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Assessing risks and mitigating impacts of harmful algal blooms on mariculture and marine fisheries

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Abstract

Aquaculture is the fastest growing food sector globally and protein provisioning from aquaculture now exceeds that from wild capture fisheries. There is clear potential for the further expansion of marine aquaculture (mariculture), but there are associated risks. Some naturally occurring algae can proliferate under certain environmental conditions, causing deoxygenation of seawater, or releasing toxic compounds (phycotoxins), which can harm wild and cultured finfish and shellfish, and also human consumers. The impacts of these so-called harmful algal blooms (HABs) amount to approximately 8 $billion/yr globally, due to mass mortalities in finfish, harvesting bans preventing the sale of shellfish that have accumulated unsafe levels of HAB phycotoxins and unavoided human health costs. Here, we provide a critical review and analysis of HAB impacts on mariculture (and wild capture fisheries) and recommend research to identify ways to minimise their impacts to the industry. We examine causal factors for HAB development in inshore versus offshore locations and consider how mariculture itself, in its various forms, may exacerbate or mitigate HAB risk. From a management perspective, there is considerable scope for strategic siting of offshore mariculture and holistic Environmental Approaches for Aquaculture, such as offsetting nutrient outputs from finfish farming, via the co-location of extractive shellfish and macroalgae. Such pre-emptive, ecosystem-based approaches are preferable to reactive physical, chemical or microbiological control measures aiming to remove or neutralise HABs and their phycotxins. To facilitate mariculture expansion and long-term sustainability, it is also essential to evaluate HAB risk in conjunction with climate change.

Key words: food production, food quality, HABs, mariculture, phycotoxins, risk mitigation.

Introduction

Managing global food security is one of the greatest challenges of the twenty-first century. Currently, around 820 million people (1 in 9 people) suffer from malnutrition (FAO, IFAD, UNICEF, WFP and WHO, 2018) and this is projected to rise as the human population grows from 7.6 to a projected 11.2 billion by 2100 (UN, 2017). While agricultural productivity and yields from wild capture fisheries have plateaued or are in decline, aquaculture has grown substantially over the last forty years, particularly in Asia, a region which now supplies ~90% of the global aquaculture market (FAO, 2018). Future food production in all sectors, however, may be limited by increasing climate variability, including extremes in rainfall intensity and temperature. These changes in climate in combination with increasing human population numbers, pollution events, impaired nutrient cycling, outbreaks of disease and pestilence are likely to result in future shortfalls in food production (FAO, 2018; FAO, IFAD, UNICEF, WFP and WHO, 2018). For aquaculture production, one of the most critical threats is the occurrence of harmful algal blooms (HABs).

Increasing frequency of HABs is associated with climate change, nutrient enrichment and habitat disturbance and is leading to growing impacts, including the poisoning or asphyxiation of finfish, shellfish and poisoning of human consumers (Hallegraeff 1993; GESAMP, 2001; Smayda 2004; Anderson 2012; Berdalet *et al.* 2016). Harmful algal blooms can also cause a variety of other impacts affecting water quality, water flow and amenity value. Therefore, estimating the economic costs of HABs is complex and requires consideration of many different issues (see reviews by Berdalet *et al.* 2016; Adams *et al.* 2018). Among the biggest economic impacts of HABs are precautionary closures of fisheries and aquaculture farms to prevent human poisoning (see Section 'Global distribution and characterisation of HABs affecting human health through seafood consumption' on human poisoning). Annual costs of precautionary closures (US$ at first point of sale) are estimated at $3–4 billion: >$0.03 billion in the UK (ASIMUTH, 2014); $0.9–1.2 billion in the EU (Hoagland & Scatasta 2006; S-3 EuroHAB, 2019); $0.1–1.0 billion in Korea, Japan and China (Kim 2006; Trainer & Yoshida 2014); and >$0.10 billion in the USA (Hoagland *et al.* 2002). Furthermore, the worldwide economic impacts of marine phycotoxins on human health are estimated to be approximately $4 billion a year (GESAMP, 2001; references in Berdalet *et al.* 2016). These estimates are very much 'best approximations' rather than detailed economic assessments (as conceded by some of the authors, e.g., Hoagland & Scatasta 2006; Adams *et al.* 2018). According to conservative epidemiological assessments, around 2000 cases of HAB-related food poisonings occur each year globally, following human consumption of contaminated finfish or shellfish, and around 15% of these cases prove fatal (FAO, 2012; CTA, 2013). The proportion of farmed versus wild-caught finfish and shellfish that contain phycotoxins and subsequently poison human consumers is not currently known.

Food fish production from aquaculture (80 million tonnes, US$232 billion per year) now exceeds capture fisheries (Table 1, adapted from FAO, 2018). Growth projections see this production from aquaculture rising by 37%, from 70 million tonnes to 109 million tonnes, by 2030 (FAO, 2018), with a significant contribution coming from the global expansion of mariculture (Kapetsky *et al.* 2013). Food fish production from mariculture currently amounts to 28.7 million tonnes, of which more than half comes from bivalve shellfish. Bivalves are among the most sustainable mariculture products, since they derive their food entirely from naturally occurring food sources, predominantly marine planktonic microalgae. The growth of these algae is fuelled by natural (and anthropogenic) nutrient supplies from land runoff and coastal upwelling (Huston & Wolverton 2009). Farming of aquatic plants and algae, dominated by seaweeds (macroalgae), has also increased recently to >30 million tonnes (FAO, 2018), worth an estimated US $11.7 billion. The largest share of seaweed production is for human food products (polysaccharide carbohydrates and micronutrients), and the remainder is for animal feeds, fertilisers and biopolymers (Nayar & Bott 2014).

Around 200 marine species are currently farmed, with the greatest variety in tropical seas (FAO, 2015; Froehlich *et al.* 2016). Species can be divided into two broad categories: (i) fed species, including finfish and some crustaceans and (ii) 'extractive' species, including (a) unfed filter-feeding bivalves, algal grazers, detritivores and (b) autotrophic plants, mainly macroalgae. Each of these categories has different environmental susceptibilities, interactions and installation planning issues (Gentry *et al.* 2016), particularly at inshore sites (≤1 km from the coast). At inshore sites, mariculture is directly influenced by anthropogenic activities (agricultural and urban runoff, municipal and industrial effluent inputs, ships and mariculture itself), which potentially increase HAB risk (Anderson *et al.* 2008; Anderson 2012). Recent calculations have suggested that current seafood consumption could be met by extending mariculture offshore, into less than 1% of Exclusive Economic Zones belonging to coastal states (Gentry *et al.* 2017). Some HABs, however, originate in open oceanic waters (Davidson *et al.* 2009, 2016; Trainer *et al.* 2012; Shutler *et al.* 2015; Gobler *et al.* 2017), indicating that some algal species may present similar or even greater risks as mariculture moves offshore.

Mariculture represents the nexus of environment–food–health systems, with food productivity and quality depending on clean coastal waters and healthy intact marine ecosystems (FAO, IFAD, UNICEF, WFP and WHO, 2018). To ensure long-term sustainable growth of the industry, a collection of interconnecting issues covering biosecurity, economic and environmental aspects (including climate

Table 1 Global food fish production from aquaculture in 2016

Aquaculture production	Finfish	Molluscs	Crustacea	Other	Total for aquaculture	Total as % of total food fish
By weight (million tonnes)	54.1	17.1	7.9	1.0	80*	53
By value (billion US$)	138.5	29.2	57.1	6.8	232	64

*Mariculture currently provides 36% (28.7 million tonnes) of food fish production from all forms of aquaculture (including freshwater and recirculating systems) and is dominated by molluscs (17.1 million tonnes; FAO, 2018).

change and HABs) need to be addressed (De Silva & Soto 2009; Lovatelli *et al.* 2013). Here, we critically review national and international HAB monitoring data records and published literature, to evaluate the occurrences, causes and impacts of HABs on shellfish and finfish mariculture in inshore and offshore waters. We identify environmental factors contributing to HAB risk and establish whether mariculture practices themselves can influence (increase or reduce) risks of HAB occurrence and impact. Methods for predicting and mitigating HAB risk are then reviewed. The risks of HABs to wild capture fisheries, as well as mariculture, are considered in this review also, since mariculture has the potential to attract and promote aggregations of wild finfish and shellfish. Building improved understanding of HAB risk for these related industries is of paramount importance to ensure future marine food security and safety.

Impacts of HABs on marine fisheries and mariculture

Nature of HABs and their impacts

Harmful algal blooms are proliferations of certain microalgae, macroalgae or blue/green algae (cyanobacteria), which under favourable environmental conditions reach certain levels that can have negative impacts on humans or the aquatic environment (Hallegraeff 1993; Anderson 2012; Bresnan *et al.*2013; GlobalHAB, 2017). Some HAB species or strains synthesise phycotoxins that are ingested by marine plankton grazers and potentially bioaccumulate in higher food chain organisms, including humans. Ephiphytic HAB species including *Prorocentrum lima*, *Ostreopsis* spp. and *Gambierdiscus* spp. have the potential to contaminate seaweeds, but human poisonings are generally caused by the consumption of seaweed grazing herbivorous shellfish, finfish or their predators, rather than from direct consumption of seaweeds. Globally, around 300 HAB species have been identified, of which more than a third, mainly in the dinoflagellate group, are known to produce toxins that are harmful to aquatic organisms and/or to humans consuming them (http://www.marinespecies.org/hab/index.php; Anderson 2012). Toxin production can vary between different genetic strains for some HAB species (e.g. Touzet *et al.* 2010; Cochlan *et al.* 2012) and/or different environmental conditions (Fehling *et al.* 2004; Wells *et al.* 2005). Poisoning syndromes in humans, responsible HAB genera, phycotoxin groups, and shellfish, finfish and macro-algal vectors of these phycotoxins are summarised in Section 'Global distribution and characterisation of HABs affecting human health through seafood consumption' (Table 2). Other metabolites may also be generated from these toxins, many of which have not been characterised in terms of chemical structure, potency or public health significance (Wiese *et al.* 2010; Anderson 2012). Other HAB species cause harm to fish through gill clogging or via the production of fish toxins (ichthyotoxins). Also, when the blooms decay, the degradation of the accumulated algal biomass by bacteria results in oxygen depletion, affecting aquatic ecosystems as a whole (Smayda 2004; Svendsen *et al.* 2018).

Global distribution and characterisation of HABs affecting human health through seafood consumption

Information concerning the global occurrence and impact of HAB events is recorded in the Harmful Algae Event Database (HAEDAT, http://haedat.iode.org). Bivalve molluscs, which filter and feed directly on microalgae, including HAB species, are the principal vectors for shellfish poisoning in humans. Crustaceans that prey upon intoxicated bivalves, including crabs and lobsters (Shumway 1995; James *et al.* 2010), and also carnivorous finfish (Friedman *et al.* 2017) can also bioaccumulate and in turn act as important vectors for phycotoxins. Table 2 summarises the principal poisoning syndromes that result from humans ingesting intoxicated shellfish or finfish and the respective geographical areas of highest incidence.

The phycotoxins associated with each poisoning syndrome (column 1 of Table 2) are neurotoxins, and they are heat-stable (and thus unaffected by cooking), underlining their risk to human health. Global maps of reported shellfish poisonings are illustrated in Manfrin *et al.* (2012), and selected references on poisoning syndromes can be found in Berdalet *et al.* (2016). Microalgae can produce a broader spectrum of toxic compounds than illustrated in Table 2 and include yessotoxins (YTXs) and pectenotoxins (PTXs) that mainly cause diarrhoea (Reguera *et al.* 2014). An increasing number of toxic compounds derived from algae are being detected as monitoring and analytical tools become more advanced, including brevetoxins (Turner *et al.* 2015) and cyclic imines (Davidson *et al.* 2015).

Occurrences and impacts of HABs on marine organisms in fisheries and mariculture

Evidence on the occurrence and impacts of HAB on marine fisheries and mariculture is being gathered by ongoing regional programmes (e.g. Maguire *et al.* 2016), national programmes (e.g. UK FSA, https://www.food.gov.uk/business-guidance/biotoxin-and-phytoplankton-monitoring) and global (GlobalHAB, 2017) programmes (see section '*In situ* monitoring'). However, despite the increasing coordination and integration of HAB monitoring programmes and research, not all incidents are captured and records may not always tally between local and global databases (e.g. HAEDAT). Some HABs are difficult to detect, notably

Table 2 Most common foodborne poisoning syndromes in humans caused by HABs and details concerning their occurrence and impacts

Poisoning syndrome	Symptoms	Causal phycotoxins	Mechanism of toxicity	Responsible HAB species	Principal vectors	Impacts (examples)	Global hot spots[d]
Amnesic shellfish poisoning (ASP)	Memory loss, brain damage[a]	Domoic acid (DO)	Agonism of the neuro-transmitter glutamate	*Pseudo-nitzschia* spp.	Scallops, e.g., *Pecten maximus* Crabs, e.g., *Metacarcinus magister*	Scallop harvesting bans (months)[b] Collapse of Californian Dungeness crab fishery 2015-2016[c]	Pacific, Atlantic coasts of North and Central America, Atlantic Europe
Paralytic shellfish poisoning (PSP)	Confused speech, tingling burning sensations, nausea, diarrhoea[e]	Saxitoxins (STXs)	Inhibition of voltage-dependent sodium channels[e]	*Alexandrium catenella, A. minutum, Gymnodinium catenatum, Pyrodinium bahamense var. compressum*	Mussels, clams, oysters, crabs, lobsters	Some 2000 PSP cases are reported per year globally (for all principal vectors), with occasional fatal consequences in humans[e]	North and South America and Canada, Africa, Europe (North Sea Mediterranean), and Australasia
Diarrhetic shellfish poisoning (DSP)	Diarrhoea, nausea, vomiting and abdominal cramps[f]	Okadaic acid (OA), *Dinophysis* toxins (DTXs)	Inhibition of protein phosphatases in intestine and neurons[f]	*Dinophysis* spp. *Prorocentrum* spp.	Mussels, clams, oysters Edible crabs (*Cancer pagurus*)	Harvesting bans for bivalves in Europe (weeks-months)[g] Closure of edible crab fishery in Norway (weeks-months)[h]	Reported globally and particularly in NW Europe
Azaspiracid poisoning (AZP)	Diarrhoea, nausea, vomiting and abdominal cramps[i]	Azaspiracids (AZAs)	Modulation of gamma amino butyric acid (GABA)[i]	*Amphidomataceae: Amphidoma, Azadinium*	Mussels, king scallops and edible crabs[j]	Harvesting bans (months) for shellfisheries (principal vectors) and mariculture in Atlantic Europe[j]	Norway coast, UK and Atlantic coast of France and Spain
Neurotoxic shellfish poisoning (NSP)	Loss of motor control, nausea muscular ache, including abdominal[k]	Brevetoxins (BTXs)	Inhibition of voltage-dependent sodium channels[k]	*Karenia* spp.	Clams, oysters and mussels[l]	Seafood poisoning. The formation of toxic aerosols by wave action also produces respiratory irritation and asthma-like symptoms	East and West coasts of North America, Florida and the Gulf of Mexico
Ciguatera fish poisoning (CFP)	Gastrointestinal, neurologic and cardiac distress[m]	Ciguatoxin (CTX), maitotoxin (MTX)	Agonism of voltage-gated sodium channels	*Gambierdiscus* spp.	Herbivorous fish (grazing HABs on macrophytes macroalgae) and their predators	CFP is one of the most common poisoning syndromes resulting from the consumption of contaminated finfish[m]	Caribbean, Florida, East Africa, Madagascar, Northern Australia, Pacific Islands

References: (a) Lundholm *et al*. (1994); (b) Campbell *et al*. (2003); (c) California Ocean Science Trust (2016); (d) Manfrin *et al*. (2012); (e) Anderson (2012); (f) Munday (2013); (g) Reguera *et al*. (2014); (h) Castberg *et al*. (2004); (i) Furey *et al*. (2010); (j) Twiner *et al*. (2008); (k) Kirkpatrick *et al*. (2004); (l) Watkins *et al*. (2008); (m) Friedman *et al*. (2017).

for species which bloom below the sea surface and evade *in situ* monitoring and satellite imaging (Shutler *et al.* 2015). It is also often difficult to attribute cause(s) to observed impacts on complex marine systems, particularly when they involve cryptic species and nonspecific mechanisms, such as the depletion of dissolved oxygen and suffocation of (shell)fish by HABs such as *Karenia mikimotoi* (Davidson *et al.* 2009; Shutler *et al.* 2015). Since the 1960s, the number of hypoxic or anoxic 'dead zones' in coastal waters has doubled every decade (Diaz & Rosenberg 2008). This has occurred in conjunction with increasing eutrophication caused by nutrient enrichment and excessive algal growth. In some cases, notable asphyxiation impacts on finfish and shellfish have been attributed to high biomass blooming HAB species such as *Phaeocystis* spp., *Karenia* spp. and *Aureococcus anophagefferens* (Peperzak & Poelman 2008; Davidson *et al.* 2009; Gobler *et al.* 2011).

Evidence of acute toxicity from HABs on finfish and shellfish in wild fisheries and mariculture

Harmful algal bloom species from different taxonomic groups with few commonalities (dinoflagellates, dictyophytes, haptophytes, prymnesiophytes, raphidophytes) have been implicated in major finfish kills in marine fisheries and mariculture. In some cases, the toxicity can be transmitted up the food chain to seabirds and marine mammals. Widely cultured finfish species affected by HABs include Atlantic salmon (*Salmo salar*), Rainbow trout (*Onchorhynchus mykiss*) and Yellowtail amberjack/kingfish (*Seriola quinqueradiata*) (reviewed by Landsberg 2002; Clément *et al.* 2016). Nevertheless, the mechanisms of toxicity for 'fish killing HABs' are not well understood. An example illustrating the complexity associated with HAB toxicity in finfish is presented for *Heterosigma akashiwo*. Here, effects may be due to the production of reactive oxygen species, brevetoxin-like compound(s), excessive mucus production that impedes oxygen exchange, gill tissue damage by mucocysts and/or haemolytic activity. Uncertainties arise when there are differences in the toxicity of wild HAB populations versus laboratory cultures; for example, reduced toxicity has been shown to result from the long-term culturing of *H. akashiwo* (Cochlan *et al.* 2012). There may also be variability in mucocyst production by different strains of microalgae (in the case of *Pseudochattonella farcimen*; Andersen *et al.* 2015).

Marine fisheries (and other wildlife). Some of the largest and most regular finfish (and other wildlife) kills occur annually along Florida's Gulf coast. Here, epidemiological assessments have attributed these to brevetoxin poisonings from blooms of the dinoflagellate *Karenia brevis* (Landsberg *et al.* 2009; Flaherty & Landsberg 2011). A recent bloom of *K. brevis* lasted over a year, beginning in November 2017, extending for a distance of 150–200 miles along Florida's Gulf coast and killed hundreds of tonnes of marine life, including thousands of small fish, numerous large fish (including groupers and a 21-ft whale shark) and marine mammals, including dolphins (Pickett 2018). The 2017–2018 bloom is one of the longest and most severe outbreaks recorded over the last 70 years and illustrates the scale of impacts possible from a single HAB outbreak (Krimsky *et al.* 2018). Elsewhere, for example in the UK (1978, 1980) and Ireland (1976, 1978, 1979 and 2005), major finfish and shellfish kills have been attributed to *Karenia mikimotoi* (a.k.a. *Gyrodinium* (*or Gymnodinium*) *aureolum*; e.g. Silke *et al.* 2005; Mitchell & Rodgers 2007). These blooms have caused widespread death of wild and cultured fish, through either acute toxicity attributed to phycotoxins with neurotoxic, haemolytic or cytotoxic effects, or via oxygen depletion caused by decaying blooms (e.g. Boalch 1979; Jenkinson & Connors 1980; Jones *et al.* 1982).

Saxitoxin produced by *Alexandrium* spp. may also be lethal to larvae and juveniles of commercially important finfish and shellfish species, such as Atlantic mackerel (*Scomber scombrus*) and American lobster (*Homarus americanus*; Robineau *et al.* 1991). Biomagnification of saxitoxin in the marine food chain has also been linked to significant fish kills, and both seabird and marine mammal deaths (Pitcher & Calder 2000; Sephton *et al.* 2007).

Mariculture. Harmful algal blooms often lead to finfish kills in caged environments, where the fish cannot escape phycotoxins or oxygen depletion from the decaying algal biomass. Risks from HABs are particularly high for finfish confined in sheltered inshore embayments, where the HABs may be concentrated by onshore winds and currents. As an example of this, between 1972 and 1982 in the Seto Inland Sea, Japan, at least 21.8 million cultured yellowtail amberjack (*Seriola quinqueradiata*) were killed by the raphidophyte *Chatonella antiqua* (Okaichi 1989). In 1972, the economic loss for the summer outbreak amounted to US $70 million. Since then, annual losses have been lower, but recurring severe impacts have continued (Fukuyo *et al.* 2002). Recurring threats have been reported also from another toxic raphidophyte, *H. akashiwo*, causing finfish kills in Iceland, Spain, British Columbia and Chile (Landsberg 2002). The losses caused by outbreaks of *H. akashiwo* to wild and net-penned finfish off Puget Sound, Washington, have been estimated to cost in the region of US$2–6 million per episode. The outbreaks of *H. akashiwo* are believed to have been increasing generally in scope and magnitude in various global regions over the past two decades (Landsberg 2002).

Originating offshore around the UK (Davidson *et al.* 2009; Shutler *et al.* 2015), high biomass blooms

(>1000 cells/mL) of *Karenia mikimotoi* have been increasingly frequent and have been associated with significant finfish kills, including for caged fish in inshore waters (Jenkinson & Connors 1980; Silke *et al.* 2005; Davidson *et al.* 2009). Farmed shellfish including mussels, oysters and clams (*Tapes semidecussatta*) in the UK and Ireland, and hatchery raised juvenile bivalve spat have also periodically suffered significant mortalities, along with crustaceans and other benthic invertebrates, in conjunction with *K. mikimotoi* blooms (Raine *et al.* 2001; Silke *et al.* 2005).

Evidence of chronic toxicity from HABs in wild fisheries and mariculture

Symptoms of chronic toxicity in finfish are wide ranging for different HABs. These symptoms include liver pathologies caused by ciguatoxins released from *Gambierdiscus* spp. and microcystins produced by *Microcystis* spp., gill pathologies caused by cytotoxins from, for example *Prymnesium* spp. and *Heterosigma* spp., narcosis (loss of balance and swimming ability) caused by neurotoxins from *Karenia* spp. and paralysing saxitoxin from *Alexandrium* spp., and excess gill mucus production, for example, caused by *Chaetoceros* spp. (review by Burkholder 1998; Svendsen *et al.* 2018).

Chronic sublethal effects of HAB toxins in bivalve molluscs include reduction in feeding rates in scallops and oysters (e.g. caused by exposure to *Prorocentrum minimum*), reduction in growth and byssus production in blue mussels (*Mytilus edulis*), growth reduction in Eastern oysters (*Crassostrea virginica*), for example caused by *Gymnodinium aurelium/Karenia mikimotoi* (Burkholder 1998) and by *Alexandrium tamarense* (Li *et al.* 2002), reproductive impairment in blue mussels and Bay scallops (*Argopecten irradians*), for example caused by *Chrysochromulina polylepis*, reduction in the recruitment of juvenile Bay scallops, for example caused by *Karenia brevis* (reviewed by Burkholder 1998; Basti *et al.* 2018). Thus, in addition to toxin accumulation rendering shellfish unsafe for harvesting for human consumption, toxin presence can have a longer term effect, impacting on shellfish abundance and time taken to grow to marketable size. Slower pumping and filtering rates are also likely to increase the time taken to evacuate toxic material from shellfish tissues. Most shellfish species can eliminate phycotoxins within a few weeks, but retention of some toxins (e.g. saxitoxins) in some species, such as sea scallops (*Placopecten magellanicus*) and Atlantic surfclams (*Spisula solidissima*), can last up to 5 years (Shumway *et al.* 1990; Landsberg 2002). Harmful algal blooms also have the potential to impact adversely on the supply of larval 'seed' or 'spat' for aquaculture. Examples of this include *Karenia brevis* impacting on larval recruitment in Bay scallops (Burkholder 1998), Pacific oysters (*Crassostrea gigas*) and Northern quahog (*Mercenaria mercenaria*); (Rolton *et al.* 2018). For these shellfisheries, the estimated annual economic losses due to *K. brevis* along Florida's Gulf coast alone are estimated to be up to US$6 million (NOAA 2004; Adams 2017). *Karenia brevisulcata* has also been shown to be toxic to larvae of Greenshell mussel (*Perna canaliculus*), Pacific oyster and New Zealand abalone (*Haliotis iris*); (Shi *et al.* 2012).

Consumption of intoxicated finfish and shellfish can also lead to chronic toxicity in organisms higher in marine food chains. For example, domoic acid derived from *Pseudo-nitzschia* sp. can cause neuropathic injury in both finfish and shellfish eating mammals and birds (Lefebvre *et al.* 2007; Ramsdell & Zabka 2008; Soliño *et al.* 2019).

Environmental factors contributing to HAB risk

Environmental factors promoting HABs

HABs are natural phenomena within the seasonal cycles of planktonic micro-organisms in aquatic ecosystems (Glibert *et al.* 2005; Shumway *et al.* 2018). In recent decades, harmful events appear to be increasing in frequency, duration and impact globally. Verifying them is a research priority (GlobalHAB, 2017; e.g. Wells *et al.* 2015, 2019). Apparent increased frequencies of HABs may be due to a combination of factors (see Figure 1) including: (i) warming sea surface temperatures, and associated water column stratification and range extensions of tropical organisms, including toxic species; (ii) increased frequency and intensity of storm events and flooding and associated increasing nutrient inputs, upwelling intensities and wider HAB dispersal; (iii) increasing anthropogenic pressures on the marine environment, notably land- and sea-based nutrient enrichment and disturbance of coastal habitats; and (iv) increased awareness and improvements in HAB monitoring systems (Hallegraeff 1993; Raine *et al.* 2008; Anderson 2012; Bresnan *et al.* 2013; Wells *et al.* 2015; Gobler *et al.* 2017; Anderson *et al.* 2019).

Evaluating HAB risk in any 'system' is highly challenging, since environmental drivers include a range of physical, chemical and biological factors, which can combine to influence (i) the initiation/development of a HAB; (ii) its impact/toxicity and (iii) the termination of a HAB (Roelke & Buyukates 2001; Anderson *et al.* 2012a). These factors operate from micro- (mm) to meso- (10–100 km) to macro (>100 km) spatial scales and over a range of temporal scales (from seconds to minutes and from days to months; Dickey 2001). For example, an abundant supply of dissolved nutrients, calm sea state, warming, increasing stratification and increased sunlight over a period of weeks may allow the algae to grow in high concentrations, and then, dramatic and significantly increased turbulent sea state (causing increased vertical mixing) over several hours can result in bloom termination (e.g. Shutler *et al.* 2015). The challenge of

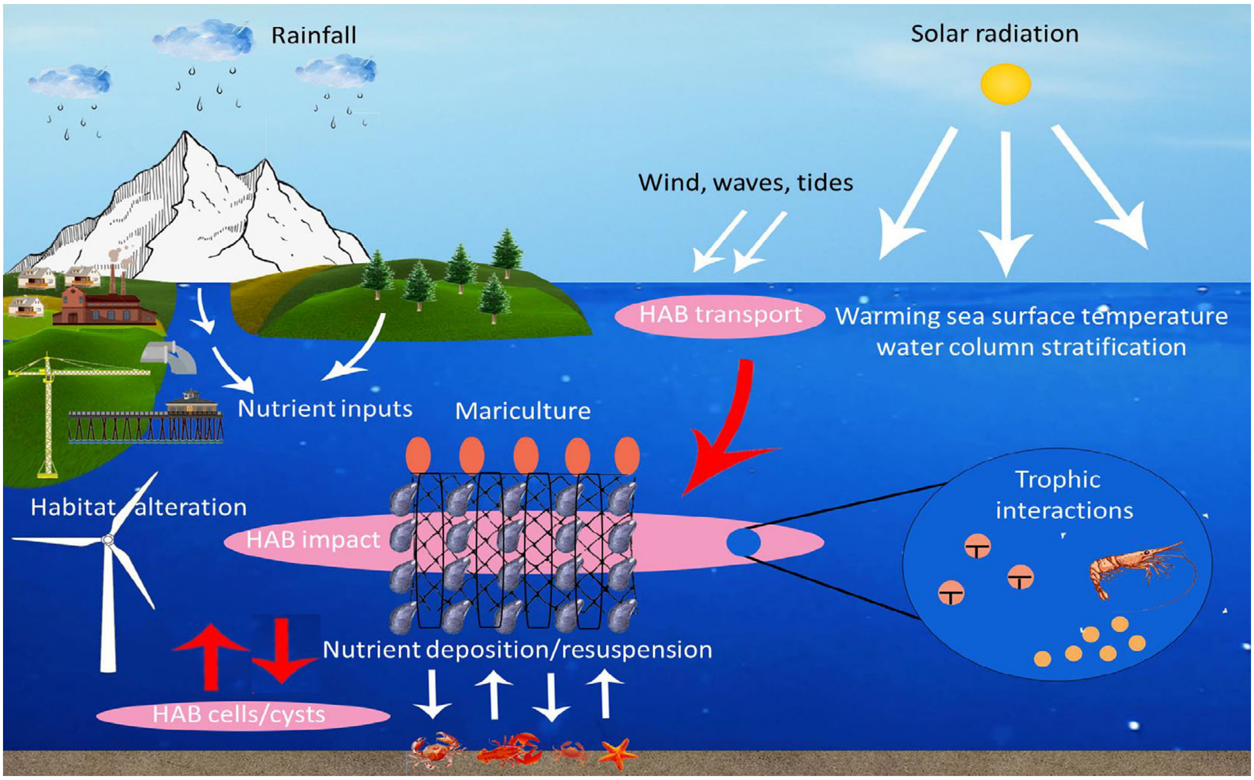

Figure 1 Environmental factors promoting HABs. Complex interactions among environmental factors (solar radiation, wind, waves, tides, rainfall, nutrients), ecological and trophic interactions and biological processes (e.g. cyst formation) can facilitate the proliferation of phytoplankton in general and harmful algal species as well. Excess and unbalanced nutrient supply and habitat alteration can increase the risk of HAB occurrence. HABs negatively impact mariculture production and product quality. (However, some mariculture practices can mitigate the occurrence and impact of HABs, for example, through the use of integrated multitrophic aquaculture approaches; see Figure 2).

understanding HAB occurrence and toxicity is further complicated by ecological interactions between HAB species and other members of plankton communities, which vary both spatially and temporally in species composition, genetic diversity and physiological status (Anderson *et al.* 2012a; Davidson 2014). Despite these complexities, some of the key factors driving HAB dynamics are well characterised and are outlined in sections ‘Environmental factors contributing to HAB initiation and toxicity’, ‘Environmental factors contributing to HAB termination’ and ‘Regulation of HABs by filter feeding shellfish’ below.

Environmental factors contributing to HAB initiation and toxicity

The pre-requisites for any HAB event are the presence of algal cells, spores or cysts; suitable conditions of light and nutrients for their growth and reproduction; and physical conditions that facilitate their accumulation in favourable growing conditions. Cells can accumulate either by horizontal transport (advection) in water bodies by wind and/or tide, or by resuspension from sediments by wave action, or upwelling of bottom water (e.g. Farrell *et al.* 2012; Pitcher *et al.* 2017). The source of propagules that initiate blooms may be local, or distant, though the origin of propagules for any particular harmful bloom is typically difficult to determine. There is evidence that HABs in some areas originate in the ocean, rather than in coastal embayments (Hinder *et al.* 2011; Whyte *et al.* 2014; Berdalet *et al.* 2017; Pitcher *et al.* 2017). The majority of HABs, including dinoflagellates and diatoms, are holoplanktonic, relying on vegetative cells to survive inhospitable conditions and to seed blooms. In some cases, when growth conditions are suboptimal, highly toxic HABs such as *Alexandrium* spp. reproduce sexually and form resting cysts. These cysts settle on sediments (Smayda & Trainer 2010) and then undergo resuspension during storms or coastal upwelling, enabling (re)colonisation of existing and new areas (e.g. Anderson *et al.* 1994; Pitcher *et al.* 2017).

Nutrient availability is another key requirement for HAB initiation and maintenance. Most HAB species are primarily photoautotrophs, and their requirements for autotrophic growth include inorganic nitrogen (N), phosphorus (P) and silicate (Si, in the case of diatoms).

High-biomass HABs in estuaries and coastal zones have been linked to elevated inorganic nutrient inputs (eutrophication; Rabalais *et al.* 2010; Paerl *et al.* 2014) and organic nutrients (e.g. urea from fertilisers, following heavy precipitation and land runoff, Heisler *et al.* 2008). However, the effects of nutrient inputs may be confounded by many other factors, including natural occurrence of HABs, transport of HAB species via mariculture and other marine activities, variable meteorological forcing, and longer-term climate change (Callaway *et al.* 2012; Gowen *et al.* 2012). There is increasing evidence that many HAB species can use dissolved and particulate organic forms of N and P (through prey ingestion), in addition to autotrophy; this combination of trophic modes is termed mixotrophy (Burkholder 1998; Anderson *et al.* 2002; Lin *et al.* 2018). Mixotrophic HAB species are therefore able to proliferate both under high organic N concentrations and by engulfing prey under nutrient limited conditions. Examples of mixotrophic HAB species include low biomass (100–1000 cells/L) blooming dinoflagellates, such as *Alexandrium* spp. (Anderson *et al.* 2012b; Lee *et al.* 2016) and *Dinophysis* spp. (Jacobson & Andersen 1994), and also high biomass (>10 000 cells/L) blooming species such as *Pseudo-nitzschia* spp. (Loureiro *et al.* 2008) and *A. anophagefferens* (Gobler *et al.* 2011). Furthermore, changes in nutrient ratios (far from the classic stoichiometric Redfield N:P ratio of 16:1) may be important in stimulating the growth of some HABs and influencing their toxin content (Anderson *et al.* 2002; Kudela *et al.* 2010; Glibert *et al.* 2014a) and responses may be highly species-specific (Wells *et al.* 2015).

Reduced turbulent mixing and increased thermal stratification are key factors promoting HABs, especially those comprised of dinoflagellates. Water column stratification and nutrient enrichment caused by river plumes, jets, upwelling areas and tidal fronts are also particularly conducive for HAB development (Pitcher *et al.* 2017). Phytoplankton and other planktonic organisms tend to collect passively in boundary layers in stratified water bodies – motile dinoflagellate HAB species have the added advantage of being able to visit both nutrient-rich deeper water and irradiance-saturated shallower water either side of these boundary layers (e.g. Smayda 1997). HABs are also more likely to occur in sheltered zones of lagoons, estuaries and coasts, as a result of increased water residence times, warmer temperatures and increased penetration of photosynthetically active radiation (PAR; e.g. Smayda 1989). Although strong turbulent mixing may be disadvantageous to bloom development by causing the breakup of chains of individuals and by inhibiting cell division (Estrada & Berdalet 1997), low level turbulence can enhance nutrient availability by facilitating increased transfer of molecules in or out of plankton cells, especially in passively floating diatoms (Peters *et al.* 2006). Other biological processes, including inter-cell quorum sensing and encounter rates with competitors and grazers (Gowen *et al.* 2012), are also modulated by fine scale turbulence and this can also favour HABs (e.g. Berdalet *et al.* 2017).

Environmental factors contributing to HAB termination

Advection and dispersion of HABs, increasing turbulent shear forces breaking up cells, and/or nutrient limitation are all understood to contribute to the termination of HABs (Gentien *et al.* 2007; Lenes *et al.* 2013), and consequently, HAB prediction models are often driven by these physical processes and biogeochemical fluxes. However, models that only include these processes often 'over-predict' HAB duration, indicating that inter-species biotic interactions play important roles in terminating harmful blooms (Roelke & Buyukates 2001; Lenes *et al.* 2013; Davidson *et al.* 2016).

Plankton grazers or predators play an important role in regulating the abundance of marine planktonic micro-algae, including HAB species. In nutrient limited (oligotrophic) offshore marine environments, mesozooplankton (e.g. copepods 0.2–20 mm) consume 10–40% of marine phytoplankton, while micro-zooplankton (20–200 μm) consume around 60–70% (Calbet 2008). In temperate nutrient-rich (eutrophic) upwelling and estuarine ecosystems, micro-sized heterotrophic and mixotrophic dinoflagellates (including HAB species) can dominate phytoplankton grazing (Calbet 2008). More detailed, mechanistic understanding concerning how and to what extent grazers regulate or terminate HABs is lacking. Plankton community interactions can vary markedly in temperate waters displaying a seasonal succession of different blooming species and also in (sub)tropical waters with relative constant standing stocks of microplankton. In both cases, food web dynamics can alternate between resource (bottom-up) and predatory (top-down) control (Calbet 2008) and outcomes for HABs are highly situation-specific (Turner & Tester 1997).

Marine parasitic microbes (micro- and nano-sized protists 10–100 μm, pico-sized bacteria 0.2–10 μm and femto-sized viruses ≤ 0.1 μm) target all of the main phytoplankton groups (Gachon *et al.* 2010). They have been shown to play a significant role in terminating some major algal blooms (Wilson *et al.* 2002) and have also been linked to the decline of HABs (Chambouvet *et al.* 2008; Roth *et al.* 2008; Jones *et al.* 2011). In turn, this has prompted research into the microbial control and bioremediation of HABs (Brussaard 2004; Sun *et al.* 2018; see section 'Spatial and temporal planning to minimise HAB risk'). Larger micro-sized parasites such as the dinoflagellate *Amoebophyra* spp. may also be responsible for the termination

(Rosetta & McManus 2003; Montagnes *et al.* 2008) or regulation (Nishitani *et al.* 1985) of dinoflagellate HABs such as *Alexandrium* spp.

Adaptive responses in HAB species to avoid or combat grazers and parasites include sensing and moving away from grazers (Wolrhab 2013); adapting/optimising colony size (chain length) versus swimming speed (Selander *et al.* 2012); synthesising and releasing phycotoxins and/or other allelochemicals (Stüken *et al.* 2011; Anderson 2012); undergoing or prolonging encystment (Rengefors *et al.* 1998; Toth *et al.* 2004); and undergoing auto-lysis (i.e. programmed cell death) (Franklin *et al.* 2006; Lenes *et al.* 2013). Combinations of mechanisms underlying predator–prey and host–parasite interactions can vary greatly since algal prey/host and predator/parasite niches are highly species-specific (Amin *et al.* 2015; Ramanan *et al.* 2016).

Regulation of HABs by filter feeding shellfish

Filter-feeding shellfish can exert considerable (top-down) grazing pressure, limiting phytoplankton (and zooplankton) biomass, particularly in shallow, well mixed estuaries and coastal waters, where bottom-living bivalves can come into contact with and filter the majority of the water column (Newell 2004; Lucas *et al.* 2016). Bivalves such as mussels, suspended on ropes hanging vertically in the water column can also be effective at filtering plankton at deeper water sites (Stadmark & Conley 2011; Hedberg *et al.* 2018). Physical factors such as water column exchange, turbulent mixing, temperature and stratification, and the influence of mariculture infrastructures on each of these (see Section 'Physical alteration of habitats and hydrodynamic regimes'), can be important in modulating shellfish grazing, phytoplankton sinking, and phytoplankton community composition – for example reduced vertical mixing favours motile dinoflagellates, while nonmotile phytoplankton such as diatoms sink below the euphotic zone and are more easily intercepted by grazers (Lucas *et al.* 2016). The influence of selective filter feeding by shellfish on plankton community structure, including HABs species, is relatively poorly understood (Newell 2004; Petersen *et al.* 2008; Lucas *et al.* 2016). Simple size selection for nano-sized plankton and above (>4 μm) and higher filtration rates in the warmer summer months may serve to reinforce seasonal succession from nano- to pico-plankton dominated communities (Newell 2004). Sensing of food particles and their surface chemistry have been suggested to play a role in selective filtering of nutritious plankton in preference to detrital and mineral particles (Ward & Shumway 2004; Espinosa *et al.* 2009; Yahel *et al.* 2009). Phycotoxins, particularly paralytic shellfish toxins (PSTs) as well as other toxin classes (e.g. NSTs and ASTs), are capable of inducing valve closure and/or reducing filtration rate in bivalves, as well as impairing growth and reproduction and inhibiting byssus production (Burkholder 1998; Landsberg 2002; Manfrin *et al.* 2012). Nevertheless, some bivalves show preferential uptake of harmful algal cells. This has been shown in the laboratory in five bivalve species (Bay scallop, Eastern oyster, Northern quahog, softshell clam (*Mya arenaria)* and the blue mussel (*Mytilus edulis*). All bivalves, with the exception of softshell clam, ejected intact cells of three HAB species (*Prorocentrum minimum* (PST and DST), *Alexandrium fundyense* (PST) and *Heterosigma akashiwo* (NST)) in their faeces or pseudo-faeces. Only oysters exposed to *H. akashiwo* showed partial or complete valve closure and reduction in filtration rate. These results confirm that feeding responses of bivalves in the presence of HABs can be highly species-specific. Furthermore, clearance of HABs from the water by bivalves may simply result in the transfer of intact/live cells to the sediment, from which they could be resuspended (Hégaret *et al.* 2007).

Environmental impacts of mariculture and contribution to HAB risk

Long-term time-series data are required to demonstrate the influence of finfish, shellfish and/or macro-algal mariculture on HAB risk as recognised in the Science Plan of the international programme on HABs (GlobalHAB, 2017). Accumulating evidence from China, which has the longest running, largest and highest concentration of mariculture in the world, indicates that the frequency and extent of HABs has been increasing concurrently with the industry growth since 1960 (Wang *et al.* 2008; Lu *et al.* 2014; Wartenberg *et al.* 2017). The occurrence of HAB events in China increased sharply in 2009 with ~80 episodes, covering > 15,000 km^2 of China's coastline in just one year. The increasing trend, however, also follows increasing urbanisation of coastal fringes (Liu & Su 2017). Potential environmental effects of mariculture are listed in Table 3, and the tendencies for these effects to promote HAB formation and impact (either directly or indirectly) are discussed in sections 'Nutrient emission versus assimilation', 'Chemical treatments used to control pathogens and parasites', 'Escapees and introduction of invasive and/or harmful species', 'Physical alteration of habitats and hydrodynamic regimes' and 'Transmission of HAB species and alteration in the abundance and composition of plankton communities'.

Organic and inorganic nutrient emission versus assimilation

Nutrient emissions from mariculture operations are predicted to increase substantially due to industry expansion (up to sixfold by 2050). The majority of these emissions

Table 3 Environmental effects of mariculture that can promote HAB risk

(i) Organic and inorganic nutrient emission versus assimilation;
(ii) Disease and use of preventative chemical agents;
(iii) Escapees and genetic interactions with wild populations;
(iv) Physical alteration of habitats and hydrodynamic regimes;
(v) Increase in HAB transmission (between relay sites) or alteration of the abundance and composition of plankton communities.

References for (i–iv): Lovatelli *et al.* (2013), Kapetsky *et al.* (2013), Wartenberg *et al.* (2017).
References for (v): Gibbs (2004), Grant *et al.* (2007).

comprise nutrient waste, primarily from finfish (fed mariculture) and also from shellfish, released in a dissolved form directly to the water column (Bouwman *et al.* 2013). These nutrient emissions may promote the growth of harmful algal species in the vicinity of mariculture farms (Anderson *et al.* 2002; Hallegraeff 2003). However, causal linkages between fish farming and eutrophication (Pitta *et al.* 2005; Modica *et al.* 2006) and HABs (Anderson *et al.* 2008) are often not clear (Smayda 2004; Gowen *et al.* 2012). In some cases (e.g. farming of extractive shellfish), mariculture can cause net assimilation of nutrients leading to deficits (Ferreira *et al.* 2014), while elsewhere nutrient emissions may exceed local environmental assimilation capacities (Bouwman *et al.* 2013). Problems are likely to be more acute for farms with higher stocking densities (Sellner *et al.* 2003; Bouwman *et al.* 2013). Intensive bivalve cultivation can alter the nitrogen:phosphorus (N:P) nutrient stoichiometry and change the major N species to reduced forms, especially ammonia, as well as particulate organic nitrogen, and these N forms are preferred by various harmful algae – predominated by dinoflagellates (e.g. Arzul *et al.* 2001; Glibert *et al.* 2014a, but see Davidson *et al.* 2012). Conversely, diatoms have also been shown to decline as a result of nutrient excretion by bivalves (Lucas *et al.* 2016). A further concern arises because of low assimilation efficiencies (typically 30–40% for N, or less under bloom conditions), such that shellfish can become point sources of regenerated nutrients. Benthic regeneration of the accumulated faeces and decomposing feed can be significant in shallow well mixed coastal waters (Bouwman *et al.* 2013).

Disease and use of chemical treatments to control pathogens and parasites

Infections by pathogens and infestations of parasites, exacerbated by aggregations of wild fish around mariculture installations (Dempster *et al.* 2004), present a risk to human and (shell)fish health and have similar financial impacts to those for HABs (e.g. impacts of white spot virus on shrimp farming in Southeast Asia ~6 US$ billion/year) (Lafferty *et al.* 2015). Consequently a range of antimicrobial chemicals and pesticides are licensed for use in mariculture, specifically for finfish culture (Johnston & Santillo 2002; Read & Fernandes 2003). Cumulative environmental exposures to these chemicals can be significant in some coastal waters (Baker-Austin *et al.* 2008; Uyaguari *et al.* 2013) and may exceed environmental quality standards (EQSs), which can be as low as 1 part in 1 trillion for some highly potent compounds (Gilliom 2007; Watts *et al.* 2017). Impacts of antimicrobial chemicals on beneficial microbes and associated ecosystem services (e.g. nutrient cycling, water quality and HAB regulation) could be significant (Woolhouse & Ward 2013; Watts *et al.* 2017). Research on the impacts of chemicals on HAB regulation has been extremely limited to date and has generally focused on the effects of pesticides on HABs in freshwater systems (Relyea 2009; Beketov *et al.* 2013; Harris & Smith 2015; Staley *et al.* 2015).

Escapees and introduction of invasive and/or harmful species

Macro-algal blooms (seaweed blooms) leading to oxygen depletion, alteration of ecosystem biodiversity and production of certain toxins (Anderson 2009) have been shown to originate from open water suspended culture systems. For example, significant escapes may occur from *Porphyra* culturing spanning more than 40 000 km^2 in some instances in the South China Sea. Bloom-forming species including sea lettuce (*Ulva* spp.) and gutweed (*Enteromorpha* spp.) can cause major economic loss by inundating waterways and beaches, leading to widespread asphyxiation of organisms when the blooms biodegrade (Liu & Su 2017).

Physical alteration of habitats and hydrodynamic regimes

Reduced hydrodynamic flows are known to lead to reduced turbulence, which in turn tends to promote the blooming of dinoflagellate species, including HAB species (Smayda & Reynolds 2001). Mariculture structures, including longlines for shellfish and kelp and net pens for finfish can significantly change surface current speed and direction, induce down-welling, increase stratification and reduce water exchange in sheltered and enclosed bays (Zeng *et al.* 2015; Lin *et al.* 2016; Wartenberg *et al.* 2017). Expansion of suspended mariculture in Sanggou Bay reduced the average speed of currents by 40% and the average half-life of water exchange was prolonged by ~70% (Shi & Wei 2009). It is also possible that disturbance of sediments by aquaculture and fishing operations may promote the resuspension of HAB cysts.

Transmission of HAB species and alteration in the abundance and composition of plankton communities

Risks of HAB impacts may increase directly with the future expansion of mariculture, via the movement (relaying) of 'contaminated' shellfish stocks and equipment between sites (Hégaret *et al.* 2008), including from the coast to offshore and *vice versa,* or via regular aquaculture operations and ballast water transfers (Hallegraeff & Bolch 1991, 1992). Indirect impacts include alteration of the abundance and composition of plankton communities, including HAB competitors, parasites and grazers (Roth *et al.* 2008; Eckford-Soper *et al.* 2016). Over-intensification of mariculture can also lead to depletion of planktonic larvae (including finfish, shellfish and other invertebrates) and reduced food availability for wild shellfish populations (Gibbs 2004; Ferreira *et al.* 2014; Pastres *et al.* 2018), especially in regions with low primary productivity (Gibbs 2004; Grant *et al.* 2007). This may have consequences for negative feedback control of the abundance and composition of plankton communities by native filter feeders.

Detecting and forecasting HAB events

Maximising the profitability and environmental sustainability of mariculture requires surveillance monitoring and early warning systems, forecast-based financing and strong risk governance structures (FAO, IFAD, UNICEF, WFP and WHO, 2018). The following systems are outlined in sections '*In situ* monitoring', 'Satellite remote sensing (Earth observation)' and 'Predictive modelling' below.

In situ monitoring

In situ monitoring for HAB species abundance and phycotoxin concentrations in (shell)fish is the principal method for 'official control' monitoring and safeguarding of food fish safety for human consumption in Europe, North America, Asia and Australasia. *In situ* monitoring is generally conducted via the collection and analysis of representative field samples; using microscopic analysis for phytoplankton identification and enumeration, and using mass spectrometric analysis for phycotoxin identification and quantitation. The use of autonomous *in situ* molecular (qPCR) and flow cytometry methods has also proved capable of real-time sensing of algal blooms (e.g. Campbell *et al.* 2013). These *in situ* devices can be located on smart buoys or underwater gliders (Davidson *et al.* 2014). Integrative solid-phase adsorption toxin tracking (SPATT) deployed in the field for the passive sampling of algal toxins has also been validated recently, and improved enzyme-linked immuno-sorbent assay (ELISA)-based methods with lower detection limits for more toxins have become commercially available for both screening and routine monitoring purposes (Zhang & Zhang 2015).

In Europe, routine HAB monitoring (EU Directives 2000/60/EC and 2006/113/EC) is used to quantify HAB species abundance and phytotoxin levels (Higman *et al.* 2014). Shellfish toxin concentrations are evaluated against EU action levels triggering harvesting bans (ASP > 20 mg Domoic/epi-Domoic acid; PSP > 800 µg STX equivalents (eq.); Lipophilic toxins (DSP) OA/DTXs/PTXs together > 160 µg OA eq.; AZAs > 160 µg AZA eq.; YTXs > 3.75 mg YTX eq. – see Table 2 and underlying text for expansion of abbreviations), allowing for cross-border trade of aquaculture products. While individual HABs and their toxins vary in concentration on a seasonal basis, HAB events can occur year-round, as can aquaculture harvesting. Responsibility for 'official control' resides with respective statutory authorities within EU member countries and results are published online for each designated site. *In situ* HAB monitoring data can be combined with satellite imagery (Section 'Satellite remote sensing (Earth observation)') and numerical models (Section 'Predictive modelling') to give a better indication of HAB risk, as implemented in Ireland (Leadbetter *et al.* 2018). In some cases, more proactive monitoring can occur, such as in Scotland where a group of finfish farmers collectively pay for weekly satellite remote sensing observations of *Karenia mikimotoi* surface distributions (Davidson *et al.* 2016).

In the United States, both the National Oceanic and Atmospheric Administration (NOAA) and the Environmental Protection Agency (EPA) monitor for, and provide some indication of, impending HABs. In the Gulf of Mexico, a twice-weekly risk assessment is provided during the summer-autumn HAB season, based on a regular *in situ* monitoring programme (and using meteorological models, particularly to provide warning of toxic aerosol events, e.g., caused by *Karenia brevis*). The rest of the US coastline is monitored routinely for HAB events by a volunteer network; the 'National Phytoplankton Monitoring Network', sampling twice monthly. In some locations in the United States, more intensive programmes are in place, such as the SoundToxins programme which is funded by NOAA and Washington Sea Grant and monitors 31 sites on a weekly basis in Puget Sound in Washington State, or the California Harmful Algal Bloom Monitoring and Alert Program (Cal-HABMAP) funded by US Congress and the National Aeronautics and Space Administration (NASA; Kudela *et al.* 2015).

Across Southeast Asia, some countries operate a regular programme of shellfish monitoring (e.g. Japan, Indonesia, Vietnam, Korea), while other countries lack the resources to have a robust programme or initiate sampling when blooms are detected (e.g. Laos, Myanmar; Eong & Sulit 2015). In Australasia, monitoring effort varies, with frequent sampling of high risk locations in western Australia (Dias *et al.* 2015), but overall being less well sampled and leading to high instances of human poisonings (Hallegraeff *et al.* 2017). In Chile and wider Latin America, after many intoxication events, a standardised sampling programme was developed across the region in 2009, although maintaining the network and regular sampling is dependent on continued resource availability (Cuellar-Martinez *et al.* 2018).

In scaling up from regional monitoring to a Global Ocean Observing System (GOOS) for HABs, it is recognised that there is no universal 'one-size-fits-all' solution, but that communication is key and stakeholders require affordable, easy to understand, real-time information, for example, in the form of spatial and temporal risk mapping (Anderson *et al.* 2019).

Satellite remote sensing (Earth observation)

The use of satellite remote sensing, alongside *in situ* sensing or ground truthing, has wide-scale potential for detecting increases in potential surface dwelling HAB species or high concentrations of all surface algae (reviewed by IOCCG, 2014; Davidson *et al.* 2016) in relation to fisheries and aquaculture/mariculture (IOCCG, 2009). Images of ocean colour from visible and infrared spectrum wavelengths can be correlated statistically with HABs events or in some cases the HAB species can be observed if they are spectrally distinct (https://www.shelleye.org/index; https://www.s3eurohab.eu/en/). For example, correlations have been found between ocean colour, chlorophyll and algal biomass (Sourisseau *et al.* 2016), with some correlations incorporating the use of artificial neural networks (El-Habashi *et al.* 2017). *K. mikimotoi* and *K. brevis* are both species that have spectral signatures that allow successful identification when they are present in large abundances (Kurekin *et al.* 2014; Shutler *et al.* 2015; El-Habashi *et al.* 2017). In general, HAB species that are detectable by remote sensing are those that form significant blooms of >1000 cells/mL at the sea surface or near-surface (e.g. *Karenia mikimotoi*, Kurekin *et al.* 2014; *Karenia brevis,* El-Habashi *et al.* 2017). Satellite imaging however cannot detect species that form harmful blooms at greater depths or at low densities of ~100 cells/L (e.g. *Dinophysis* spp.) (Reguera *et al.* 2014). Remote sensing techniques are also unable to detect HABs when observation of ocean colour is obscured by cloud cover (Maguire *et al.* 2016).

Predictive modelling

Early warning of the onset of HAB events over time scales of several days, and their likely movement and changing magnitude (i.e. relative to safe limits), would be highly beneficial to the mariculture industry, allowing proactive, rather than reactive, responses to minimise impacts on businesses, customer confidence or human health (Davidson *et al.* 2016). Immediate responses may include advanced (or delayed) harvesting of stock (limited by storage capacity and by supply chain logistics) or deployment of mitigation measures (Section 'Analysis of options for mitigating HAB risk to mariculture'). Longer-term, more strategic business planning is dependent on knowing when harvesting bans imposed by HAB outbreaks are likely to be lifted, in order to better manage business operations, staffing and supply chains. HAB predictions based on readily available physical (hydrographical and meteorological) data offer a simple, tractable solution for forewarning mariculture operators in locations where these physical 'forcing factors' are principle drivers of HAB initiation. These physical models are generally better at predicting HAB initiation than HAB termination, but in any event forecasting is generally limited to 1 week in advance (Davidson *et al.* 2009; Cusack *et al.* 2016; Schmidt *et al.* 2018), which corresponds with general extent and accuracy of meteorological forecasting (Davidson *et al.* 2016). Furthermore, the majority of models, which are driven predominantly by meteorological and hydrographical processes, often 'over-predict' HAB duration (Davidson *et al.* 2016). This is reassuring for human safety, but not so appealing for businesses desperate for harvesting bans to be lifted, as soon as it is safe to do so. Hydrophysical models coupled with HAB population models, which also incorporate biological and geochemical processes, can improve HAB predictions, by taking into account life-history data and environmental and physiological optima for HAB species (Roelke & Buyukates 2001; McGillicuddy *et al.* 2005; Glibert *et al.* 2014b; Aleynik *et al.* 2016; Gillibrand *et al.* 2016). Modelling changes in trophic mode (autotrophy versus mixotrophy) (Lee *et al.* 2016) and interactions with other plankters, including HAB parasites and grazers (Lenes *et al.* 2013) can also help to improve predictions of bloom duration. However, increasing trophic complexity in community and ecosystem models can lead to reduced resolution of species-specific dynamics, including HAB population dynamics (Flynn & McGillicuddy 2018). Other trade-offs in implementing more elaborate ecosystem models include greater specificity (spatial limitation) of model predictions and increasing requirements for input data for model parameterisation, computational processing power and expert operators (Butenschön *et al.* 2016).

Combining bio-physical modelling of HABs with satellite remote sensing data has been used successfully in short-term national forecasting systems for public health and aquaculture protection in the US and EU for example (Kudela *et al.* 2015; Shutler *et al.* 2015; Davidson *et al.* 2016; Ruiz-Villarreal *et al.* 2016) with the potential for wider detection of HABs (Anderson *et al.* 2019). There is also the potential to extend forecasting of HAB events from days to several weeks or even months in advance, by tracking successional changes in plankton community composition over time, in conjunction with traditional *in situ* monitoring and real-time sensing of impending blooms (Roelke & Buyukates 2001; Campbell *et al.* 2013). Inter-annual predictions of HAB trends and the identification of hotspots prone to recurring HAB events are also highly beneficial for strategic marine spatial planning, including for new or expanding mariculture infrastructure. These longer-term predictions are more circumspect, as the biogeographical niches of different HAB genera or species are likely to shift with a changing climate and/or become more variable (Callaway *et al.* 2012; Wells *et al.* 2015; GlobalHABs, 2017).

Analysis of options for mitigating HAB risk to mariculture

Options for mitigating HAB impacts to mariculture fall into three basic categories: (i) spatial and temporal planning of mariculture operations to avoid or minimise the risk of HABs; (ii) holistic environmental management options to minimise local HAB risk around mariculture farms (e.g. multi-species, multi-trophic, ecosystem-based options favouring nutrient assimilation and recycling and/or cultivation of species which are more resistant to, or less prone to accumulate, HAB toxins); (iii) direct interventions for controlling the presence or abundance of HAB species (physical, chemical, biological control options). The advantages of various options in each of these categories and their state of readiness for application in commercial mariculture are discussed below (Sections ‘Spatial and temporal planning to minimise HAB risk’, ‘Holistic environmental management options for minimising HAB impacts’ and ‘Direct interventions for controlling HAB impacts’).

Spatial and temporal planning to minimise HAB risk

Spatial planning for new mariculture infrastructure can be targeted to avoid HAB hotspots, while planning harvesting outside peak HAB risk periods can be implemented at already established/licensed mariculture farms, with both options being informed by existing HAB detection and forecasting systems (outlined in Section ‘Detecting and forecasting HAB events’). Development of offshore sites with significant exposure to tides, wind and wave action (Drumm 2010; Froehlich *et al.* 2017; Buck *et al.* 2018) can potentially mitigate HAB risks linked to mariculture itself e.g. elevation of nutrient levels, physical alteration of habitats and hydrodynamics and modification of local planktonic (and benthic) communities (Section ‘Environmental impacts of mariculture and contribution to HAB risk’). However, HABs often originate naturally offshore (independently from anthropogenic activities) (Whyte *et al.* 2014; Davidson *et al.* 2016; Díaz *et al.* 2016; Gobler *et al.* 2017) and there is some evidence that some HAB species may present even greater risk here compared to inshore areas (Trainer *et al.* 2012). Regulatory policy for sustainable offshore aquaculture has only recently been developed in the United States (NOAA, 2016) and is not yet formulated and published in other countries or continents, such as New Zealand, Australia and Europe (Froehlich *et al.* 2017). Emerging guidelines for assuring minimal impacts from offshore mariculture on water quality and pelagic and benthic communities relate to: minimum water depths (twice the depth of mariculture infrastructure) and minimum water flow rates (>0.05 m/s) (Belle & Nash 2008; Froehlich *et al.* 2017). In such localities, the probability of ecological effects on neighbouring natural habitats diminishes significantly beyond a distance of 90 m (Froehlich *et al.* 2017). This distance also provides a nominal guideline for the proximity/density of neighbouring offshore mariculture infrastructure. However, some ecosystem models predict significant trophic interactions between large offshore installations and more distant coastal mariculture sites, indicating wide-ranging implications for nutrient budgets and biosecurity (spread of microbial pathogens). These ecological interactions have been modelled and verified for the large (15 km^2) Ria Formosa Mariculture Park located >3 nm offshore from coastal sites in the Algarve region of Portugal (Ferreira *et al.* 2014). Ecological linkages between extensive mariculture installations and the periodic occurrence of HABs along the Algarve coast have yet to be established.

Holistic environmental management options for minimising HAB impacts

Holistic environmental management of HABs addressing causative factors (e.g. minimising nutrient inputs from land-based sources and from mariculture itself) or preserving habitats and ecosystem services that help regulate HABs, may be simpler, more effective and more environmentally friendly (WHO, 2003; Wells *et al.* 2019) than attempting to control HAB outbreaks directly (Section ‘Direct interventions for controlling HAB impacts’). For example, nutrient enrichment can be managed through the use of ‘extractive’ shellfish and macro-algal species. Furthermore, restoration of coastal habitats, for example with seagrasses that harbour algicidal bacteria (Inaba *et al.* 2019), or cultivation of seaweeds that secrete algicidal chemicals (Zerrifi *et al.* 2018), can also help mitigate against HABs. This follows Ecosystem Approaches to Fisheries and Aquaculture (EAF/EAA) (Soto & Aguilar-Manjárrez 2009; FAO, 2018), which cover three main aspects: (i) minimising environmental impacts and waste; (ii) sustaining wider ecosystem functions and services; and (iii) promoting human well-being and equity among marine stakeholders.

(i) Minimising environmental impacts and waste – Shellfish and macro-algal culturing can have a positive influence on the regulation of HABs, either by reduction of high biomass blooms through filter feeding or via nutrient removal (Stadmark & Conley 2011; Petersen *et al.* 2014). Nutrient removal by mariculture, curbing eutrophication, in EU coastal waters alone is valued at US$20 to 30 billion per year (Ferreira *et al.* 2009). Furthermore, mariculture reduces the exploitation of natural shellfish stocks, which can also help regulate HABs. For example, overfishing of shellfish around Long Island, USA, has coincided with the increased occurrence of *Aerococcus anophagefferens* brown tides (Glibert *et al.* 2005).

(ii) Sustaining wider ecosystem functions and services – Mariculture farms can provide sheltered nursery habitats for marine/estuarine organisms, with the potential to enhance local fisheries and to support biodiversity in neighbouring marine protected areas (Le Gouvello *et al.* 2017). Maintaining biodiversity is important, since impoverishment of planktonic species and reduced species succession have been correlated with increased HAB risk. In some cases, such community changes can forewarn HAB outbreaks several months before the detection of the HAB species (e.g. *Microsystis* sp.; Roelke & Buyukates 2001).

(iii) Promoting human well-being and equity among marine stakeholders – Marine spatial planning is required to effectively locate mariculture and fisheries conservation areas and avoid conflicts with other uses of the marine environment. To facilitate planning, environmental models can be used to assess nutrient budgets, productivity versus eutrophication risk, the risk of transmission of pathogens, pests associated with mariculture (Ferreira *et al.* 2014; Pastres *et al.* 2018) and the risk of advection of HABs to mariculture sites (Dabrowski *et al.* 2016; Paterson *et al.* 2017).

A promising approach for delivering on each of these EAA/EAF aspects, including the potential to minimise HAB risk, is integrated multi-trophic aquaculture (IMTA) (Wartenberg *et al.* 2017). IMTA employs cultureable 'extractive' species (e.g. suspended bivalve shellfish and macroalgae, and benthic deposit feeders) to remove/reuse waste nutrient material discarded from the culturing of 'fed' species (finfish and crustaceans) thereby providing a self-sustaining and more productive food web (Figure 2) (Soto 2009; Troell *et al.* 2009; Chopin *et al.* 2012). Macroalgae can also play a direct role in inhibiting the growth of microalgae, including HAB species, through competition for nutrients (Soto 2009; Holdt & Edwards 2014), inhibitory allelopathy (Tang & Gobler 2011; Ben Gharbia *et al.* 2017; Zerrifi *et al.* 2018), and/or by reducing light penetration (Zhou *et al.* 2006; Wang *et al.* 2007; Yang *et al.* 2015).

Further developments in IMTA, including deploying aquaculture species that are less sensitive to, or less likely to accumulate, toxins from locally re-occurring HAB species, are likely to be required to maximise benefits in terms of mitigating against HAB impacts. The long-term sustainability of IMTA for mitigating HAB risk with climate change also requires further research (Wells *et al.* 2019). For example, China has some of the world's largest and longest established IMTA systems, including a multi-trophic system established in 1996 in Sanggou Bay, Yellow Sea (Fang *et al.* 2016). Since 2010, however, Sangou Bay has regularly experienced brown tides of *A. anophagefferens* (Kong *et al.* 2012). Coincidentally, large-scale *A. anophagefferens* brown tides extending over 3000 km^2 have occurred in the north western Bohai Sea each year in early summer since 2009 and have caused significant negative impacts on scallop (*Argopecten irradians*) culture (Zhang *et al.* 2012). Other HAB species including *Karenia mikimotoi* and *Prorocentrum donghaiense* also continue to form annual blooms in nearshore waters of the Yellow Sea and neighbouring East China Sea (Li *et al.* 2009), with *K. mikimotoi* causing substantial losses to mariculture from 2005 to 2015 (Liu & Su 2017).

Direct interventions for controlling HAB impacts

Physical and chemical control methods can remove HABs efficiently and are used operationally as a last resort in mariculture, but they can be costly, lack specificity to HABs, and are generally less effective in coastal situations in comparison with enclosed or semi-enclosed aquatic systems. Alternatively, biological control methods can be potentially more specific for individual HAB species, minimising impact on other non-target species, but they are more difficult to constrain in non-enclosed systems and have not progressed beyond laboratory or field trials for mariculture applications (reviewed in NOAA, 2015; Sellner & Rensel 2018; Sun *et al.* 2018; Gallardo-Rodríguez *et al.* 2019).

Physical control methods include the use of barriers or skirts, for example, around fish net pens and/or the removal of HAB cells by water column mixing, filtering, flocculation, settlement, sediment burial and dredging, or HAB cell lysis using ultrasound (Sellner & Rensel 2018). Water column mixing using water or air pumping systems leads to disruption of thermal stratification and impairment of algal buoyancy or alteration of their daily

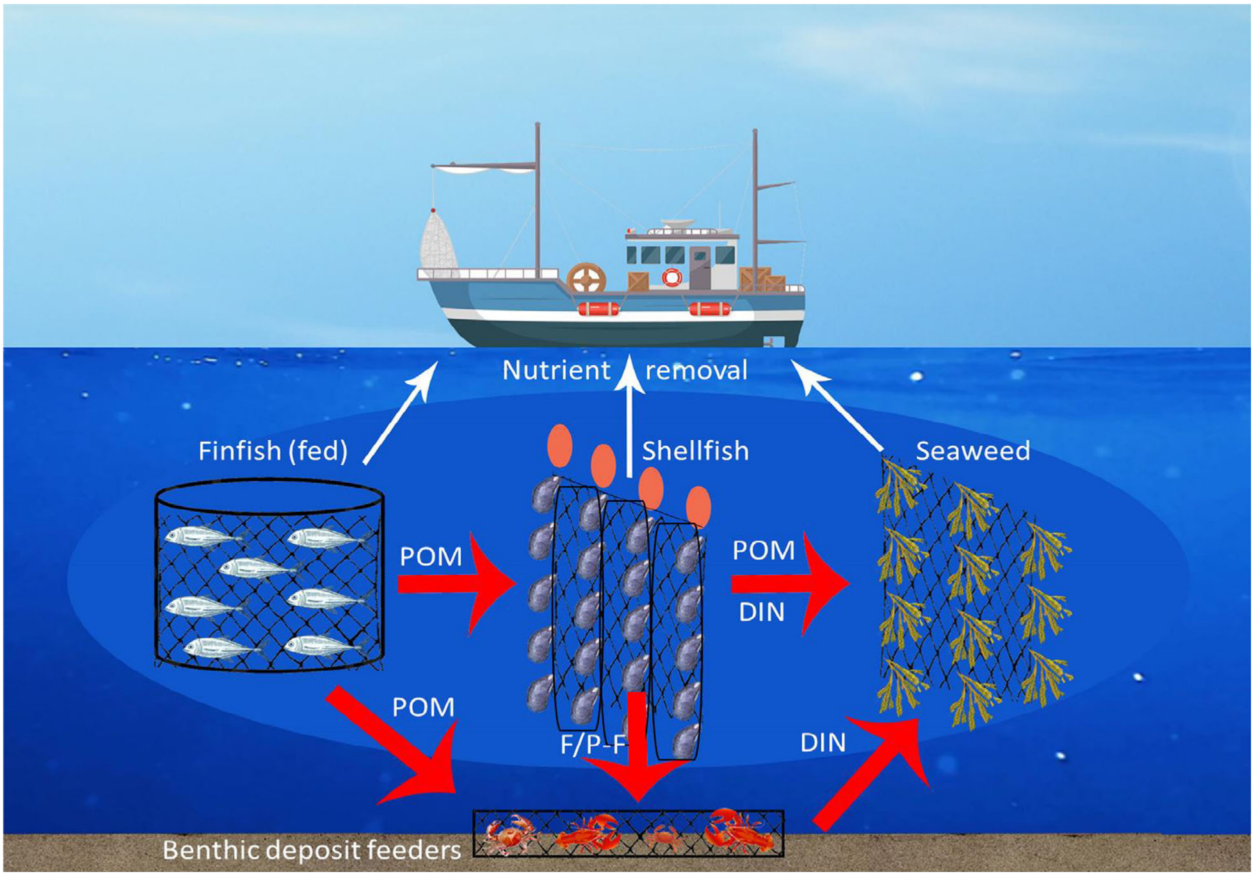

Figure 2 Integrated multi-trophic aquaculture (IMTA). POM – particulate organic matter; DIN – dissolved inorganic nitrogen; F/P-F – faeces/pseudo-faeces. IMTA incorporating suspended filter-feeding shellfish, and benthic deposit feeding shellfish can reduce the proliferation of HABs and recycle POM (capable of fuelling HAB growth) associated with 'fed' species (finfish and crustaceans). Suspended macroalgae can also reduce the growth of microalgae, including HAB species, through shading, competition for nutrients (e.g. fine POM and DIN) and inhibitory allelopathy.

migration patterns, removing them from the photic zone and preventing photosynthesis. Direct cell removal from the water column can be achieved by hydrodynamic separation, centrifugation, pump filtration, plankton net trawling or membrane filtration. A measure which has proven effective for HAB control in the open sea has been the use of clays to induce bloom flocculation. As considerable quantities of clay are needed, from 100 to 400 g/m^2 (Park *et al.* 2013), physical resuspension of local sediments or importation on ships are a practical solutions. Subsequent flocculation, sinking and burial of HAB cells and/or cysts can be followed by dredging and physical or chemical treatment before discharging the sediments back to the removal site (NOAA, 2015; Sellner & Rensel 2018). Potential drawbacks include the removal of non-harmful algae. More efficient flocculation can be achieved by spraying the sea surface with modified clays containing inorganic (e.g. aluminium sulphate or polyaluminium chloride) or organic (e.g. polyacrylamide or chitosan) modifiers, which can be up to 100 times more efficient in adsorbing HAB cells (and other plankters) than natural clay sediments. This enables a reduction in application levels and time windows – reducing the risk of clay build-up and helping to reduce impacts on non-blooming (non-HAB) species (reviewed in Gallardo-Rodríguez *et al.* 2019). Furthermore, modified clays have been shown to kill HAB cells (Beaulieu *et al.* 2003), adsorb and remove extracellular HAB toxins (Pierce *et al.* 2004; Seger *et al.* 2015, 2017) and particulate nutrients (Yu *et al.* 2017), and to also reduce HAB toxin accumulation in benthic filter-feeding bivalves (Yu *et al.* 2017). Consequently, they have been used in Japan (Shirota 1989) and employed as a standard method for controlling HABs in China, since 2014 (Yu *et al.* 2017). A remaining concern, preventing uptake of these physical control methods in other countries, is their lack of specificity for controlling harmful species and possible unknown impacts on other phytoplankton and the ecosystem as a whole.

More direct chemical treatments for controlling HABs include the use of natural biosurfactants, biocides or allelochemicals (e.g. biochemical extracts from macroalgae), or the use of synthetic chemicals, including hydrogen peroxide and isolated algicidal compounds, or metallic compounds such as copper sulphate. These various chemicals (metals and organic compounds) can interfere with HAB cell survival (algicidal chemicals), growth and reproduction (algistatic chemicals) through a variety of mechanisms (NOAA, 2015; Gallardo-Rodríguez *et al.* 2019). Biochemicals are advantageous in terms of their higher diversity, biodegradability and, in some cases, specificity and potentially lower toxicity to the wider environment (Ahn *et al.* 2003). Although many effective aqueous algicidal treatments exist, few are approved for use in open marine systems, due to environmental concerns, although some have restricted use in antifouling paints and surface treatments (NOAA, 2015; Gallardo-Rodríguez *et al.* 2019). Several biocidal chemicals have been tested and approved for use in mariculture, for controlling shellfish and finfish pathogens or parasites (Johnston & Santillo 2002; Read & Fernandes 2003) and some of these may be effective in killing some HAB species.

Biological control measures include the application of microbial (viral, bacterial, fungal and/or protistan) parasites that infect HABs and play a significant role in the natural termination of major blooms (Brussaard 2004; Chambouvet *et al.* 2008; Roth *et al.* 2008; Jones *et al.* 2011; Demuez *et al.* 2015; Pokrzywinskia *et al.* 2017). Algicidal and growth inhibitory bacteria and viruses have potential for controlling HABs, due to their ability to replicate rapidly and target-specific hosts (Bibak & Hosseini 2013; Sun *et al.* 2018). However, it is possible for these parasites to be too specific, rendering them unable to infect different genetic strains of HAB species, or adapt to changing environmental conditions (Sun *et al.* 2018; Gallardo-Rodríguez *et al.* 2019). Therefore, rather than using single cultured microbial species, employing a range of microbes may be more effective. Aggregates (biofilms) immobilised on substrates may be more effective in reducing HAB cell density by inhibiting HAB cell growth via nutrient uptake and allelochemical secretion, and causing cell lysis (Alex *et al.* 2014; Sun *et al.* 2018). Research is needed to quantify the release of toxins following HAB cell lysis and the potential for microbes to degrade them. Further research is also needed to isolate, purify and identify microbial allelochemicals/exudates and to demonstrate their efficacy for controlling different HAB species and genetic strains, while incurring minimal effects on non-harmful algae and other marine organisms, including cultured shellfish and finfish species (NOAA, 2015, Sun *et al.* 2018). Other potential biological interventions include selective breeding of shellfish with resistance to HAB toxins and using them as HAB biofilters and bioremediators (NOAA, 2015). Unquantified biosecurity risks for biological control measures currently prevent their operational use in controlling HABs at mariculture sites.

Conclusions and recommendations

Marine aquaculture (mariculture) is playing an increasingly important role in global food security. One of the most significant risks to mariculture expansion, both inshore and offshore, is the occurrence of Harmful Algal Blooms (HABs).

Global impacts from HABs on mariculture (due to finfish or shellfish mortality, poisoning of human consumers and preventative harvesting bans) currently amount to something in the region of 8 US$ billion/year; however, HAB risk assessment is not a standard requirement in the planning and classification of mariculture sites. This is, in part, because HABs are natural phenomena, and because risk factors are diverse, varying greatly both spatially and temporally. For example, HABs may originate offshore, far from anthropogenic activities, and can be advected over large distances to other areas conducive for HAB development. Further research is required to guide and enable pre-emptive measures for mitigating HAB risks, including the strategic siting of mariculture infrastructure and scheduling of harvests.

Adaptive management of HAB risk, involving the prediction of HAB events and the tactical use of appropriate and approved physical, chemical and/or biological control measures, is needed as part of the sustainable development of mariculture. However, successful application requires improved understanding on the efficacy and biosafety/specificity of the available options. There is a need also for improved understanding on the interactions among physical forcing factors (meteorological and oceanographical), and chemical (nutrient) and biological (community) factors, in order to predict where and when blooms are most likely to occur. In support of this, research should exploit the widespread occurrence of HABs, which provides opportunities for comparative assessments of HAB drivers around the world, including the extent to which HAB species, their population dynamics, and community interactions show similarities in responses within comparable ecosystem types. There is considerable scope to capitalise on advances in automation and (bio)sensor (DNA, RNA, protein and metabolite)-based technologies, with applications in: real-time, *in situ* monitoring of HAB population dynamics; defining physiological processes and underlying regulatory gene networks linked to growth and/or toxin production in HAB species; and building robust, mechanistic models for predicting HAB events.

Harmful algal bloom risks are generally perceived to be higher at coastal sites, which experience nutrient enrichment from agricultural runoff and municipal effluent discharges. Winds and tides can also transport and accumulate HABs into coastal areas, including sheltered embayments, where less turbulent and warmer waters are conducive for the growth of various HAB species. In these and other areas with low water exchange rates, mariculture itself can have a significant influence on HAB risk by affecting local water quality (e.g. nutrient eutrophication levels), hydrodynamics (artificial structures reducing water circulation) and plankton communities (e.g. through selective filter feeding by shellfish). More studies are required to quantify HAB risks against each of the above factors and their interactions and the degree to which they are influenced by different types of mariculture.

Harmful algal bloom risks associated with nutrient enrichment and eutrophication (from terrestrial sources and mariculture itself) may be mitigated by establishing mariculture sites offshore, away from the coast and/or in areas with high horizontal water exchange rates and vertical mixing. Greater understanding is required on how hydrodynamic conditions (e.g. influenced by wind, waves, tides) and bathymetry (water depth) influence dispersal versus local deposition and resuspension of nutrients and HAB propagules/cysts.

Further capacity for HAB mitigation is offered by integrated multi-trophic aquaculture (IMTA), which employs extractive bivalve shellfish and macroalgae alongside fed finfish and crustaceans, in order to recycle nutrients, thus maximising productivity and water quality simultaneously. Macroalgae (in addition to filter-feeding shellfish) can also have a direct influence on local plankton community composition and abundance – via nutrient competition, light shading and allelochemical mechanisms. Further research is required to understand how IMTA systems could be further optimised for the additional purpose of HAB attenuation, through selection of suitable, resilient finfish, shellfish and macroalgal species, and appropriate spatial deployment and stocking densities.

A key remaining question for mariculture, both inshore and offshore, is 'How will HAB risk transpire in a future warmer climate, typified by increased sea surface temperatures and water column stratification, or alternatively in a future characterised by increased atmospheric energy and more turbulent waters?' Climate change is also likely to be accompanied by HAB range extensions towards the poles. To address these issues, collaborative effort is needed that seeks to unify research themes on 'HABs, climate change and aquaculture/mariculture', as exemplified by GlobalHAB, an international programme sponsored jointly by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO.

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