasites can alter bivalve behaviour, for example by reducing burrowing depth and/or speed, or enhancing feeding activity, ultimately making bivalves more vulnerable to predation (Thomas & Poulin, 1998; Addino *et al.*, 2010). However, parasites can also affect predators, changing their behaviour, metabolism, digestive efficiency or foraging ability. All of these could lead to changes in their feeding behaviour and impact the quantity of prey consumed (Bishop & Cannon, 1979; O'Shaughnessy, Harding & Burge, 2014).

## VI. FUTURE DIRECTIONS

Although bivalves are one of the better studied prey taxa in aquatic ecosystems, several knowledge gaps remain. Most studies focus on predation at the individual level, with few assessing effects at the population or community and ecosystem level. Such studies would be informative, given the ecosystem functions and services that bivalves often supply, including their commercial value. We need to understand not only the lethal effects of bivalve predation that reduce their provision of ecosystem services like filtration and nutrient cycling, which can be density dependent, but also sub-lethal effects such as those caused by behavioural or morphological changes in response to predators (Dzierżyńska-Białończyk *et al.*, 2019). Because sub-lethal effects can compromise the physiology and behaviour of bivalves, they are likely to affect their provisioning of ecosystem services even if their density is unchanged. These aspects are not unique to bivalves, but given the suitability of bivalves for field and laboratory manipulations they are a useful taxon to explore these impacts. However, studies at the population, community or ecosystem level are logistically complex because these manipulations involve many more species and usually have to be conducted in the field.

Developing techniques and technologies could be useful to allow data to be collected in a less time-consuming manner, although each has their strengths and weaknesses. For example, the use of metabarcoding to analyse diet contents can allow us to identify niches and diets without lengthy direct observations or predation trials; however, for freshwater and marine predators, the results might not be sufficiently accurate. This is especially true in the case of generalist omnivores, because gut contents can reflect organisms ingested accidentally or indirectly (Bowser, Diamond & Addison, 2013; Terceel, Symondson & Cuff, 2021). In these cases, metabarcoding analysis perhaps describes the surrounding ecosystem better than the diet itself. Despite these limitations, metabarcoding can offer a simplified quantitative index of diet diversity, and when combined with stable isotope analysis, could increase insights into dietary differences between predators sharing the same niches and patterns of resource allocation (Berry *et al.*, 2017; Cordone *et al.*, 2021; Nalley *et al.*, 2022). Remote sensing has been used to assess stress on bivalves caused by environmental conditions, such as increases in toxin levels or predation risk (Nagai *et al.*, 2006; Wilson, Arnott & Elwood, 2012; Andrewartha *et al.*, 2015; Dzierżyńska-Białończyk *et al.*, 2019). Microsensors can be used to monitor the rate and duration of bivalve shell closing in response to surrounding stressors. Monitoring the heart rate of mussels in the presence of predatory snails demonstrated differences according to predation methods (i.e. drilling and valve penetration followed by muscular paralysis) (Nagai *et al.*, 2006). Sensors can also be used to track predators and evaluate their behaviours (e.g. telemetry sensors and time-depth recorders), but also to assess physiological costs and impacts on bivalves (e.g. heart effect sensors and heart sensors) (Aquiloni, Ilhéu & Gherardi, 2005; Robson, Wilson & Garcia de Leaniz, 2007; Robson *et al.*, 2010; Bajer, Chizinski & Sorensen, 2011; Richard *et al.*, 2020; Banet, Fieberg & Sorensen, 2022). Biosensors can be equipped with features that can signal if an animal is consumed (Boulêtreau *et al.*, 2020). In addition, by creating smaller sensors with improved storage capacity and autonomy this technology could be extended to more species, and to provide new information, especially on sub-lethal effects of predation.

Because predation and environmental conditions may affect restoration and conservation measures (Brumbaugh *et al.*, 2006; Wilcox & Jeffs, 2019), it is also important to investigate how these factors interact, especially considering the current rate of climate change and projected future changes (Karl & Trenberth, 2003; Cheung *et al.*, 2009). Both environmental stress and the introduction of non-native species can impact bivalves, making them more vulnerable to predation and also changing predation pressure, thus it would be interesting to expand our knowledge of such effects on the predation of bivalves and how they affect species interactions. For example, future studies could design experiments to study population dynamics while manipulating environmental conditions (e.g. temperature, salinity, pH). The results could be used to develop species distribution models to predict future distribution of bivalves while accounting for future

predator distributions, and to allow us to predict future key zones of impacts (Hof, Jansson & Nilsson, 2012; Jokinen *et al.*, 2019; Zhang *et al.*, 2020).

Citizen science is increasingly employed (Haklay *et al.*, 2021) and has been used to monitor and assess the range and movement patterns of invasive species including bivalve predators such as *C. maenas* (Grason *et al.*, 2018). Using citizen science, it was possible to determine the recruitment envelope of the giant clam *Tridacna gigas* in the Philippines and to track the mortality and health status of pen shell *Pinna nobilis* in Spain (Cabanellas-Reboredo *et al.*, 2019; Requilme *et al.*, 2021). Citizen science could be used to gather more data on predators, bivalve predation and its effects at individual, population and community levels. This could be especially important for bivalve species of commercial importance, with information gathered by fishermen potentially extremely valuable.

Lastly, while bivalves may be unique prey due to their low mobility and high armouring, they currently provide one of the best windows into understanding predator–prey interactions. We do, however, need to understand how generalisable the effects of predation on bivalves are to other taxa.

## VII. CONCLUSIONS

(1) This review of 1334 published studies identified 2682 records of bivalve predation, predominantly located in North America and Europe. These records mostly focus on impacts of predation on bivalves using predation trials and most were conducted in marine systems.

(2) In marine ecosystems, mytilids were the most studied bivalves and crustaceans the most common predators. In freshwater ecosystems dresenids were the most studied bivalves, and fishes the most common predators.

(3) Marine records were mostly from native (81%) and commercially important (63%) bivalves; percentages for freshwater species records were lower in both categories (50% native; 4% commercial).

(4) Most studies focused on studying predator attributes (50%) and used predation trials (trials where predators were added to experimental cages or tanks, with or without the use of tethering) to assess bivalve predation.

(5) There is a lack of information on the effects of bivalve predation at the population and community and ecosystem levels with only 7% and 0.5% of the studies reporting evidence of these, respectively.

(6) New methods and technologies hold promise for the study of the interactions between bivalves and their predators, including remote sensing and metabarcoding. Because climate change and global stressors such as acidification could affect predator–prey interactions, it is essential to integrate these aspects in future studies.

(7) Lastly, the patterns described in this review could apply to other prey taxa. Bivalves provide a unique opportunity for holistic studies and could provide insights for researchers working on other taxa.

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## X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Search terms used in the ISI-Web of Knowledge database.

**Table S1.** Bivalve species that could be identified and their respective predators found in our literature review within freshwater studies.

**Table S2.** Bivalve species that could be identified and their respective predators found in our literature review for marine studies.

**Table S3.** List of predators of predated bivalves that could not be identified found in our literature review for marine and freshwater studies.

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