Exotic asphyxiation: interactions between invasive species and hypoxia

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ABSTRACT

Non-indigenous species (NIS) and hypoxia (<2 mg O_2 l^{-1}) can disturb and restructure aquatic communities. Both are heavily influenced by human activities and are intensifying with global change. As these disturbances increase, understanding how they interact to affect native species and systems is essential. To expose patterns, outcomes, and generalizations, we thoroughly reviewed the biological invasion literature and compiled 100 studies that examine the interaction of hypoxia and NIS. We found that 64% of studies showed that NIS are tolerant of hypoxia, and 62% showed that NIS perform better than native species under hypoxia. Only one-quarter of studies examined NIS as creators of hypoxia; thus, NIS are more often considered passengers associated with hypoxia, rather than drivers of it. Paradoxically, the NIS that most commonly create hypoxia are primary producers. Taxa like molluscs are typically more hypoxia tolerant than mobile taxa like fish and crustaceans. Most studies examine individual-level or localized responses to hypoxia; however, the most extensive impacts occur when hypoxia associated with NIS affects communities and ecosystems. We discuss how these influences of hypoxia at higher levels of organization better inform net outcomes of the biological invasion process, i.e. establishment, spread, and impact, and are thus most useful to management. Our review identifies wide variation in the way in which the interaction between hypoxia and NIS is studied in the literature, and suggests ways to address the number of variables that affect their interaction and refine insight gleaned from future studies. We also identify a clear need for resource management to consider the interactive effects of these two global stressors which are almost exclusively managed independently.

Key words: anoxia, anthropogenic impacts, climate change, dissolved oxygen, introduced species, literature review, non-native species, selection regime modification.

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I. INTRODUCTION

Non-indigenous species (NIS) continue to invade and spread, especially in aquatic environments (Lodge, 1993; Byers *et al.*, 2015; Gollasch, Minchin & David, 2015). In some areas, establishments of NIS are increasing exponentially with time (Cohen & Carlton, 1998; Ruiz *et al.*, 2000; Wonham & Carlton, 2005). The impacts of these NIS on native biota can often alter ecosystem functions (Parker *et al.*, 1999; Dukes & Mooney, 2004), and they are a leading cause of the extirpation and endangerment of native biota (Czech & Krausman, 1997; Wilcove *et al.*, 1998).

There are various reasons for the increased introduction and impact of NIS. Two leading mechanisms are the increased movement of transport vectors (i.e. enhanced propagule pressure) and increased levels of environmental disturbance (e.g. Ruiz & Carlton, 2003; Eschtruth & Battles, 2009). Anthropogenic transport of aquatic NIS propagules, such as *via* the hulls and ballast water of transoceanic or canal-crossing ships, or deliberate introductions of biota for the aquarium trade or the establishment of novel fish stocks, helps to overcome natural dispersal barriers (Lockwood, Cassey & Blackburn, 2005; Byers, 2009; Wonham *et al.*, 2013). For example, tens of millions of metric tons (MT) of ballast water are discharged yearly into US ports, with each MT on average containing ~1,000–10,000 zooplankton organisms (Verling *et al.*, 2005). Additionally, disturbances may alter the receptiveness of a community to such an influx of NIS. For example, disturbances can reduce native population abundances or biomass, thus reducing resident biotic resistance to invasion (e.g. Gribben *et al.*, 2018; Bulleri *et al.*, 2020). Disturbances also alter abiotic conditions, habitat, and resources in ways that in many cases can favour NIS (D'Antonio, Dudley & Mack, 1999; Lear *et al.*, 2020). Many nearshore aquatic habitats are highly disturbed. Marshes and estuaries, for example, are heavily filled and channelized, receive high quantities of sedimentation and contaminants from runoff (e.g. Kennish 2001; Valiela, Rutecki & Fox, 2004; Birrer *et al.*, 2021), and contain relatively large numbers of invasive species (Cohen & Carlton, 1998, Ruiz *et al.*, 2000).

One influential environmental disturbance that is increasing in aquatic systems is the frequency and duration of low levels of dissolved oxygen (Diaz, 2001; Jane *et al.*, 2021; Sampaio *et al.*, 2021). Hypoxia is typically defined as dissolved oxygen (DO) levels below 2 mg O_2 l^{-1}, and anoxia is the complete lack of oxygen (Diaz & Rosenberg, 1995, 2008). These low-oxygen conditions are often driven by an overload of limiting nutrients, especially phosphorus and nitrogen that run off from wastewater facilities, polluted storm water, land-based concentrated animal feedlot operations, and fertilizer applications. The input of excessive nutrients creates eutrophic water bodies that cause algal blooms, followed rapidly by bacterial blooms that capitalize on the algae as a new plentiful food source. The rapid bacterial degradation of the algal biomass abruptly boosts oxygen consumption, creating hypoxia. Inland waters and the coastal zone are particularly susceptible to eutrophication effects because these areas are proximate to land-based nutrient runoff and have lower volumes of water to dilute the incoming nutrients as compared to the open ocean.

Hypoxia can also be created or exacerbated by physical processes. Because warmer water holds less dissolved gases, including O_2, increases in temperature due to seasonal or long-term climate trends increase hypoxia. Also, reduced winds, in combination with higher temperatures, can reduce mixing, creating stratification of the water column, with warmer, less-dense water on top. In some cases, freshwater runoff can create salinity-driven density stratification that also reduces vertical mixing. As stratification progresses, a strong pycnocline develops, and the water at the bottom has little opportunity to contact air or mix with better oxygenated surface waters; thus, once bottom water is depleted of O_2, for example through respiration of benthic organisms, it cannot readily be replenished (e.g. Lenihan *et al.*, 2001).

Diaz & Rosenberg (1995) and Diaz (2001) argued that the drastic change in dissolved oxygen in coastal waters over recent decades has been greater and more influential than any other ecological variable, leading to the widespread degradation of coastal environments. The number of coastal sites where hypoxia has been reported has increased with an

exponential growth rate of 5.54% per year (Vaquer-Sunyer & Duarte, 2008). The most extreme examples of hypoxia are large-scale dead zones where most aerobic organisms are killed or excluded (Rabalais *et al.*, 2002; Diaz & Rosenberg, 2008; Altieri & Gedan, 2015). Such dead zones are increasing in area and frequency over time (Vaquer-Sunyer & Duarte, 2008). Some dead zones can be extensive and persistent, such as a recurring dead zone that began just seaward of the Mississippi River delta in the Gulf of Mexico more than 100 years ago and now often grows in excess of 20,000 km^2 in the summer months (Rabalais *et al.*, 2002, 2007; Osterman *et al.*, 2009).

Thus, two influential anthropogenic stressors – NIS and hypoxia – are increasing in extent, frequency, and impact. The responses of species and systems to multiple stressors have received much attention (e.g. Lenihan *et al.*, 1999; Gunderson, Armstrong & Stillman, 2016, Breitburg *et al.*, 2015), including the examination of NIS as a stressor (Ruiz *et al.*, 1999; Orr *et al.*, 2020). Although NIS and hypoxia have been examined in many individual studies, a smaller number has examined them in concert, and none has synthesized their interactive roles as multiple stressors. Thus, here we seek to summarize quantitatively how the invasion biology literature has examined these two stressors and how they operate and interact in aquatic systems. Because NIS can be both a cause and a consequence of hypoxia (Costa, Martins & Chainho, 2017), we explore how the literature has addressed how NIS are both contributing to, and possibly benefiting from, hypoxia.

If hypoxia differentially impacts native species relative to NIS, their decline could potentially allow an NIS to expand within the vacated niche space and utilize the associated liberated resources of its depleted competitors (Tilman, 2004). In an extreme case, hypoxia might wipe out an entire system leaving little to no biotic resistance. NIS can handle, or are at least hypothesized to handle, stress and disturbance better than native species (e.g. Hobbs & Huenneke, 1992; Altman & Whitlatch, 2007; Lembrechts *et al.*, 2016). Hypoxia could be one such stress that NIS tolerate well (e.g. Byers, 2000; Lagos *et al.*, 2017). In fact, the high frequency and duration of hypoxia that is occurring at present could be a prime example of selection regime modification (Byers, 2002), whereby extreme disturbances shift the local environment sufficiently to erase a native species' prior advantage of local environmental adaptation accrued during its long-term incumbency over evolutionary time. Selection regime modification may suddenly put even previously well-adapted native species at a competitive disadvantage with NIS. Furthermore, in any of these hypoxia scenarios, the NIS could not only be tolerating hypoxia, but also contributing to it.

We conducted a literature review to examine the extent of interactions between NIS and hypoxia. Because hypoxia and its effect on organisms varies based on many influential variables (e.g. scale, duration, cause, intensity), the invasion literature seldom quantifies NIS–hypoxia interactions in a standardized way. Therefore, our objectives were to quantify the breadth of published studies addressing the interactions

between NIS and hypoxia, to identify what species, regions and environments have been targeted in these tests, and whether there are any generalities arising from these studies. In particular, we wanted to summarize how the invasion literature has captured the ways and degrees to which NIS both tolerate and create hypoxia, and how this in turn can affect native species. Specifically, we quantified how the NIS literature has examined (*i*) whether and how NIS create hypoxia at an organismal- or community-relevant scale; (*ii*) how well NIS tolerate hypoxia; and (*iii*) how co-resident native species respond to hypoxia relative to NIS. Additionally, we sought to summarize evidence for various mechanisms involved in the creation and tolerance of hypoxia by NIS; provide case studies for different mechanisms of a few well-studied examples; and discuss key research gaps and provide recommendations for future research that could improve our understanding of NIS–hypoxia interactions including at larger population-level scales.

State-of-the-literature reviews like ours have provided salient results and important knowledge about research biases in other fields, including climate change, conservation biology and general invasion biology (Pysek *et al.*, 2008; Darwall *et al.*, 2011; Martin, Blossey & Ellis, 2012; Wernberg, Smale & Thomsen, 2012; Thomsen *et al.*, 2014). We hope that this review will stimulate research about NIS–hypoxia interactions, describe the state of the field in terms of emergent principles, biases, and knowledge gaps, and suggest areas of future investigation into these two increasingly important stressors in aquatic environments globally.

II. METHODS

Throughout this paper we use the term hypoxia to refer to oxygen levels in the water that are ≤2 mg O_2 l^{-1}, a threshold that is harmful to most aerobic organisms (Rosenberg, Hellman & Johansson, 1991; Diaz & Rosenberg, 2008). This definition also includes anoxia, which is the complete lack of O_2. We searched the biological literature for studies that reported the effects of hypoxia on aquatic NIS and on co-occurring native species. Specifically, we searched the literature using the ISI *Web of Science* (All Databases) for combinations of the following key words: (exotic or invas* or introduce* or nonnative or nonindigenous) and (anoxia or hypoxia or "hydrogen sulf*") and species not "oxygen species" not "sulfur species" not cancer not tumor not tumour not "invasive tissue". Studies published before October 31, 2019 were collected for the analysis. This search yielded an initial 547 publications.

We excluded papers where there was no clear interaction between an aquatic NIS and hypoxia. This was often the case if the association of NIS and hypoxia was not investigated; many papers simply assumed or invoked this association without presenting data. A few papers were excluded from the main analysis because they examined hypoxia strictly within the sediment rather than hypoxia in the water column

where the mechanisms of hypoxia operation and impact are different. However, if papers described sediment hypoxia that spilled over to affect hypoxia in the water column, including the benthic boundary layer, these were included. Six additional papers were deemed inaccessible because they were in obscure journals or not in English. We added in a few relevant papers that we discovered in the bibliographies of selected papers that were not captured by the original search. After applying these criteria, we had slightly over 100 publications, which pared down to exactly 100 in applying the following final steps.

First, papers were categorized along two axes; we determined if the study examined an NIS tolerating hypoxia or creating hypoxia. For hypoxia-tolerance studies we examined whether an NIS was found to tolerate hypoxic conditions as well as or better than normoxic conditions. Tolerance was measured by several metrics including survival, abundance, physiology, and behaviour. Three studies examined trait changes (gill dimensions) in the presence of hypoxia, but because they did not demonstrate whether the trait changes affected hypoxia tolerance *per se*, we excluded them. For hypoxia-creation studies, we examined whether the NIS created hypoxia in its environment, and if so, how. Second, we determined if the study compared the response (in survival, abundance, physiology, or behaviour) of the NIS to hypoxia against the responses of native species in the system. If so, for hypoxia-tolerance studies we asked whether under hypoxia the NIS performed better than the majority of the native species against which it was tested, and how similar the compared native species were taxonomically. For hypoxia-creation studies we asked whether the study found that an NIS generated enough hypoxia to affect the native species negatively.

Next, we recorded important attributes of each study, including: (*i*) the examined organismal response variables to hypoxia (i.e. mortality, abundance, physiology, behaviour); (*ii*) the cause of hypoxia as physical or biological, with the latter category subdivided into the respiration of macroorganisms *versus* associated microbes (as in eutrophication); and (*iii*) whether hypoxia triggered indirect effects in the community. In these cases, low oxygen did not necessarily affect the focal species directly, but caused a change in the system that in turn affected the focal species. For example, hypoxia could decrease a predator population, resulting in a benefit for a focal NIS prey species that was itself not directly affected by hypoxia. We also recorded whether the study: (*iv*) used an experimental or observational approach; and (*v*) collected data in a field or laboratory setting (or both). Note that if a study was conducted in both the field and the laboratory, we recorded the cause of hypoxia (point *ii*, above) from the field portion of the study because that was deemed most relevant to natural conditions (laboratory experiments often generate hypoxic conditions in the most expedient manner). Finally, we documented (*vi*) the taxa examined; (*vii*) biome represented (marine or freshwater); and (*viii*) geographic location.

To understand the nexus of NIS and hypoxia reported in the literature, we probed our database to address eight central questions: (*i*) do NIS create hypoxia at an organismal- or community-relevant scale? (*ii*) How specifically is hypoxia created? (*iii*) Does hypoxia simply result from species respiring O_2 and depleting it from the system, and does that result from collective respiration, i.e. due to high population density, or from a high *per capita* rate of respiration? (*iv*) Do NIS create enough hypoxia to affect native species negatively? We note that studies examining native species' responses inherently consider the relevant scale of response, because their responses serve as bioindicators of the impact of NIS-generated hypoxia at the population and community level. For hypoxia tolerance, we asked: (*v*) what is the source of hypoxia? (*vi*) What are the common metrics used to quantify species responses to hypoxia? (*vii*) For the given study conditions, are NIS tolerant of hypoxia (compared to normoxic conditions)? (*viii*) Are NIS more tolerant of hypoxia than native species? Finally, we quantified the distribution of hypoxia–NIS studies based on the aforementioned study aspects: laboratory *versus* field, taxa examined, marine *versus* fresh water, geographic location, and the occurrence of indirect effects of hypoxia, i.e. where hypoxia extends to affect species interactions in the community.

We primarily examined responses at the study (=publication) level because we were trying to characterize the literature, and thus we wanted to examine the breadth of conditions and methods with which hypoxia is investigated in NIS. Our focus on studies allows us to assess if the literature collectively is biased toward a handful of 'marquee' species. To avoid over-inflation by certain favoured subject species or by research groups with multiple studies in the same system, we also report on many patterns at the level of species, that is, by scoring the average response of each species across all studies in which it was found. We used each study's conclusion as the ultimate decision in how to score a publication. The study conclusions indicate *potential* for hypoxia and organismal response, i.e. the conclusion is not a guarantee of a universal hypoxia effect, since hypoxia tolerance and creation are highly context-dependent processes. We emphasize that findings of hypoxia tolerance and creation will most always be influenced by experimental conditions and study approaches, as opposed to being a universal characteristic of an NIS. Thus, we summarize the range of measurement conditions across the studies, and add caveats to those few studies that reported the creation of NIS-driven hypoxia, but observed it only under limited or specific conditions.

III. RESULTS

(1) Hypoxia creation

Of the 100 studies reviewed (see Table S1 for full data set), 24 examined the ability of a NIS to create hypoxia

(Table 1, Fig. 1). Of these, 19 studies (on 11 species) found that the NIS created hypoxia. Of the remaining five studies (on three species), three found evidence of oxygen reduction, but not to hypoxic levels (Effler *et al.*, 1998; Caraco *et al.*, 2000; McKinnon *et al.*, 2009), and two reported the opposite effect, i.e. hypoxia alleviation (Norkko *et al.*, 2012; Isaev *et al.*, 2017), in both cases by NIS polychaetes, *Marenzelleria* spp. in the Baltic Sea. Widespread invasion of these polychaetes, which through their movements and excavation aerate sediments and alleviate hypoxia at the benthic boundary layer, can reportedly restore normoxia over large areas, including the water column. The bioirrigation activities of dense *Marenzelleria* populations increase oxygen transport into sediments which increases retention of sedimentary phosphorus. This in turn appears to facilitate a switch from a seasonally hypoxic system back to normoxia by decreasing the potential for sediment-induced eutrophication in the upper water column (Norkko *et al.*, 2012; Isaev *et al.*, 2017).

Of the species that created hypoxia, all but one were plants or seaweeds, including several species that were the subject of multiple studies, including *Caulerpa taxifolia*, *Trapa natans*, *Hydrilla verticillata*, *Eichhornia crassipes*, and *Egeria densa* (Table 1). The single non-indigenous animal species reported to create hypoxia was the freshwater clam, *Corbicula fluminea*; however it was caused by researchers experimentally simulating the clam's mass mortality, which was followed by microbial decomposition of its organic matter (Cherry *et al.*, 2005). In every case where the NIS created hypoxia, it took place as a collective function of its high biomass or density as opposed to a particularly high *per capita* respiration rate. The majority of hypoxia-creation studies were observational and conducted in the field (Fig. 2), which may be important study attributes in order to capture an NIS affecting O_2 under natural conditions. A few of the studies that found hypoxia only did so under certain conditions, such as the highest organism densities or areas with lowest flow (Cherry *et al.*, 2005; Ribaudo, Bertrin & Dutartre, 2014). Two studies were conducted in the laboratory in small containers with no flow (Teixeira, Budd & Strayer, 2015; Saenz & Adams, 2017).

Of the 13 studies that examined the consequences for native species from an NIS potentially creating hypoxia, 11 found that the NIS created enough hypoxia to generate a significantly negative response in the natives. Of the two that found no effect on native species, one was because hypoxia was not generated (McKinnon *et al.*, 2009). Almost two-thirds of these studies were experimental. Most studies compared the NIS against a single native species; however, two studies examined effects of the NIS on five and six native species, and three others assessed dozens of native species (see Table S1).

(2) Hypoxia tolerance/sensitivity

A majority of studies (75%) addressed hypoxia tolerance by an NIS. Almost twice as many studies found NIS to be tolerant of hypoxia than not (Fig. 1). Analysed at the level of species, this ratio was also nearly 2:1. Mortality and abundance were the
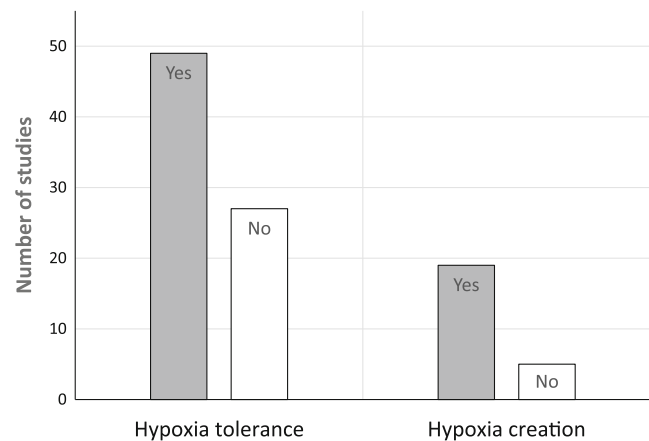

Fig. 1. Binary conclusions (yes/no) of studies in the biological invasion literature examining the relationship of non-indigenous species (NIS) with hypoxia, including those addressing tolerance of hypoxia by NIS ($N = 76$), and those addressing creation of hypoxia by NIS ($N = 24$). For hypoxia-tolerance studies we assessed the question: did the NIS tolerate hypoxia relative to normoxia? For hypoxia-creation studies we assessed the question: did the NIS create hypoxia? Two studies that were categorized as 'No' for hypoxia creation in fact reported hypoxia alleviation.

two organismal response variables used most often to assess tolerance of NIS and native species (Fig. 3). In fact, over half of the abundance studies measured changes in abundance over time, and thus could theoretically be converted into a mortality response. Physiological measurements were the next most commonly measured category of responses, with respiration (oxygen uptake rate) the single most common variable, followed by various other physiological responses, such as swimming speed, oxidative stress, metabolic by-product production, consumption rates, and growth. Behavioural responses included hypoxia avoidance and mitigation behaviours such as the rate of surface air gulping. Behavioural responses were most commonly recorded together with another response variable (Fig. 3). Of the 25 studies examining multiple response variables, 15 included behavioural responses, four studies paired mortality and abundance, and three paired mortality with physiology measurements.

In hypoxia-tolerance studies, low DO arose from various sources (Fig. 2). In the case of laboratory experiments, hypoxia was induced by researchers, and thus does not necessarily replicate the causes of hypoxia in the field setting. Hypoxia in these laboratory studies is almost always physically induced, for example by bubbling N_2 into the water to displace dissolved oxygen (e.g. Wright *et al.*, 2010). By contrast, hypoxia in field settings is predominantly of biological origin, including eutrophication and macro-organism respiration (Fig. 2). Occasionally, physical factors like warm temperatures and low circulation also contributed. With few exceptions, field studies were observational and laboratory studies were experimental; a handful of papers reported both laboratory and field components (e.g. Byers, 2000).
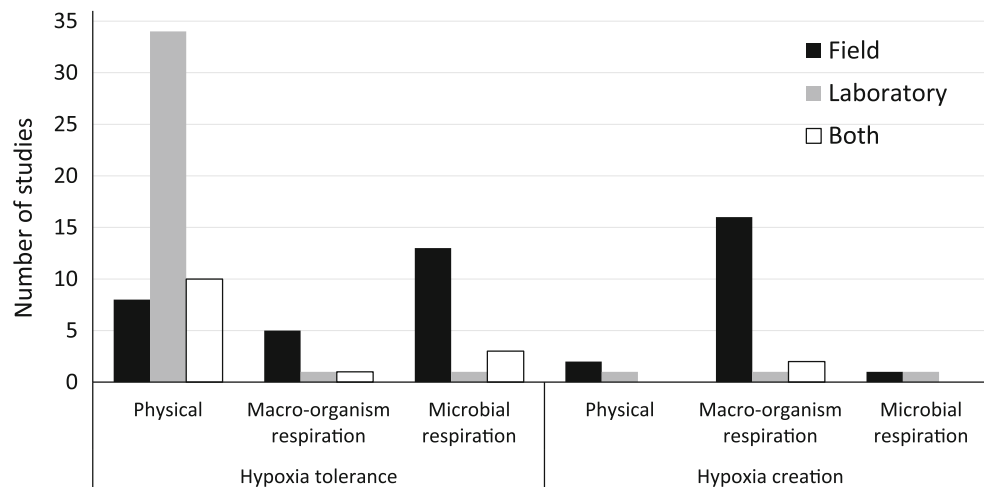
Fig. 2. The causes of hypoxia as a function of type of study (hypoxia tolerance or hypoxia creation), and also whether the study was conducted in the field, laboratory, or both. Causes of hypoxia are physical, such as low water flow, high temperatures, or inputs of gases that displace oxygen; and biological from either macro-organism respiration or microbial respiration, the latter of which is essentially eutrophication.

Half of the hypoxia-tolerance studies compared the response of the NIS to native species. When native species were studied they almost always matched taxonomically (e.g. NIS bivalve *versus* native bivalve; NIS fish *versus* native fish; Table S1), making these comparisons more relevant since they involved a likely competitor that might be displaced. When NIS tolerance of hypoxia was compared against that of native species, 62% of studies determined the NIS to be more tolerant (Fig. 4). Most studies compared an NIS against one or two native species (median = 2.0 species). But several studies compared an NIS against multiple native species, which greatly increased the average (mean = 7.7 species). Thus, the tolerance decision for the latter studies reflects whether the invader tested better than the majority of the natives included in that study. About 30% of papers discussed or quantified the population- or community-level ramifications of differential tolerance by NIS and native species. Studies with a larger scope than the physiological response of a few individuals of a single species can potentially detect hypoxia-mediated interactions and indirect effects of hypoxia on a community. For example, Byers (2000) showed that an NIS tolerated hypoxia better than a native competitor, and that this enabled displacement of the native species. Non-native Nile perch (*Lates niloticus*) provide an interesting counter-example of community-wide ramifications where an invasive top predator is disadvantaged by low oxygen levels (Chapman *et al.*, 1996; Schofield & Chapman, 1999; see Section IV.5.*b*).

The NIS most commonly examined in hypoxia-tolerance studies include Nile perch (8 studies); Asian clam, *Corbicula fluminea* (*N* = 7); carp, *Cyprinus carpio* (*N* = 4); zebra mussel, *Dreissena polymorpha* (*N* = 4); and the polychaetes *Marenzelleria* spp. (*N* = 4) (Table 1). The best-studied of these – the Nile perch – is a large-bodied predator with high metabolic demands that is typically intolerant of hypoxia. Its over-representation in

our data set thus affects our count of studies showing NIS to be intolerant of hypoxia. Fish, molluscs and crustaceans were the three most common NIS taxa examined, accounting for ∼80% of all tolerance studies and 75% of species represented in tolerance studies (Tables 1 and S1). Native taxa whose hypoxia responses were compared to NIS were also focused heavily on certain taxa, especially fish, crustaceans, and bivalves (Table S1).

(3) Distribution of hypoxia–NIS studies

The 100 studies were split roughly equally between marine and freshwater systems (marine = 44; fresh water = 56). Studies were geographically biased, as is often the case for ecological studies, including those on NIS (Byers, 2009), with the majority conducted in North America and Europe (Fig. 5). A moderate proportion were located in Australia and Africa; however, eight of the 11 African studies were on one species, Nile perch.

IV. DISCUSSION

(1) Hypoxia tolerance and creation by NIS

Studies of hypoxia tolerance in NIS are three times more common than hypoxia-creation studies. The higher frequency of hypoxia-tolerance studies implies that NIS are more often studied as responders to degraded environmental conditions, as opposed to drivers of low oxygen levels. More explicit consideration of some of the potential literature biases associated with NIS as drivers of hypoxia would be worthwhile. For example, many studies of hypoxia, ecosystem metabolism, or biological oxygen demand do not identify species involved in these processes, much less whether they are NIS or not.
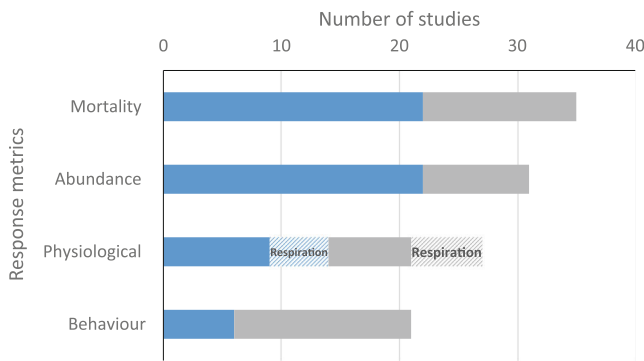
Fig. 3. Organismal responses of non-indigenous species (NIS) and native species examined in all hypoxia-tolerance studies ($N = 76$ studies) and in the hypoxia-creation studies that examined native species responses ($N = 13$ studies). Studies that solely examined hypoxia creation by NIS are not included because there was no information on organismal responses in those studies. The hashed bars within the physiology bar depict respiration, which is a subset of physiological responses. Most studies ($N = 64$) examined a single category of response (blue). However, in 25 studies, two categories of response variables were recorded; grey colouration represents the 50 variables enumerated across those 25 studies. Behaviour was the least common response variable to be examined singly (blue), but the most common response variable to be paired with another (grey).
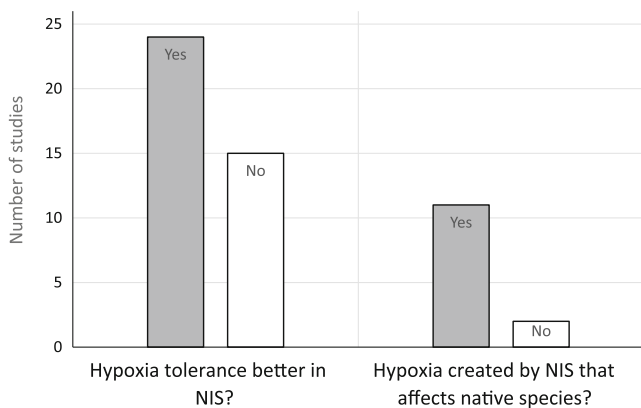

Fig. 5. Study location by continent for studies included in our database. The majority of African studies were on a single non-indigenous species (NIS) Nile perch (*Lates niloticus*).

Fig. 4. Effects of hypoxia on native species. For hypoxia-tolerance studies (left), we asked whether the non-indigenous species (NIS) tolerated hypoxia better than the native species it was tested against. For hypoxia-creation studies (right) we asked whether the NIS created hypoxia that significantly negatively affected the native species. These are study-level conclusions, thus if multiple natives were examined in a study, the response of the majority of the species in that study is how the study was tallied. These studies that examined native species responses are a subset of the hypoxia-tolerance and hypoxia-creation studies summarized in Fig. 1.
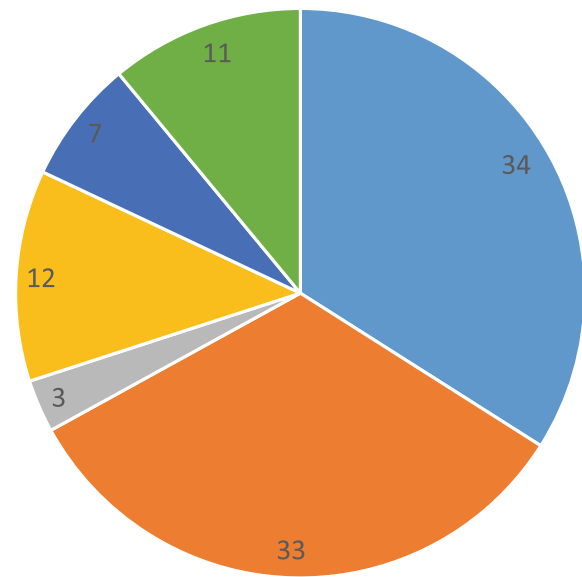
Second, we have a poor understanding of the invasion status of many of the species likely involved in deoxygenation processes, such as phytoplankton, microphytobenthos, and microbes in general (Litchman, 2010). Thus, it may be that NIS are substantially involved in hypoxia dynamics, but we just do not have proper documentation of this to date.

At the level of the individual, which is the level analysed in most studies in our review, 64% of hypoxia-tolerance studies found that NIS tolerate hypoxia (Fig. 1). At face value this number suggests a preponderance of NIS could take advantage of low-oxygen conditions to invade, establish, and even outperform native counterparts. However, this high proportion is almost certainly due to a literature bias, given that NIS are usually not selected randomly for study, but rather because they are commonly observed in hypoxic areas or have a suspected tolerance of hypoxia. Given this potential bias in selection of species for study, plus a likely publication bias for positive results, the large proportion of studies confirming hypoxia tolerance among NIS in the literature is perhaps not surprising.

The distribution of studied taxa also contributes to tolerance outcomes because of phylogenetic constraints on hypoxia tolerance (Vaquer-Sunyer & Duarte, 2008). Molluscs in general tend to be hardy, with lower median lethal oxygen concentrations (LC_{50}) and longer median lethal times (LT_{50}) upon exposure to acute hypoxia (Fig. 6). As an extreme example, the oyster *Crassostrea virginica* is resistant to complete anoxia at temperatures of 10 °C for 28 days (Stickle

et al., 1989). Fish and crustaceans tend to be more oxygen sensitive, and in fact, native species examined for responses to hypoxia relative to NIS often were fish and copepods. Mobile organisms such as these may have evolved fewer adaptations to hypoxia because they have the capacity to avoid hypoxic waters (Fig. 6). Benthic fish and crustaceans often move to better oxygenated shallower waters when bottom waters become hypoxic (Lenihan *et al.*, 2001; Bell, Eggleston & Wolcott, 2003). Furthermore, because hypoxia-tolerance studies were most often conducted in the laboratory, they may have disallowed important behavioural responses like emigration that are possible in field settings, thus overestimating hypoxia impacts on species that rely on escape and avoidance as a primary hypoxia defence.

For cases of hypoxia creation by NIS, it may seem paradoxical that primary producers are the most prominent hypoxia creators since photosynthesis produces oxygen. However, there are at least two reasons why they can create low-oxygen conditions. First, the vegetation, especially the roots and rhizomes, can harbour microbes whose respiration generates hypoxia at the benthic boundary layer, and also within the sediment; the NIS seaweed *Caulerpa taxifolia* is particularly noteworthy in this regard (see Section IV.5.*d*). Clarifying the role of microbes associated with an NIS in hypoxia creation requires additional work; often a study ceased after identifying that an increase in NIS abundance increased hypoxia without uncovering the mechanism involved. Second, vegetation can grow so dense (often in thick vegetative mats)

that oxygen consumed in the lowest levels of the vegetation cannot be replaced by diffusion from the atmosphere or hydrologic exchange (Caraco *et al.*, 2006; Ribaudo *et al.*, 2014). The progressive accumulation of vegetative biomass also makes it more likely that respiration can exceed photosynthesis rates, especially under low-light conditions like during the night or autumn when oxygen production declines (Loverde-Oliveira *et al.*, 2009; Ribaudo *et al.*, 2014). Such biological depletion of DO can be exacerbated by physical conditions such as high temperatures or reduced flow (e.g. Bradshaw, Allen & Netherland, 2015). Examples in the literature presently show that hypoxia creation by NIS at population and community scales seems relegated to a handful of species (Fig. 6). However, one glaring gap in the NIS–hypoxia literature is that there are no harmful algal blooms (HABs) or microalgae identified as NIS in the studies in our database. Although the ecological origin of many microscopic organisms, including microalgae and HABs, is not well known (Litchman, 2010), given the ability of these organisms to drive low oxygen, especially under eutrophic conditions, the confirmed status of even a portion of these as NIS could boost the number of NIS hypoxia creators.

A rare category of NIS interacting with hypoxia was the hypoxia alleviator, with only one representative species complex composed of the polychaetes *Marenzelleria arctia*, *M. neglecta*, and *M. viridis* in the Baltic and North Seas (Fig. 6). This species complex was initially found living in hypoxic areas, and so was first examined as a hypoxia
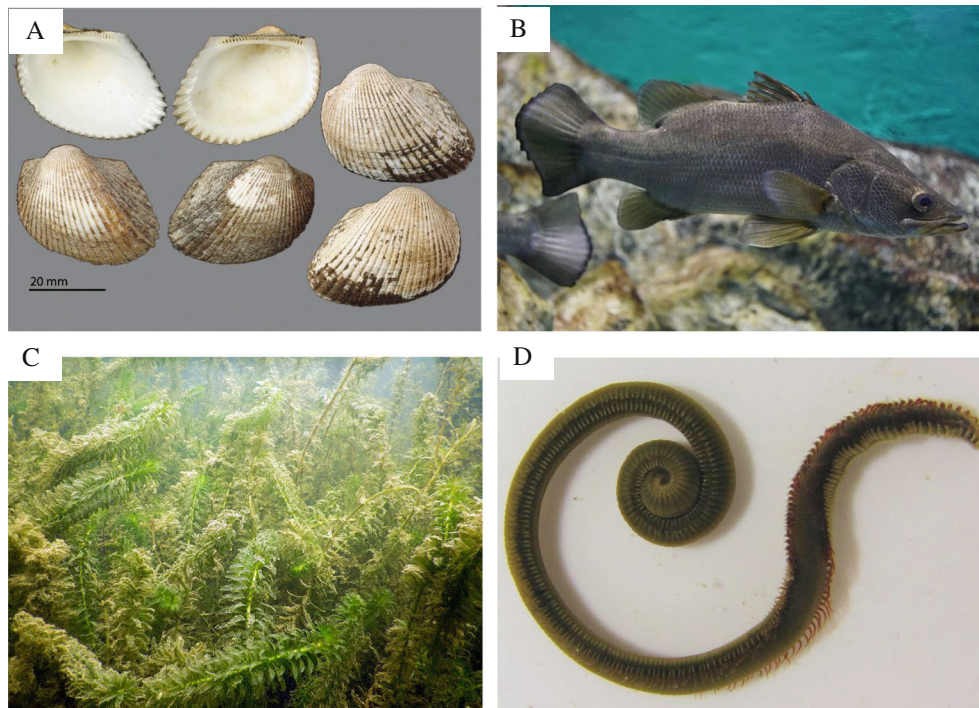
Fig. 6. Four representative aquatic non-indigenous species (NIS) studied in relation to hypoxia. The species here exemplify four broad categories of NIS in relation to their hypoxia associations: (A) hypoxia tolerant (ark clam, *Anadara inaequivalvis*); (B) hypoxia intolerant (Nile perch, *Lates niloticus*); (C) hypoxia creator (Brazilian waterweed, *Egeria densa*); and (D) hypoxia alleviator (red gilled mud worm, *Marenzelleria viridis*).

Table 1. Taxonomic distribution within NIS–hypoxia studies included in our literature review. (A) Non-indigenous species (NIS) examined in hypoxia-creation studies grouped according to whether they created hypoxia or did not. (B) NIS examined in two or more hypoxia-tolerance studies. See Table S1 for full list of NIS examined in hypoxia-tolerance studies. Native species that were included in our database of hypoxia-creation and hypoxia-tolerance studies are also listed in Table S1.

(A) Hypoxia-creation studies

Species	Taxonomy	No. of studies	Reference
Species that created hypoxia			
Caulerpa taxifolia	Alga	4	Gribben *et al.* (2009a,b); Byers *et al.* (2010); Wright *et al.* (2010)
Corbicula fluminea	Bivalve	1	Cherry *et al.* (2005)
Egeria densa	Aquatic plant	2	Ribaudo *et al.* (2014, 2018)
Eichhornia crassipes	Aquatic plant	2	Masifwa *et al.* (2001); Waltham & Fixler (2017)
Hydrilla verticillata	Aquatic plant	2	Bradshaw *et al.* (2015); Wilson *et al.* (2015)
Lagarosiphon major	Aquatic plant	1	Ribaudo *et al.* (2018)
Lophocladia lallemandii	Alga	1	Deudero *et al.* (2010)
Myriophyllum spicatum	Aquatic plant	1	Kauffman *et al.* (2018)
Potamogeton crispus	Aquatic plant	1	Vilas *et al.* (2017)
Trapa natans	Aquatic plant	4	Caraco & Cole (2002); Goodwin *et al.* (2008); Kornijow *et al.* (2010); Teixeira *et al.* (2015)
Triadica sebifera	Plant	1	Saenz & Adams (2017)
Species that did not create hypoxia			
Dreissena polymorpha	Bivalve	2	Effler *et al.* 1998; Caraco *et al.* (2000)
Marenzelleria spp.	Polychaetes	2	Norkko *et al.* 2012; Isaev *et al.* (2017)
Caulerpa taxifolia	Alga	1	McKinnon *et al.* (2009)

(B) Hypoxia-tolerance studies

Species	Taxonomy	No. of studies	References
Ciona spp. (*C. intestinalis* and *C. savignyi*)	Tunicate	3	Pool *et al.* (2013); Atalah *et al.* (2016); Lagos *et al.* (2017)
Corbicula fluminea	Bivalve	7	McMahon (1979); Byrne *et al.* (1991); Owen & Cahoon (1991); Johnson & McMahon (1998); Ilarri *et al.* (2011); Wittmann *et al.* (2012); Rosa *et al.* (2015)
Cyprinus carpio	Fish	4	Bajer and Sorensen (2010); Bajer *et al.* (2012); King *et al.* (2012); Benito *et al.* (2015)
Dreissena bugensis	Bivalve	2	De Ventura *et al.* (2016); Nowicki & Kashian (2018)
Dreissena polymorpha	Bivalve	4	Johnson & McMahon (1998); Tamburri *et al.* (2002); De Ventura *et al.* (2016); Nowicki & Kashian (2018)
Ficopomatus enigmaticus	Polychaete	2	Tamburri *et al.* (2002); Jewett *et al.* (2005)
Gambusia holbrooki	Fish	2	King *et al.* (2012); Stoffels *et al.* (2017)
Lates niloticus	Fish	8	Chapman *et al.* (1995, 2002); Rosenberger & Chapman (1999); Schofield & Chapman (1999, 2000); Reid *et al.* (2013); Chretien & Chapman (2016); van Zwieten *et al.* (2016)
Limnoperna fortunei	Bivalve	2	Oliveira *et al.* (2010); Perepelizin & Boltovskoy (2011)
Marenzelleria spp.	Polychaete	4	Schiedek *et al.* (1997); Karlsson *et al.* (2010); Kauppi *et al.* (2015); Gammal *et al.* (2017)
Mytilus galloprovincialis	Bivalve	2	Zardi *et al.* (2006); Atalah *et al.* (2016)
Palaemon macrodactylus	Shrimp	2	Gonzalez-Ortegon *et al.* (2010, 2013)
Perna perna	Bivalve	2	Hicks & McMahon (2002, 2005)
Perna viridis	Bivalve	2	Huhn *et al.* (2016, 2017)
Rhodeus ocellatus ocellatus	Fish	2	Morosawa (2011, 2017)
Anadara inaequivalvis (= *Scapharca inaequivalvis*)	Bivalve	2	Dezwaan *et al.* (1991); Munari & Mistri (2011)

tolerator (e.g. Schiedek *et al.*, 1997; Karlsson *et al.*, 2010). But it appears through their burrowing activities these worms aerate the sediment, helping to reverse hypoxia in shallow sediments and the benthic boundary layer (Norkko *et al.*, 2012; Maximov, 2015; Isaev *et al.*, 2017). As discussed in Section III.(1), its influence extends into the water column because its irrigation helps bind phosphorus and thus reduce eutrophication-driven hypoxia outbreaks in the water column (Norkko *et al.*, 2012; Isaev *et al.*, 2017). It remains unclear whether such hypoxia alleviation is rare, or whether such effects have been seldom investigated. Given the number of organisms that burrow in soft sediments, it will be

useful if future research can determine if aeration is a universal characteristic of such burrowing species (Gonzalez *et al.*, 2019). Hypoxia alleviators could have potential for restoring oxygen-deteriorated ecosystems.

Many variables influence oxygen concentrations and their measurement, such as depth, flow rate, time of day, tidal cycle, temperature, season, and organismal densities. Encouragingly, most studies in our review used realistic and relevant conditions, and made an effort to capture a range of spatial and temporal variability. For example, 88% of hypoxia-creation studies in our database measured O_2 levels in the field. They often examined O_2 along a gradient of distances away from the focal organism, often on the scale of many meters. They typically measured O_2 at different depths, flow rates, temperatures, seasons, and densities. We suggest that the *in situ* field settings, realistic conditions, and larger scale measurements are aspects that enhance their applicability to the population and system scales.

(2) Native species differential response to hypoxia

Nearly half of all hypoxia-tolerance studies (37 out of 76) examined an NIS in isolation. Confirmation that an NIS taxon is tolerant of hypoxia is of greater value when measured in the context of the hypoxia tolerance of the native species that it may displace. For example, reduced relative performance or abundance of native species may in turn give NIS an advantage in subsequent interspecific interactions like competition. This is an area in which future research could improve. For the 39 studies that did compare the hypoxia tolerance of NIS with that of native species, 62% of studies showed that the NIS tolerated hypoxia better than the natives (Fig. 4). In tolerance comparisons, the native taxa were typically chosen to be a functional or taxonomic match for the NIS, to allow direct comparisons between species that were likely to be competitors. Similarly, 85% of hypoxia-creation studies that also examined effects on native species found the NIS to create enough hypoxia to generate a negative response in the native species.

A negative influence on native species may be accentuated if hypoxia is chronic or frequent. Chronic and frequent hypoxia may shift selective environments sufficiently to devalue advantages gained from local adaptation due to long-term incumbency by native species (Byers, 2002). This could place even previously well-adapted native species at a competitive disadvantage to hypoxia-tolerant NIS species. However, even short-term hypoxic episodes can cause extensive damage. In a comprehensive meta-analysis of marine species, Vaquer-Sunyer & Duarte (2008) showed that the median LT_{50} upon exposure to acute hypoxia was <5 days. Almost every species above this median was a mollusc or priapulid worm, meaning that most other taxa were vulnerable in far shorter time periods. The median LT_{50} for the bottom 10% of species (i.e. the least hypoxia-tolerant) was <7 h.

In ∼35% of studies, NIS did not tolerate hypoxia, either compared to conspecifics in normoxic conditions or compared to native species. Nile perch and the NIS freshwater clam, *Corbicula fluminea*, were the two species most often studied in relation to hypoxia tolerance, perhaps reflecting their status as high-profile, successful invaders. Whereas Nile perch was consistently found to be hypoxia intolerant, *Corbicula fluminea* showed variability in tolerance. As with native species, fish and crustaceans tended to be more oxygen sensitive. There were a few species like *C. fluminea* that were found tolerant of hypoxia in one study and intolerant in another, e.g. *Perna perna* and *Dreissena polymorpha*. Such variation in tolerance results seems unsurprising given differences in influential experimental conditions, such as temperature, oxygen levels, and hypoxia duration.

(3) Role of other anthropogenic disturbances in exacerbating NIS–hypoxia interactions

Co-occurring anthropogenic disturbances, such as contamination, overfishing, and turbidity, likely exacerbate the effects of NIS and hypoxia and their interaction. One of the most influential anthropogenic disturbances in this regard may be habitat degradation and modification, specifically the coastal infrastructure that dominates many nearshore aquatic environments. Lagos *et al.* (2017) conducted a study of the hypoxia tolerance of eight NIS and six native fouling species, coupled with field measurements of O_2 in human-dominated infrastructure such as marinas and piers. Artificial structures are prolific in nearshore coastal environments and are often closely associated with NIS invasions (Tyrrll & Byers, 2007; Airoldi *et al.*, 2015). Furthermore, such structures can disrupt local hydrodynamics, leading to the formation of oxygen-depleted microsites. Thus, these areas provide a ripe opportunity to look at NIS–hypoxia interactions. Lagos *et al.* (2017) confirmed that these manmade structures, especially marinas, reduce water flow, and that hypoxia, and even anoxia, is common in low-flow conditions. They also showed that the NIS they studied could tolerate much lower levels of oxygen relative to the native species: 30% of available microhabitats within low-flow environments were physiologically stressful for native species, while only 18% of the same habitats were stressful for NIS. Thus artificial habitats can boost NIS abundance, hypoxia, and their interactive impact.

(4) Trait-based and plastic responses as mechanisms of hypoxia tolerance

Several studies explored the mechanisms enabling hypoxia tolerance, specifically if plastic or evolved trait changes were involved. Huhn *et al.* (2016) tested whether local adaptations through stress-induced selection or phenotypic plasticity were responsible for inter-population differences in hypoxia tolerance in the highly invasive mussel *Perna viridis*. They reciprocally transplanted mussels between a healthy bay and an anthropogenically impacted bay and tested them and resident controls for hypoxia tolerance 2 months later. Mussel tolerance to hypoxia depended more on the environment in which they had lived for the last 2 months than on the quality of their natal habitat. Phenotypic plasticity and high

body condition were suggested as the most likely causes of population-specific differences in hypoxia tolerance in *P. viridis* as opposed to chronic stress-induced selection for robust genotypes.

For both NIS and native species, the response variables reported in most hypoxia studies were abundance, mortality, and physiology (usually respiration rates) (Fig. 3). But there is some suggestive evidence that morphological and trait-based changes, either plastic or evolved, can be important mitigators of the effects of low oxygen. These trait changes, if sufficiently rapid, may ameliorate detrimental effects of NIS–hypoxia impact on natives, complementing behavioural and avoidance strategies often employed. For example, changes in gill morphology may enable native soft-sediment bivalves to survive hypoxic conditions generated by invasive algae (Wright *et al.*, 2012). Similarly, although most studies indicate that Nile perch are intolerant of hypoxia, Paterson, Chapman & Schofield (2010) found that the Nile perch occupying low-DO wetland ecotones of an invaded lake had significantly larger gills compared to conspecifics living in better oxygenated open waters of the lake. However, the few studies that have measured morphological trait changes associated with hypoxia and NIS have often not quantified linkages between the trait changes and physiological or fitness-related responses, and hence were excluded from our database. However, even with a quantified fitness effect, whether a trait change scales up to a population-level impact, for example by affecting NIS establishment or native species decline, would remain unresolved.

(5) Community effects of NIS–hypoxia interactions

All studies included in our database examined the impacts of hypoxia on individuals, with a few considering population-scale effects. But the furthest-reaching impacts of hypoxia–NIS interactions are manifested where hypoxia affects communities and ecosystems. For scientists interested in biological invasion processes, the population-, community-, and even landscape-level effects of hypoxia may be the most important to consider because these levels of ecological organization are important in the invasion process, i.e. establishment, spread, and impact. Although community-level studies are often more speculative, they are important because they address the indirect effects of hypoxia on other species in the ecosystem, i.e. the mechanisms by which hypoxia operates beyond asphyxiation or compromised physiology at the level of individuals. We have categorized several broad, community-wide impacts of hypoxia–NIS interactions that we highlight with examples below.

(a) Hypoxia killing competitors

If NIS and native species compete in the presence of hypoxia, a hypoxia-tolerant NIS can gain advantages due to the lower relative performance or abundance of its native competitors. The Asian clam *Corbicula fluminea* is a ubiquitous freshwater NIS that exemplifies this process. Early conventional wisdom

on this clam and its rapid worldwide spread argued that its success was due to negative impacts on native species (Strayer, 1999). More recent evidence suggests that it may invade empty niches vacated by native species extirpated by other causes, including poor water quality (e.g. Atkinson, Julian & Vaughn, 2014; Vaughn, Atkinson & Julian, 2015). In fact, *C. fluminea* can itself be forcefully affected by hypoxia and temperature-related stress (McDowell, McDowell & Byers, 2017), but it is an *r*-selected species that, following alleviation of the stressor, can rebound quickly. Furthermore, following mass die-offs, its rotting flesh reduces DO and increases ammonia levels exacerbating the mortality of native bivalves, whose populations are much slower to recover when water quality recovers (Cherry *et al.*, 2005).

(b) Hypoxia hindering predators

There could be a net positive indirect effect of hypoxia for some native fauna if hypoxia affects an NIS predator more harshly. One of the few ways in which hypoxia has been documented to benefit (some) native species was when native species used hypoxic areas as a refuge from predators that are intolerant of hypoxia (Altieri, 2008). The most prominent example of this is the introduction of Nile perch in Africa (Fig. 6B). This predatory fish is at the centre of one of the most dramatic cases of hypoxia intolerance shaping an entire ecosystem. This large piscivorous fish, which can exceed a body mass of 200 kg was introduced into Lake Victoria, Uganda and the surrounding watershed for commercial fishing in the late 1950s and has caused massive declines of up to 50% in native fish populations (Witte *et al.*, 1992). Several species of native fish survive almost exclusively in shallow, heavily vegetated wetlands around the edges of the lake that are chronically hypoxic (Chapman *et al.*, 1995). The Nile perch is hypoxia intolerant and avoids these areas, which thus provide spatial refugia for the native prey species (Chapman *et al.*, 2003).

Several native cichlid fishes living in these low-oxygen zones appear to have developed physiological adaptations and dietary changes. For example, in these hypoxic refugia, the native species dagaa (*Rastrineobola argentea*) exhibits a larger number of gill filaments that were suggested to enhance its capacity to extract oxygen from the water (Wanink & Witte, 2000). As numbers of Nile perch are increasingly diminished by heavy human fishing, populations of some of these native fishes have begun to rebound and they once again utilize more open areas of the lake outside their refugia (Chapman *et al.*, 2003).

In the literature, the Nile perch is the most common NIS discussed in the context of hypoxia. However, several of these papers were not included in our review because they did not gather direct evidence on the poorer tolerance of low DO by Nile perch compared to its prey, instead citing seminal papers that do, such as Chapman *et al.* (1995) and Schofield & Chapman (2000). Chapman *et al.* (1995) measured responses of several native fishes to hypoxia, and Schofield & Chapman (2000) quantified the hypoxia tolerance of Nile perch. Recent

studies have focused on the spatial distribution and abundance of native fish populations in the lake, referencing the Nile perch and their intolerance to low DO levels as background context, but not providing new data on the NIS and its hypoxia intolerance. This statement is not meant as a negative judgement on those latter papers, because once the hypoxia response of a system or species has been established, it may not need to be repeatedly verified, i.e. studies can build on accepted baseline knowledge. The Nile perch system is one with a rich storyline and receives heightened interest and attention given drastic native species declines and important accompanying socioeconomic aspects.

(c) Hypoxia causing predator switching

In a study investigating predator responses to hypoxia (Munari & Mistri, 2011), under normoxic conditions three prey bivalve species (two NIS and one native) were consumed by the NIS molluscan predator *Rapana venosa* in almost equal numbers when offered separately (no-choice experiments); but when a choice was offered, *R. venosa* strongly preferred the NIS *Scapharca inaequivalvis*. However, in choice trails conducted under hypoxic conditions, one of its prey, the NIS clam *Tapes philippinarum*, decreased its burial depth and *R. venosa* modified its predatory behaviour to attack preferentially the more vulnerable *T. philippinarum*. Thus, the NIS predator switched its preference from one NIS prey to the other under different oxygen conditions. The native prey was always less preferred but may suffer more from direct effects of hypoxia. The authors suggested this was an environmentally mediated indirect interaction between the two NIS prey species, due to the different reactions of the prey to hypoxia, with the net result being that hypoxia may facilitate the coexistence of the two NIS bivalves *via* predator switching.

(d) Hypoxia altering sediment biogeochemistry

Anoxia may also affect NIS and native species relative performance through changes to belowground oxygen processes like sediment sulphate reduction, as commonly occurs in salt marshes and seagrass and seaweed beds (e.g. Holmer *et al.*, 2004; Neira *et al.*, 2006; Gribben *et al.*, 2018). Entire infaunal communities can be altered by these oxygen-driven biochemical changes. Studies that exclusively examined sediment oxygen processes were not included in our database due to our focus on hypoxia in the water column. However, in some cases such as the NIS seaweed *Caulerpa taxifolia*, the oxygen-depleting activity of bacteria associated with its underground rhizomes or sediments spills over to affect organisms living at the benthic boundary layer; such cases were included in our review (Byers, Wright & Gribben, 2010; Wright *et al.*, 2010).

Within dense *C. taxifolia* beds, hypoxia concentrated in the sediment can extend 3–5 cm above the sediment surface into the water column (Gribben *et al.*, 2009b). This likely results from a combination of reduced water flow

and high microbial activity in shallow sediments consuming the available oxygen both below and above ground at the benthic boundary layer. Laboratory and field experiments demonstrate that hypoxic water column conditions can alter the behaviour (reduced burial depth) and increase stress on the native infaunal bivalve *Anadara trapezia* (Gribben *et al.*, 2009a; Wright *et al.*, 2010). Moreover, *A. trapezia* experiences higher mortality when forced to bury in *C. taxifolia* sediments (Byers *et al.*, 2010; Wright *et al.*, 2010), and adult and juvenile *A. trazepiza* were in poorer condition and showed higher mortality when grown on the sediment surface in *C. taxifolia* beds compared to unvegetated sediments (Gribben *et al.*, 2009b; Wright & Gribben, 2008). Thus, sediment anoxia appears to play an important role in the spread and impact of *C. taxifolia*, with impacts on native fauna related to the creation of low-oxygen conditions within sediments (Gallucci *et al.*, 2012), but also in the overlying water column.

(e) Hypoxia compromises hosts infected with NIS parasites

Gollock, Kennedy & Brown (2005) showed that an NIS nematode parasite compromises its eel host's ability to tolerate hypoxia by damaging internal organs such as the swimbladder. Because this study did not neatly fit into our categories of an NIS tolerating or creating hypoxia, it was not included in our database. However, it is noteworthy because it exemplifies a likely, but understudied effect of NIS parasites. Namely, parasites commonly deteriorate their host's performance, but this deterioration may be intensified under stressful conditions, such as hypoxia (Byers, 2021). Infected hosts under such conditions would presumably be greatly disadvantaged in community interactions like competition and predation (Gooding *et al.*, 2020).

(6) Ecosystem-level/management needs

Two deficient areas in which future research on NIS and hypoxia could aid ecosystem management are scaling and interactive effects. Knowledge of the interactions of NIS and hypoxia at larger ecological organizational scales, especially the ecosystem scale, would be most useful. Some of the largest influences of NIS occur when they affect broad emergent ecosystem properties including productivity, habitat structure, connectivity, succession, stability, biodiversity and carbon sequestration (Levin & Crooks, 2011). If hypoxia alters the influence of NIS on these properties, that could result in some of the largest system-wide effects. We found several papers that holistically evaluated small-scale studies to explicate the major threats to specific aquatic ecosystems, often with the goal of improving ecosystem management (Kennish, 2002; Purcell, Uye & Lo, 2007; Khim *et al.*, 2018; Kennish, Brush & Moore, 2014; Chagaris *et al.*, 2019). A noteworthy characteristic of these reviews is the discrepancy between the large scale at which management is framed *versus* the smaller scale at which hypoxia–NIS interactions are studied.

Although these reviews often acknowledge the key roles hypoxia and NIS play in altering ecosystems and promote their focus in future studies, they do not typically consider potential interactions and synergies between NIS and hypoxia. One exception highlighted that high nutrient loading and subsequent hypoxia that can follow hurricane events may exacerbate the spread of NIS such as hypoxia-tolerant species of fish (Stevens, Blewet & Casey, 2006; Mallin & Corbett, 2006). Isaev *et al.* (2017) suggested that invasion by the bioturbating polychaetes (*Marenzelleria* spp.) in the Northern Baltic Sea may improve oxygenation over large areas that experience hypoxic events, by increasing oxygen penetration into sediments promoting phosphorus retention, which inhibits development of hypoxic eutrophic conditions in the water column. Although scaling up current approaches to investigate hypoxia–NIS interactions to inform ecosystem management will be challenging, we argue that large-scale management of entire ecosystems has much to be gained by explicitly acknowledging these interactions and their spatial dependency. For example, where there is a relationship between hypoxia and NIS success, ameliorating anthropogenic eutrophication could yield synergistic benefits, alleviating the impacts of both stressors simultaneously. Ignoring the interaction between these two global stressors will likely result in continued less-effective management and conservation efforts.

(7) Future directions

Because hypoxia is highly context dependent and research questions regarding its interactive effects with NIS so wide ranging, invasion studies should continue to examine the effects of hypoxia in the way best suited to a particular system. Studies should continue to include field-based and large community-based studies that will provide more realistic insights into the role of hypoxia in invasions. A benefit of field-based, large-scale studies is that the results may be more directly relevant for resource management. Because incorporating these realistic aspects will necessarily mean more variable conditions and less standardization across studies, this realism likely comes at a cost of being able to conduct meta-analyses. However, when more empirical studies have amassed, for future attempts at meta-analysis, mortality and oxygen consumption seem the most promising response variables because of their frequency of use, relevance, and prospects for standardizing units across studies (Fig. 3).

Another useful field-based, large-scale measurement could be the Metabolic Index (Φ), which is a species-specific measure of the environment's capacity to meet temperature-dependent organismal oxygen demand (e.g. Deutsch *et al.*, 2015; Howard *et al.*, 2020). This index is increasingly used as a means to summarize an environment's capacity to support species with various oxygen sensitivities. In theory it could be an efficient metric for summarizing ecosystem health, particularly with regard to how differently native and NIS species will respond.

Based on the potential for far-reaching effects of hypoxia–NIS interactions, future studies should widen their scope beyond physiological, individual-level responses. A minority of the field studies in our database did this by examining effects on density, but these studies were often observational and small in scale. Studies perhaps avoid focusing on large-scale effects because they are deemed too intractable or too hard to manipulate experimentally. Furthermore, hypoxia tends to be localized in space and time (Levin *et al.*, 2009), making its potential effects on NIS spread and establishment likely episodic and patchy, and such non-uniform processes can be difficult to recreate or capture in study designs. But if done well, even observational studies may allow robust inferences to be drawn. The Nile perch research is probably the best example of this, whereby the community-level responses of native species have been inferred through a collection of studies focused on shorter-term responses of movement, physiology, habitat use, and mortality (see Section IV.5.*b*).

Our review provides an initial synthesis of the relationships between NIS and hypoxia in the literature, identifying a synergy between them, but only in certain contexts. Although we identified emerging trends and commonalities of effects due to the interaction of NIS with hypoxia, we also identify that researchers have not collectively analysed a balanced subset of NIS, native species, or conditions using standardized methods and response variables. We hope that our review suggests ways to refine future studies to enhance insights.

V. CONCLUSIONS

(1) Rates of NIS invasion are increasing (Cohen & Carlton, 1998; Ruiz *et al.*, 2000; Byers *et al.*, 2015; Gollasch *et al.*, 2015), and hypoxia events are also increasing in frequency, duration, and size (Kennish, 1997; Diaz, 2001; Vaquer-Sunyer & Duarte, 2008). Climate change is predicted to accentuate hypoxia as temperatures rise because warmer water holds less dissolved gases, reduces vertical mixing by stratifying the water column, and enhances decomposition rates (Long, Deutsch & Ito, 2016).

(2) Independently, NIS invasions and hypoxia are strong selective forces and structuring agents of aquatic communities (e.g. Brett, Ivany & Schopf, 1996; Cox, 2004; Freeman & Byers, 2006; Strauss, Lau & Carroll, 2006; Interesova *et al.*, 2020). As both factors increase, understanding how these two influential factors interact will be important, especially for effective resource management.

(3) The distribution of studies that address hypoxia–NIS interactions suggests that NIS are more often considered passengers associated with hypoxia rather than drivers of it. This implies that NIS are most often opportunists of anthropogenically degraded water quality. However, this conclusion may be influenced by substantial bias in the species selected for study.

(4) Unexpectedly, of those NIS identified in the literature to create hypoxia, primary producers were most common.

(5) The majority of NIS examined to date seem to tolerate hypoxia well, although the species examined are not taxonomically comprehensive or randomly selected. Geographic bias is also strong, with most studies carried out in Europe and North America. Indeed, the hypoxia–NIS literature shares many of the same biases common to other ecological studies.

(6) The recorded metrics for the responses of NIS and native species in the creation of, and response to, hypoxia are not standardized, and studies often do not examine net outcomes on populations or even individual-based measures like fitness or mortality. Furthermore, abundance and mortality effects of hypoxia are often examined in highly localized areas or conditions, e.g. in laboratory aquaria.

(7) Two of the most important ecological responses to understand would be how hypoxia influences the establishment and spread of NIS, yet these are seldom examined directly.

(8) Selection regime modification remains a likely mechanism for associations between hypoxia and the spread and establishment of NIS (Byers, 2000; Lagos *et al.*, 2017). Frequent or intense hypoxic disturbances may have shifted selection environments sufficiently to erase a native species' prior advantage of local environmental adaptation. More data are required to investigate this hypothesis.

(9) Examining community-level and indirect effects of hypoxia could allow us to capture larger scale processes, since by their very nature they are more holistic and involve more interactions. Also, they emphasize that studying hypoxia in field settings can be important to capture the chain of hypoxia-induced effects that may be operating within a system.

VI. ACKNOWLEDGEMENTS

VII. AUTHOR CONTRIBUTIONS

J.E.B. and P.E.G. conceived the ideas and designed the study. A.C.D., H.L.H., and J.E.B. performed the literature review. J.E.B. and J.A.B. analysed the data. J.E.B. wrote the initial manuscript, and all authors contributed to revisions.

VIII. DATA AVAILABILITY STATEMENT

All supporting data, which was compiled from the primary literature, are available as supporting information in Table S1.

IX. REFERENCES

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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.

Table S1. Summary data of the 100 literature studies used in our review of hypoxia and non-indigenous species (NIS).