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Crustaceans, One Health and the changing ocean

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ABSTRACT

Crustaceans permeate every habitat on Earth but are especially impactful in the marine environment. They can be small and extremely abundant like the ubiquitous marine copepods found throughout the world's oceans, or large and highly prized by fishermen like spiny lobsters found in tropical and temperate seas, globally. The latter are among the decapod crustaceans, a group which includes crabs, shrimps, and lobsters - those targeted most commonly by fishery and aquaculture industries. Hence, crustaceans are ecologically important, but they are also directly linked to the economic and nutritional health of human populations. To most effectively manage and conserve crustacean populations in the face of a changing ocean environment, whether they are harvested or not, requires a One Health approach that underscores the linkages between crustacean, human, and environmental health. Here, we give an overview of the need, benefits, and challenges to taking the One Health approach to crustacean health and argue that when viewed through the One Health lens, there is perhaps no other group of marine animals more worthy of that perspective.

1. Introduction

Crustaceans are abundant, economically valuable, ecologically valuable, and important nutritionally (Bondad-Reantaso et al., 2012; FAO, 2020b). They are fished and farmed around the globe so their health is often linked to human health, and together they are linked to the health of the environment (Fig. 1). These connections are multi-directional with each affecting the health of the others. This interconnectedness of human health, animal health, and environmental health is known as the One Health triad. But woven through these connections are the threads of change, exploitation, and disease. In the following sections, we will demonstrate that crustaceans are model organisms for taking a One Health perspective; however, the angle of that perspective requires adjustment for the unique nature of the sea.

This article is part of a special issue of the Journal of Invertebrate Pathology entitled 'Invertebrates as One Health Sentinels', so we will use a common definition for One Health: *The collaborative effort of multiple health science professions, together with their related disciplines and institutions – working locally, nationally, and globally – to attain optimal health for people, animals, wildlife, plants, and the environment they interact with.*

1.1. *Why must we consider One Health in the sea differently?*

The sea is physically different than the terrestrial environment (Behringer et al., 2018), so marine organisms of *all types* have developed different adaptations that enable them to live there. In turn, these adaptations to life in the sea require different considerations for how marine organisms fit into the concept of One Health. For example, because seawater is far denser and more viscous than air it more readily supports the suspension of particles and organisms (Behringer et al., 2018). This is why connectivity of host and parasite populations are so much greater in the sea (McCallum et al., 2003) and why many more marine parasites have mobile infectious stages (McCallum et al., 2004). For example, populations of the Caribbean spiny lobster *Panulirus argus* are connected across the Caribbean Sea by their long-lived planktonic larvae (Butler et al., 2011), but are also connected by their waterborne parasite Panulirus argus Virus 1 (PaV1), the first member of the Mininucleoviridae (Subramaniam et al., 2020; Kough et al., 2015). Suspension and filter feeding strategies are much more common among organisms in the sea compared to the air, which may bring these organisms into contact with infectious propagules more frequently than their terrestrial counterparts. Some of these infectious propagules may not be infectious to the organisms that ingest them, but due to the nature of filter feeding they may become concentrated in that organism. This

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organism, with its concentrated load of infectious material, may then be ingested by an organism that is susceptible to infection such as a crab, a fish, or a human. The bacterium *Vibrio vulnificus* is one of the deadliest examples of this phenomenon for humans. It is found associated with a vast array of estuarine organisms, including planktonic copepods (Heidelberg et al., 2002), but molluscan shellfish are known to accumulate it through filter feeding and when subsequently consumed (raw) account for 95% of all seafood-related deaths in the US (Oliver, 2015).

1.2. *How does One Health pertain to crustaceans?*

The Crustacea (Arthropoda) are an extremely diverse group of ecologically important organisms inhabiting saltwater, freshwater, brackish, and terrestrial environments (Martin and Davis, 2001). Although often small, crustaceans can be hyper-abundant, dominating the biomass of an ecosystem. For example, planktonic copepods are considered one of the most abundant metazoans on Earth and Antarctic krill (*Euphausia superba*) in the Southern Ocean alone have an estimated biomass of 379 million tons (Atkinson et al., 2009). Although some miscellaneous crustaceans are harvested or cultured, the overwhelming majority of fished or cultured crustaceans are from the order Decapoda, which includes crabs, lobsters, and shrimps (FAO, 2020a).

While crustaceans can be found in terrestrial (e.g., isopods) and freshwater environments (e.g., crayfishes), and serve important ecological functions in those environments, here we will focus on crustaceans and One Health in the sea. We also consider crustacean health in the One Health sense as inclusive of natural and cultured crustacean populations (Fig. 2). Natural populations include exploited and non-exploited populations, whilst cultured populations include those farmed in the sea and those farmed in land-based aquaculture systems (Fig. 2). We also consider crustacean health as inclusive of not only disease caused by infectious agents but anything that impacts the condition of an organism, such as the effects of toxins (e.g., industrial or algal toxins), environmental changes (e.g., ocean warming or acidification), invasive species (e.g., increased competition or parasite exposure), or anthropogenic impacts (e.g., habitat degradation or fishing).

The One Health concept is particularly appropriate to apply to marine crustaceans because of their importance to human health and nutrition in many regions of the globe (Bondad-Reantaso et al., 2012) but also because of their importance to the marine ecosystems and communities in which they reside – whether they directly support fishery or aquaculture industries or not (Behringer et al., 2020). This is the One Health perspective at its core, so viewing the conservation and management of crustaceans through this lens is critically important.

Marine crustacean fisheries produced nearly 6 million tons of crustacean product and aquaculture contributed another 5.7 million tons in 2018 (FAO, 2020b). This corresponds to a significant source of dietary protein for coastal communities and the communities to which they sell their products. However, the health benefits to humans from fisheries and aquaculture extend beyond nutrition to include the livelihoods of people around the globe. An estimated 60 million people were engaged in the primary sectors of fishing (39 million) and aquaculture (21 million) in 2018 (FAO, 2020b), and that does not include the many ancillary industries engaged indirectly such as boat manufacturers or global shipping companies. The millions of tons of crustaceans harvested annually through fishery and aquaculture production is significant source of income for coastal communities (FAO, 2020b), which in turn supports economic and human health (Bondad-Reantaso et al., 2012; Woodhead et al., 2018). The health and sustainability of the crustacean fishery and aquaculture industries is therefore intimately linked in many places to the health of the human population.

2. Fisheries and aquaculture affect crustacean health

Fisheries can affect the health of wild crustacean populations both directly and indirectly (Behringer et al., 2020). The clearest effect of fishing on the health of crustacean populations comes from overfishing which directly affects the sustainability and ecological function of the target population (Armstrong et al., 1998). Fishing can also directly affect non-target members of the population (e.g., juveniles or gravid females) during capture or trap confinement, including physiological stress, starvation, increased disease transmission, and mortality. For example, Caribbean spiny lobsters suffer depressed nutritional condition, increased infection with PaV1, and mortality when caught in traps and confined during long trap soak periods of several weeks (Behringer et al., 2012; Butler et al., 2018a; Matthews, 2001), or when traps are lost by the fishermen but continue to attract and confine lobsters as 'ghost traps' (Butler et al., 2018b). Similarly, juvenile New Zealand rock

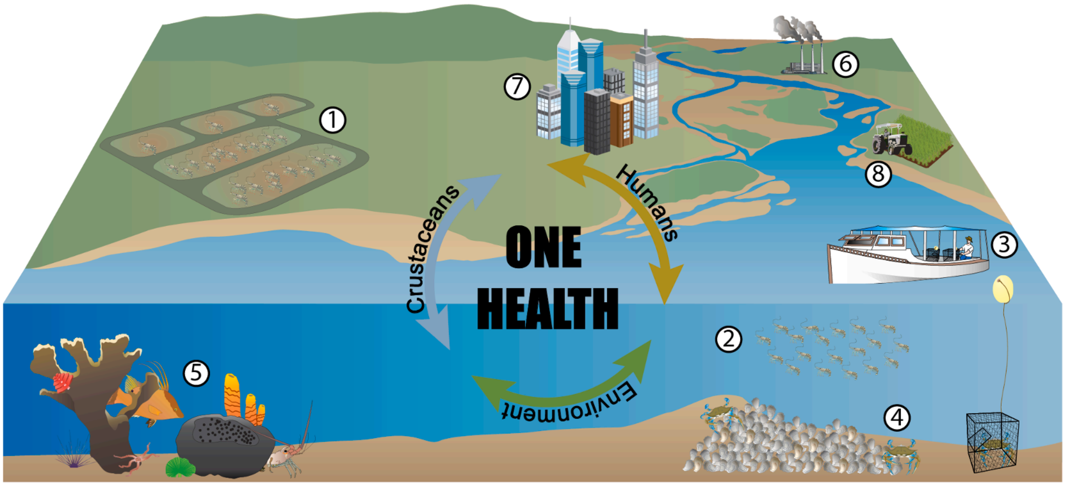

Fig. 1. Crustaceans, whether farmed, fished, or as members of natural ecological communities are part of an interconnected One Health triad, along with humans and the environment. The health of each component is dependent on the health of the others. Examples of this interdependence include: Crustacean aquaculture (1), particularly shrimp, is fundamental to human food security, but biosecurity must be improved to prevent and limit the spread of disease among aquaculture operations and to wild populations of crustaceans (2). These wild populations of crustaceans support fisheries (3), which can impact population size and biology of important ecosystem predators (4) and competitors (5). Aquaculture and wild catch of crustaceans provides a growing protein source for humans worldwide, but burning of fossil fuels (6) is causing ocean warming and acidification, coastal development (7) is leading to major habitat loss, and pollution from agriculture (8) is increasing coastal eutrophication, with resulting increases in harmful algal blooms and hypoxic zones. Vector art from the IAN image library (ian.umces.edu/imagelibrary/).

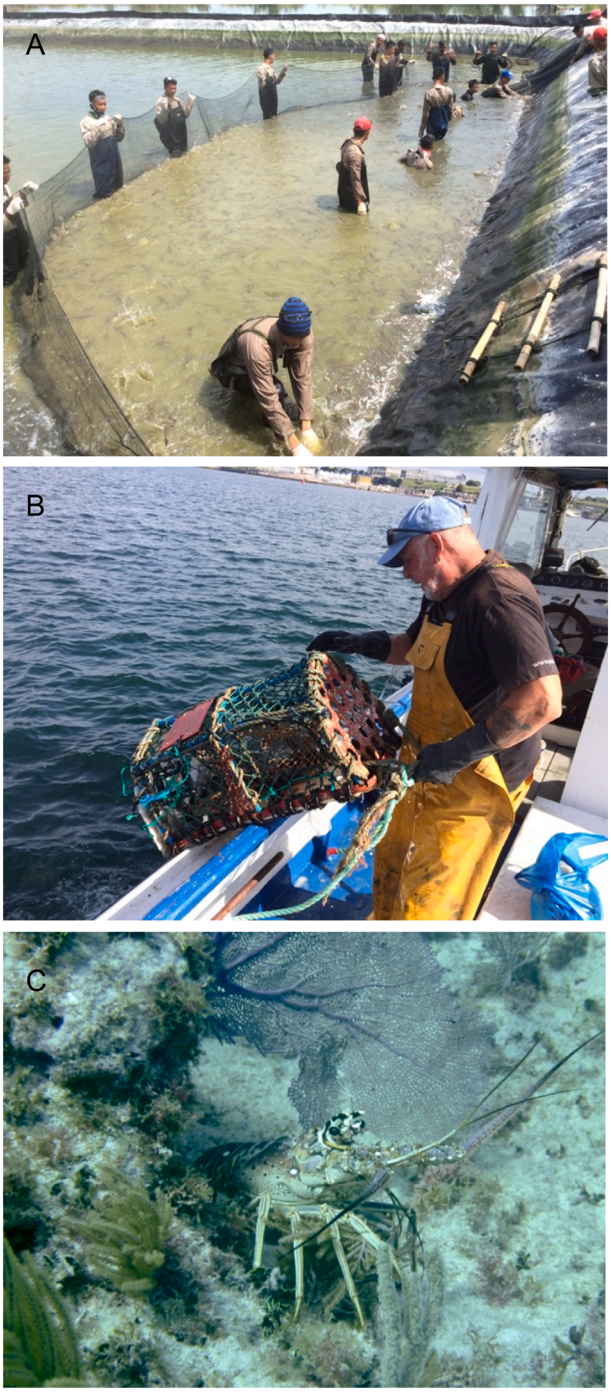

Fig. 2. Wild fisheries, aquaculture, and natural marine communities all intersect with human and environmental health. (A) Workers at a farm in Indonesia harvesting white-leg shrimp *Penaeus vannemei* from an aquaculture pond (Photo credit: Grant Stentiford), (B) fisherman in Plymouth, UK, pulling a trap for the European brown crab *Cancer pagurus* (Photo credit: D. Behringer), and (C) Caribbean spiny lobster *Panulirus argus* on a coral reef in the Florida Keys, USA (Photo credit: D. Behringer).

lobsters *Jasus edwardsii* suffer high incidence of tail-fan necrosis due to trap confinement (Freeman and MacDiarmid, 2009), and Dungeness crabs in the northeast Pacific and blue crabs in northern Gulf of Mexico suffer high mortality within derelict 'ghost traps' (Anderson and Alford, 2014; Antonelis et al., 2011). Whilst direct impacts like these from fishing are common, indirect effects are not always obvious and not always negative.

Fishing removes animals from a population and that removal has consequences for those that remain. The effects of fishing on parasite prevalence and diversity are complex, context-dependent, and more thoroughly reviewed elsewhere (Behringer et al., 2020), but here we highlight some examples of how fishing can affect the health of the fished populations. These examples transcend target organism but could be applicable to any fishery, including crustaceans. Host density often tops the list of attributes that drive disease transmission. If a disease is plaguing the population, a reduction in host density from fishing could theoretically break a density-dependent transmission threshold and reduce the impact of a parasite. However, this relationship is not always clear nor constant (Lloyd-Smith et al., 2005), and assumes there are no social behaviors (e.g., gregariousness) that would maintain density and contact rates despite the decrease in host density (frequency-dependent transmission) (McCallum et al., 2001). The portion of the population targeted (e.g., large or small, male or female, juvenile or adult) can also affect disease dynamics among those that remain. Many fisheries target the largest individuals, which have often accumulated the heaviest parasite burdens, so removing those individuals could reduce the prevalence of parasites in the population (Wood and Lafferty, 2015). Conversely, if a disease targets the juvenile segment of a population then fishing for adults could increase the prevalence of infection and the proportion of the remaining population most susceptible to infection (Behringer, 2012). The biology of the parasites themselves can also determine the effect of fishing. Directly transmitted parasites have been shown to increase in prevalence under fishing pressure whilst parasites with life-cycles requiring multiple hosts decline (Wood et al., 2014; Wood et al., 2018). These examples demonstrate how fishing can directly affect the health of crustacean populations but there are also potential indirect effects that cascade down through communities (Behringer et al., 2020), and these may not all be bad for the crustacean population. For example, the overfishing and collapse of the cod *Gadus morhua* fishery in the northwest Atlantic (Myers et al., 1997) led to an increase in the American lobster *Homarus americanus* fishery in Maine (USA) and Atlantic Canada (Boudreau and Worm, 2010).

The relationships in a One Health triad are typically bi-directional, and that holds here where crustacean health also affects the health of fisheries. Healthy crustacean populations are a boon for fisheries but if environmental stress and disease are introduced, fisheries can decline due to decreases in growth and fecundity, increased mortality, or decreased marketability. This is exemplified in the American lobster fishery in southern New England devastated by Epizootic Shell Disease (ESD), an environmental and physiological 'dysbiosis' (Shields, 2013). ESD results in all of these impacts, including females that drop clutches to rid themselves of an infected carapace, lobsters that die due to a lack of carapace integrity or molting difficulties, and a repulsive appearance that renders them unmarketable (Barris et al., 2018; Hoenig et al., 2017).

The relationship between aquaculture and crustacean health tends to be less complex than wild fisheries but arguably more impactful (Stentiford et al., 2020). Aquaculture concentrates organisms at unnatural densities and has historically moved brood stock, larvae, and product (live and frozen) around the world. These practices have resulted in the emergence and proliferation of diseases in crustacean aquaculture (Stentiford and Lightner, 2011), particularly among penaeid shrimp where losses are estimated at over 40% of global capacity (Stentiford et al., 2017). Parasites of crustaceans have also been introduced in wild populations via numerous routes, including escape from culture systems, carcass disposal, and use as fishing bait (i.e., shrimp; Bateman et al., 2012; Durand et al., 2000). The management of crustacean health within aquaculture falls under the purview of the World Organization for Animal Health (OIE), which is recognized by the World Trade Organization. The guidelines and regulations outlined by the OIE have curtailed some of the practices that have led to disease outbreaks but not all parasites of concern are considered by OIE; existing parasites such as WSSV and *Enterocytozoon hepatopenaei* continue to drive losses, and new ones emerge. Crustacean aquaculture is an increasingly essential sector of global aquaculture production and will be a driver of human and environmental health outcomes going forward (Stentiford et al., 2012; Stentiford et al., 2020). Revising and integrating crustacean fishery and aquaculture policies and practices under a One Health banner has the potential to alleviate poverty, increase human nutritional conditions, improve the health and sustainability of wild fisheries, and reduce environmental impacts (Stentiford et al., 2020).

3. Environmental change affects crustacean health

3.1. Ocean acidification

The increase in CO_2 in the Earth's atmosphere that is associated with the burning of fossil fuels and other anthropogenic causes of climate change are buffered by chemical reactions in the oceans. The ocean absorbs ~25% of this CO_2 (IPCC, 2019), resulting in a decrease in pH and reduction in the availability of calcium carbonate to marine organisms, including crustaceans, that use it to build their exoskeletons. This process is called ocean acidification (OA), i.e. "the other CO_2 problem" (Turley and Blackford, 2005). This change in ocean chemistry can increase stress on hosts and parasites alike, which could increase susceptibility of hosts and change the abundance of parasites (increase or decrease, depending on the system).

Crustaceans are able to compensate for short-term increases in CO_2 in their environment (i.e. ocean hypercapnia (McNeil and Sasse, 2016)) using existing acid-base, ion-, and osmo-regulating capabilities. Osmoregulators and species with higher metabolic activity may be better able to compensate because they have higher buffering capacities (Whiteley, 2011). Crustaceans also may be more resistant to effects of decreased calcium carbonate in the ocean, such as skeletal dissolution and decreased calcification efficiency in pteropods, corals, and echinoderms (Orr et al., 2005), because they use the more stable form of $CaCO_3$ calcite (Boßelmann et al., 2007), rather than the more soluble aragonite used by the aforementioned groups. Resistance is also conferred by the separation of hypercapnic ocean water from the internal calcification process (Cameron, 1985). However, even for species that are able to compensate, indirect effects on adults of reduced growth (Kurihara, 2008; Wickins, 1984), decreased fecundity (Kurihara et al., 2004a; Kurihara et al., 2004b), and increased oxygen consumption and mortality (Long et al., 2019); and on larvae of reduced hatching (Findlay et al., 2009; Kurihara, 2008; Mayor et al., 2007), increased mortality (Kurihara et al., 2004a; Kurihara et al., 2004b), and altered geotaxis (Gravinese et al., 2019a) are common even with short-term exposure because of the metabolic demand of these physiological processes. These issues may be compounded if acidification reduces chemosensory abilities, affecting foraging and behavioral avoidance of infected conspecifics (Ross and Behringer, 2019).

The crustacean exoskeleton is the first line of defense against predators and parasites alike. During the growth and molting process, any delay in exoskeleton hardening leaves the animal vulnerable. Time to harden for *Callinectes sapidus* doubled (from 14 to 28 days) under hypercapnic conditions (Cameron, 1985). Decreased calcification efficiency can also lead to molting difficulties and, in turn, an increased prevalence of ESD in *H. americanus* (McLean et al., 2018) and other large, long-lived crustaceans. Importantly, there are crustacean parasites that may experience similar negative effects of OA as well, notably the copepod "fish lice" of Salmonids (Costello, 2009).

Crustaceans may be more resilient to calcium carbonate dissolution than other calcifying marine organisms due to their use of calcite rather than the more soluble aragonite, ability to control intracellular pH, and exoskeleton production buffered from direct contact with acidified waters (Kroeker et al., 2010). Some studies have shown increases in calcification rates in crustaceans after temporary exposure to elevated partial pressure of carbon dioxide, pCO_2, (Whiteley, 2011), while others have produced mixed results, such as increased calcification of barnacle basal plates at low pH, but concurrent dissolution of wall plates (McDonald et al., 2009).

3.2. Ocean warming

Increased CO_2 warms the atmosphere through the greenhouse effect but also has a warming effect on the ocean. Due to the higher heat capacity of water, the ocean acts as a buffer against some atmospheric warming, taking up more than 90% of the heat in some systems, but it has undoubtably warmed over the last half century and is expected to continue warming (IPCC, 2019). Measurements indicate the sea surface has warmed at a rate of 0.13 °C per decade over the last century (EPA, 2016). Warmer waters will increase metabolic activity of most marine hosts and parasites, which could result in more interactions between them, i.e. more exposure, which increases the likelihood of infection (Anderson and May, 1978). Increase in temperature and metabolic activity is frequently associated with disease emergence and epizootics, such as infection with the parasitic dinoflagellate *Hematodinium* spp. in a wide variety of crustaceans (Messick, 1994; Stentiford and Shields, 2005) and outbreaks of the ciliate causing black gill disease in the penaeid shrimp *Litopenaeus setiferus* and *Farfantopenaeus aztecus* (Frischer et al., 2018). A warming globe will result in longer summers that will likely result in longer periods of disease proliferation and warmer winters in many locations will eliminate seasonal escape from disease, allowing year-round proliferation (Lafferty et al., 2004).

Ocean warming is also altering the range distribution of many marine organisms, which are experiencing poleward range shifts at a higher rate than terrestrial species (Pinsky et al., 2013; Lenoir et al., 2020). When host range expands, parasites can expand with them, gaining access to new populations and even new host species (Burge and Hershberger, 2020). Parasite range within its host can also expand with warming waters, as ESD in *H. americanus* has expanded from southern New England into the Gulf of Maine (Wahle et al., 2009).

Warming increases metabolism, oxygen consumption, and molting in crustaceans (Le Moullac and Haffner, 2000), even when food consumption is not increased (Long et al., 2019). This discrepancy likely accounts for the common finding of reduced survival under warming conditions. Sublethal effects of warming can also cause increased stress in individuals, increasing host susceptibility and altering transmission and proliferation of parasites.

In some cases, ocean warming may reduce parasite prevalence and transmission. The thermal tolerances of parasites and hosts may differ such that the parasite can tolerate higher temperatures (e.g. ESD in *H. americanus*) or the host may tolerate higher temperatures (e.g. the rhizocephalan barnacle *Loxothylacus panopaei* which parasitized the mud crab *Eurypanopeus depressus*) (Gehman et al., 2018; Shields, 2019). Likewise, stress from increased ocean temperatures may reduce host populations, which could result in decreased contact and parasite transmission among conspecifics. These examples illustrate the complex relationship between a warming ocean, crustaceans, and One Health.

3.3. Eutrophication

The causes and consequences of increasing eutrophication in coastal waters are tightly linked with other factors considered here. Changes in precipitation patterns may cause increasing runoff with increased nutrient load due to changes in land use for agriculture, industrialization, and urbanization (Bojko et al., 2020). In coastal waters we will see impacts of this eutrophication as increased frequency and severity of hypoxic events and harmful algal blooms with cascading effects on water quality, habitat loss, and crustacean health. These impacts will not occur uniformly, with the largest increase in nutrient load expected to occur in the tropics and subtropics where nutrients have been historically low but parasite abundance high (Johnson et al., 2010), and in Asia (Seitzinger et al., 2002), a critical supply region for aquacultured shrimp. Sea surface warming will act synergistically with rising nutrient loads to intensify negative effects of eutrophication (Moss et al., 2011).

3.3.1. Harmful algae blooms

Eutrophication is a leading factor in the increasing incidence of harmful algal blooms (HABs), but other aspects of global change are involved, such as OA, warming, and altered salinity (Fu et al., 2012). HABs often produce toxins, such as brevetoxin, domoic acid, and paralytic shellfish toxin that can bioaccumulate in benthic invertebrates (Bricelj et al., 2012; Samson et al., 2008). Crustaceans accumulate these toxins (Costa et al., 2003; Oikawa et al., 2004), displaying lethal and sublethal effects such as altered geotaxis, slower swimming speeds, reflex impairment, and decreased appetite (Gravinese et al., 2018; Gravinese et al., 2019b). Though more commonly caused by bivalve consumption, consuming crustaceans containing these toxins can lead to gastrointestinal illnesses in humans, such as neurotoxic shellfish poisoning caused by brevetoxin (Fleming et al., 2011) and amnesic shellfish poisoning caused by domoic acid (Lefebvre and Robertson, 2010).

Harmful algal blooms are on the rise in areas of increased eutrophication, where they increase primary productivity in the water column, and in turn increase secondary production and respiration (Breitburg et al., 2018). On the benthos, there tends to be more respiration and decomposition during HABs, which result in the formation of hypoxic zones (Diaz and Rosenberg, 2008).

3.3.2. Hypoxia

Hypoxia has more than doubled in recent decades in coastal marine systems due to increasing nutrient loading, HABs, and stronger haloclines formed by high freshwater discharge and warmer surface temperatures (Rabalais et al., 2009). Hypoxic events are increasing in severity, occurring earlier in the year, and persisting longer, particularly in shallow benthic areas, home to many crustaceans. Hypoxia causes behavioral and cellular changes in crustaceans (Spicer, 2014), mortality (Gravinese, 2020), and can hinder immune defense. Hypoxia, compounded by hypercapnic sea water conditions, hinders the ability of the Atlantic blue crab *C. sapidus*, white-leg shrimp *Penaeus vannamei*, and grass shrimp *Palaemonetes pugio* to clear bacterial parasites (Holman et al., 2004; Mikulski et al., 2000) because these conditions hinder critical immune defenses such as phagocytosis and the prophenoloxidase (proPO) system (Tanner et al., 2006). Disease caused by these bacterial parasites can cause mortality, affecting food security (see Section 4.1) by reducing populations of the heavily fished and cultured *C. sapidus* and *P. vannamei*, respectively. Some of these parasites (e.g. *Vibrio* sp.) are also factors in foodborne illnesses in humans (see Section 4.3).

3.4. Habitat loss

Habitat loss due to anthropogenic and natural disturbance is a key issue affecting marine environments worldwide. Loss of habitat and habitat complexity directly impact crustacean populations on coral and oyster reefs, seagrass beds, and mangrove forests (Airoldi et al., 2008). In the Florida Keys (USA), shallow hard-bottom habitat is degraded by periodic cyanobacteria blooms that kill sponges. The loss of sponges impacts populations of the commercial decapods *P. argus* and the stone crab *Menippe mercenaria* sheltering beneath sponges (Behringer and Hart, 2017; Butler, 1995) as well as snapping shrimp living in sponge interstices (Butler et al., 2017). On degraded habitats, the gregarious *P. argus* shelters in larger aggregations due to the paucity of sponge shelters. This increase in density on a small scale could be expected to increase the transmission of density-dependent parasites, however healthy *P. argus* avoid diseased conspecifics, a behavior that reduces the liklihood of epizootics (Butler et al., 2015).

Crustacean aquaculture is also the cause of habitat loss, particularly when mangroves, salt marshes, and other coastal land is cleared for shrimp farms. Millions of hectares in Asia and Latin America have been cleared to make room for this lucrative sector, resulting in loss of biodiversity and important nursery habitat (Páez-Osuna, 2001). López-Angarita et al. (2016) estimate that 40–80% of mangrove habitat in Central and South America has been lost since the 1960s and land use for aquaculture has grown by over 800% in India since the 1980s (Jayanthi et al., 2018). This habitat loss impacts water drainage patterns and carbon sequestration, increases coastal erosion, and leaves coastal communities more susceptible to storm and hurricane damage (Ahmed and Glaser, 2016; Cardoso-Mohedano et al., 2018). During aquaculture operations, discharge of nutrients, chemicals, parasites, and saltwater can further degrade remaining coastal habitats (Páez-Osuna, 2001). Better management practices are being developed in some areas to mitigate these negative impacts (Rodríguez, 2018; Sivaraman et al., 2019).

3.5. Pollution

Increasing industrialization, human population, global trade, and technological advances have inherently increased pollution in the oceans over the last century. Many pollutants persist in the environment for decades or more and are capable of affecting crustaceans through direct uptake and bioaccumulation (Bojko et al., 2020). Benthic crustaceans may be at even greater risk, due to settling and accumulation of toxins and pollutants on the benthos. Anthropogenic pollution is most commonly linked to decreases in immunocompetence and endocrine disruption in aquatic organisms (Depledge and Billinghurst, 1999; Islam and Tanaka, 2004).

Many pollutants have been linked to endocrine disruption in vertebrates (Sumpter, 2005) and molluscs (Matthiessen and Gibbs, 1998) through estrogenic effects but effects on crustaceans appear more variable (Oetken et al., 2004). Some studies have reported feminization of crustaceans in polluted areas, such as higher incidence of intersex amphipods (Ford et al., 2006), decreased egg viability (Jacobson et al., 2011), and morphological feminization in *Carcinus maenas* (Brian, 2005). However, Brian (2005) concludes that the observed changes are not consistent with hormonal changes reported in other organisms due to endocrine disrupting chemicals, possibly due to differing hormonal control of secondary sexual characteristics in crustaceans. Effects of pollution on crustacean hormonal pathways may more readily result in de-masculinization than feminization. Either pathway could affect crustaceans at the population level by altering sex ratios and fecundity. Perhaps better understood are the effects of endocrine disrupting compounds (EDCs) on crustacean molting hormone, ecdysone, and hyperglycemic hormones (LeBlanc, 2007) which are well documented impacting growth, reproduction, development, and survival (Oetken et al., 2004; Rodríguez et al., 2007).

Many compounds that have shown endocrine disruption in other taxa have been linked with increased incidence of parasitism of crustacean hosts. Tributyltin (TBT), long used in anti-fouling paints, has a long list of negative consequences for various aquatic vertebrates and invertebrates, including depressed growth, molting, and fecundity in crustaceans (Jacobson et al., 2011; Oetken et al., 2004). Low doses of TBT have also been linked to immune suppression and increased microsporidian infection (Jacobson et al., 2011). Microsporidians commonly take advantage of immunocompromised hosts and have also been linked to PCB, PFOS, heavy metal, and paper mill effluent pollution (Ford et al., 2006; Jacobson et al., 2010; Smith et al., 1995).

Heavy metals tend to bioaccumulate and are found in higher concentrations in tissues of crustaceans collected from sites with greater anthropogenic use (Reed et al., 2010). Heavy metal toxicity can reduce immunocompetence (Le Moullac and Haffner, 2000), and may affect parasitized individuals more severely than uninfected individuals (Lafferty et al., 2004). For instance, (Brown and Pascoe, 1989) found that amphipods with acanthocephalan parasites were more sensitive to cadmium exposure (i.e. had higher mortality) than uninfected conspecifics. Chronic mercury exposure also affects respiration by causing hyperplasia in the gills in some species (*Macrobrachium idae*) (Victor et al., 1990), but other species (e.g. *C. maenas*) are relatively tolerant to heavy metal stress (Truscott and White, 1990).

For other common pollutants, there is limited evidence of effects on crustaceans, likely due to research gaps. Oil spills may increase stress responses and have been linked to higher incidence of shell disease in shrimp (Gopalan and Young, 1975). Research into microplastics pollution is in its infancy, but is hypothesized to mimic carcinogens in some cases, and consumption of microplastics is tied to decreased feeding and subsequent nutritional deficiencies in the Norway lobster (Welden and Cowie, 2016a; Welden and Cowie, 2016b). Disruption in electric and magnetic fields, i.e. electromagnetic pollution, can disrupt cues used by lobster for foraging and navigation (Zoë et al., 2020).

3.6. *Storm frequency and intensity*

Changes in weather patterns are expected to increase storm frequency and intensity (Burge and Hershberger, 2020) particularly for hurricanes, which increase in strength in warmer waters. To our knowledge, storms have not been linked directly to crustacean health in the literature but we presume this is due to a lack of study rather than a lack of effect. Other marine invertebrates experience physical injury and increased susceptibility to parasites due to the violent mixing that storms cause. This mixing can also cause resuspension of particles, leading to increased exposure to pollutants (see Section 3.5) and range shifts for crustaceans and their parasites due to the movement of water (Burge et al., 2014). This mixing and disruption can alter marine habitats and communities for decades (see Section 3.4). For instance, several studies have found long-term decreases in trematode parasites in fish and snails following hurricanes (Aguirre-Macedo et al., 2011; Overstreet, 2007).

Climate change is resulting in other changes to weather patterns as well, including changes in precipitation (more or less, depending on location and season). Increased precipitation increases terrestrial runoff, leading to decreased salinity, eutrophication, harmful algal blooms, and increased frequency and severity of hypoxic events (Section 3.3) (Spicer, 2014) all of which can alter parasite-host dynamics. Decreased precipitation has the effect of increasing coastal salinity, which may allow for range expansion of stenohaline marine parasites, such as *Hematodinium* (Coffey et al., 2012) and rhizocephalan barnacles (Alvarez et al., 2002). *Hematodinium* infections are correlated with salinities over 18 ppt (Messick and Shields, 2000) and outbreaks in blue crabs have been tied to drought years (Lee and Frischer, 2016; Parmenter et al., 2012).

3.7. *Ecosystem connectivity*

Marine systems are known for their high connectivity relative to terrestrial systems (Cowen et al., 2000). Global trade has artificially increased this connectivity over the last century, with shipping accounting for 70% of international trade (Jägerbrand et al., 2019) and aquaculture already the fastest growing food production industry (FAO, 2018). Ballast water, biofouling, and aquaculture are the top three vectors spreading invasive species, accounting for more than three quarters of invasive crustaceans (Williams et al., 2013). Invasive species cost billions of dollars in economic impact (Pimentel et al., 2005) in the US alone, and two crustaceans are on the Global Invasive Species Database (GISD) list of 100 “worst” invasive species. At the same time Carlton (2005) argues that invasive crustaceans are likely extremely under-reported due to a paucity of taxonomists studying non-decapod crustaceans. Invasive crustaceans can impact native populations by altering habitat (Garbary et al., 2014), competing for resources (Gregory and Quijón, 2011), and co-introducing non-native parasites (Bojko et al., 2018).

“Pathogen pollution” (i.e. human-mediated pathogen spread) from invasive species is considered a huge and severely understudied risk to native wildlife populations (Roy et al., 2017). Horizon scanning is an important tool in predicting future invasions but must also include assessment of potential pathogen spread and host switching. Host switching is thought to affect native marine populations in three ways: 1) parasite spillover occurs when an introduced species brings non-native pathogens which then infect native species, 2) parasite spillback occurs when an introduced species is infected by a native pathogen, becoming a reservoir that can increase overall parasite transmission, and 3) parasite dilution occurs when an introduced species is infected by a native pathogen, diluting the infection prevalence in native hosts (Blakeslee et al., 2020). As one example among marine crustaceans, managers are concerned about parasite spillover from the invasive green crab *C. maenas* to the lucrative American lobster *H. americanus*. Researchers have cautioned against regional efforts to use *C. maenas* as bait in the American lobster fishery for this reason (Bojko et al., 2018), though use is currently allowed in parts of Canada (C. McKenzie pers. comm.).

4. Environmental change and human activities affect One Health

4.1. *Food security*

“Food security exists when all people, at all times, have physical and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life” (World Food Summit, 1996). Seafood is an extremely important source of protein, providing over 3.2 billion people with more than 20% of their animal protein, and is particularly important in rural areas, where food security is lower (FAO, 2018). Crustacean aquaculture and wild catch is a growing part of global food security supplying 11.7 million metric tons and worth over $50 billion (Fig. 3), but expected to become a limiting protein source due to disease (FAO, 2018; FAO, 2020b; Stentiford et al., 2012).

Nearly half (5.7 million tons) of crustacean production comes from aquaculture. Crustacean aquaculture grew 18% annually from 1970 to 2008, faster than any other aquaculture sector (Bondad-Reantaso et al., 2012). Biosecurity measures are crucial to maintaining this sector and increasing production for food security (Taw et al., 2011), but three common practices still contribute directly to disease emergence and spread. First, locating farms in direct contact with natural waterways poses threats to both farmed and wild individuals. It was traditionally thought that direct water exchange was required to maintain water quality in aquaculture ponds (Hopkins et al., 1993); however, this practice led directly to introduction and spread of virulent parasites (Moss et al., 2012).

Second, the practice of feeding frozen decapods to farmed shrimp allows for transfer of parasites between species. Stentiford et al., (2012) note that WSSV emerged after farmers fed frozen imported portunids to shrimp broodstock and that these crabs have viruses similar to WSSV. Thus, this practice may have triggered the most devastating, widespread, and costly viral outbreak in crustacean aquaculture, estimated to have caused $8–15 billion in losses as of 2012 worldwide (Stentiford et al., 2012). There are also issues with co-culturing shrimp with other decapods, as Xu et al., (2010) concluded that this practice likely transfers or increases spread of *Hematodinium* to shrimp, resulting in up to 100% mortality.

Finally, the global trade of broodstock may be the most serious practice contributing to the emergence and spread of diseases in shrimp aquaculture. One of the top five viral parasites listed by the OIE for regulation, infectious myonecrosis virus (IMNV), spread rapidly from its origin in Brazil through Indonesia due to illegal trading of broodstock (Stentiford et al., 2012). Infectious hypodermal and hematopoietic necrosis virus (IHHNV) is believed to have been an endemic parasite of *P. monodon* introduced to the Americas with devastating epizootics in *P. stylirostris* and reduced growth in *P. vannamei* (Flegel and Fegan, 2002). WSSV infects numerous wild and farmed decapod hosts (Lo et al.,

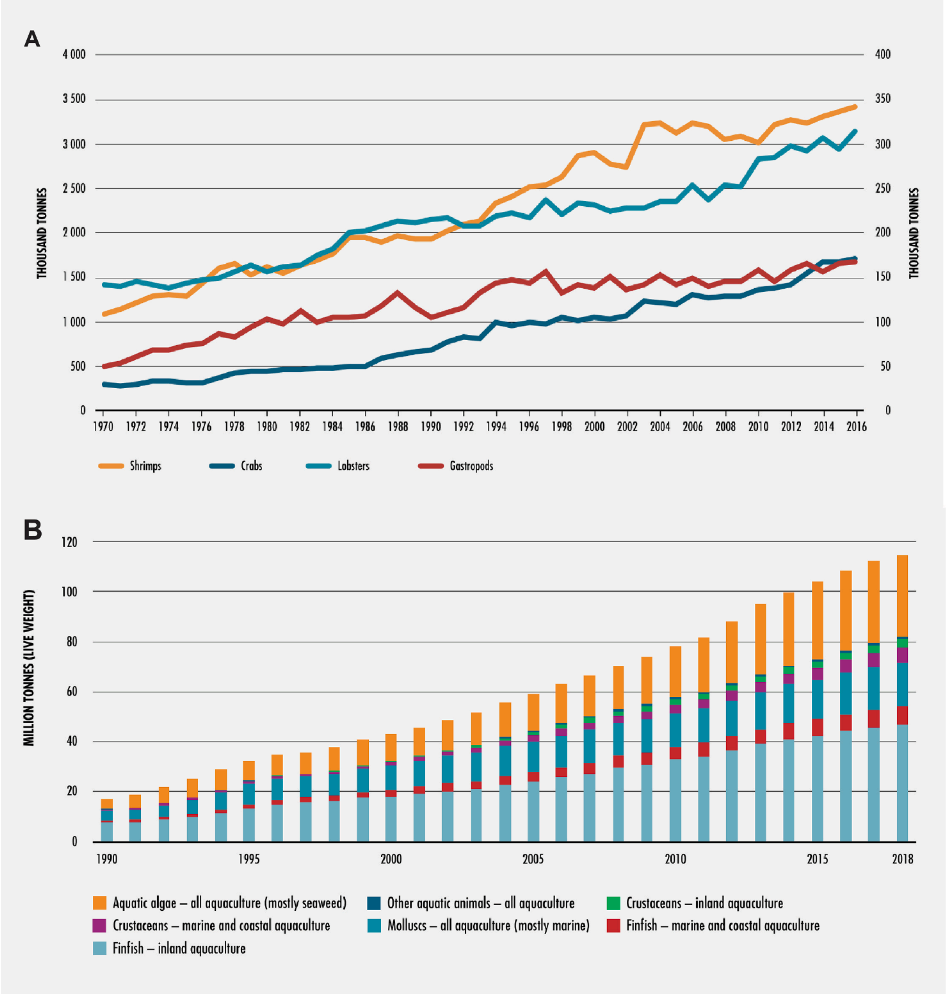

Fig. 3. (A) Wild catch of most valuable (USD per metric tonne) species groups 1970–2016. Tonnage of shrimps and crabs are on the left axis, values for lobsters and gastropods are on the right axis. Figure reproduced from FAO, 2018. (B) Aquaculture production of aquatic animals and algae 1990–2018. Figure reproduced from FAO, 2020.

1996) and has spread globally since its emergence in Japan, a process likely accelerated by exchange of live larvae and broodstock among shrimp farms (Flegel and Fegan, 2002). Better management practices and biosecurity measures, as well as development and use of specific pathogen free (SPF) lines of shrimp will help maintain aquaculture as an important and growing source of protein internationally (Flegel, 2019).

Wild catch of crustaceans is also important for food security and is impacted by global change. Snow crab fisheries are in decline due to intrusion of warm water on short (Zisserson and Cook, 2017) and long (Mullowney et al., 2014) time scales. Effects differ by location with some areas likely losers (e.g. Newfoundland) and other areas likely winners (e.g. Norway) (Lorentzen et al., 2018). Currently, pH is not affecting crab stocks in Alaskan waters, but managers are warned to brace for future impacts (Mathis et al., 2015).

Crustaceans are also involved indirectly in impacts to food security. Many coldwater systems are expected to experience declines in krill and copepod populations due to OA and warming (Bailey et al., 2017; Klein et al., 2018; Thor et al., 2018). These declines will cascade up trophic levels impacting whales, seals, penguins, and fish (Klein et al., 2018). Copepods are a main food source of pollock (Kimmel et al., 2018), the largest capture fishery in the world providing some of the cheapest protein (FAO, 2018).

Crustacean aquaculture uses more fish meal and fish feeds than other aquaculture sectors (FAO, 2018). Fish meal and feeds are sourced largely from wild fishery catch (Boyd et al., 2007) of potential food-grade quality (Tacon et al., 2006) and are thus implicated in overfishing. It takes about 2 kg of wild-caught fish to produce 1 kg of aquacultured shrimp (Tacon et al., 2006), resulting in unsustainable \consumption relative to production. This practice particularly impacts food security in developing countries, where emphasis is on production and export of high value species, such as shrimp, with less available protein for domestic consumption (Cremer et al., 1999; Tacon, 1998). FAO supports research into a variety of vegetarian proteins and oils for shrimp aquaculture, such as canola and soybean meal (Tacon et al., 2006).

Also limiting the amount of protein available directly to consumers, shrimp trawling is recognized as a large source of bycatch and discard (Bondad-Reantaso et al., 2012). Shrimp trawling accounts for nearly 50% of all discarded bycatch in the US. Despite efforts to reduce bycatch using bycatch reduction devices (BRDs), the Gulf of Mexico shrimp trawling fishery discards 4.5x more biomass than it lands (Harrington et al., 2005). Not all fisheries worldwide require the use of BRDs, and thus may lose even more; the lost value of discarded bycatch in the Gulf of California's shrimp fishery is nearly $100 million USD – one fifth of the value of the shrimp fishery itself (Ibarra, 2017).

4.2. *Food quality*

Food quality can be affected by spoilage, disease, and heavy metal toxicity. With warming temperatures, fishers and markets will need to take great care to preserve crustacean foods for consumers. Shell disease in a variety of crustaceans has been linked to warming temperatures and causes a decrease in quality, often to the point that a diseased individual is no longer marketable (Barris et al., 2018). Heavy metals, such as arsenic and chromium, accumulate in crustacean tissues, especially the hepatopancreas (Reed et al., 2010), and could be a human health concern in areas with heavy coastal industrialization.

4.3. Zoonotic parasites

The oceans host a variety of dangerous waterborne parasites that have, or have the potential, to infect humans, including viruses, bacteria, and microsporidians (Nwachcuku and Gerba, 2004). *Enterocytozoon bienusi* is an emerging parasite that infects immunocompromised humans but is found within a clade of microsporidians that typically infect fish and aquatic arthropods (Stentiford et al., 2016). This parasite species has zoonotic reservoirs (Dengjel et al., 2001), and its closest known relative, *Enterospora canceri*, is a parasite of marine crabs (Stentiford et al., 2019). Those authors propose that this clade of microsporidians, known as *Enterocytozoon* group Microsporidia (EGM), are key One Health sentinels because of their propensity to infect hosts with compromised immune systems (Stentiford et al., 2016), which may be indicative of stressors to hosts (human and wildlife) and environment.

However, our current knowledge suggests that marine crustaceans account for a relatively small portion of zoonotic parasites, most commonly causing foodborne illnesses, though still only accounting for 3% of all foodborne (CDC, 2019) and 16% of seafood-related foodborne illness (Iwamoto et al., 2010). Over 95% of crustacean foodborne illnesses are gastrointestinal illnesses caused by bacterial contamination (Iwamoto et al., 2010), mostly commonly *Vibrio parahaemolyticus*, but also including *Clostridium perfringens*, Salmonellosis, Shigellosis, and Staphylococcal intoxication (Bryan, 1980). More concerning zoonotic parasites passed from crustaceans are rare, but include nematode, trematode, *Vibrio cholera*, and, possibly, microsporidian parasites. The lung fluke, *Paragonimus westermani*, causes acute and chronic infections in humans, attacking the lungs and central nervous system (Liu et al., 2008), but is transmitted through freshwater crabs.

Despite the limited reports of crustaceans acting as direct sources of zoonotic parasites, there is growing evidence that global change and climate factors are impacting the proliferation of foodborne and contact illnesses transmitted *through* crustaceans. *V. cholera* is associated with chitinaceous plankton, such as copepods (Colwell, 1996) and epidemics are positively correlated with sea surface temperatures (Harvell et al., 1999). Warm water temperatures and storm events, such as hurricanes and extreme rain events, have increased duration, incidence, and extent of non-cholera *Vibrio* infections in marine wildlife as well (Burge et al., 2014). *Salmonella* sp. are most commonly found in marketed crabs in India (e.g. *Portunus pelagicus* and *Scylla serrata*) during monsoon season and extreme weather events (Mohamed Hatha and Lakshmanaperumalsamy, 1997). Shifts in oceanic currents, which are related to global change and ENSO events, have also been linked to complex parasites, such as nematodes, which are transmitted through krill to fish and consumed by humans (Harvell et al., 1999).

4.3.1. Microplastics

Crustaceans have a unique link between microplastic pollution and human health. Microplastics have been found in gut and muscle tissue of harvested crustaceans worldwide (Abbasi et al., 2018; Devriese et al., 2015; Murray and Cowie, 2011; Wójcik-Fudalewska et al., 2016). While microplastics are commonly found in a variety of seafoods (Barboza et al., 2018; Sharma and Chatterjee, 2017), they are typically found in the gut, which is more commonly consumed with crustaceans (e.g. shrimp) and other shellfish (Wright and Kelly, 2017). Microplastics can introduce a myriad of toxic substances, microbes, and parasites when ingested (Barboza et al., 2018). Effects of microplastics on human health are not yet well understood, but may include chromosome alterations, immunosuppression, inflammation, and further severe chronic effects with bioaccumulation (Barboza et al., 2018; Wright and Kelly, 2017).

4.4. Crustacean population health affects ecological community health

All components of the One Health triad are interconnected so that changes to one component can affect the others (Fig. 1). Changes such as ocean warming, overfishing, or disease emergence can all directly affect the health of the crustacean component (see Sections 2 and 3), but those direct effects can also carry indirect ecological consequences for the population, and the health and stability of the wider marine community. Crustaceans are integral members of natural communities, serving nearly every trophic role from detritivore (e.g., fiddler crabs), to primary consumer (e.g., krill), to predator (e.g., lobsters). Thus, impacts to crustacean populations from environmental changes (natural or anthropogenic) or exploitation can have consequences that reverberate from the community to the ecosystem (Bascompte et al., 2005). A classic example lies in the Channel Islands (USA) where the California spiny lobster *Panulirus interruptus* is heavily fished in some areas and protected in others. Where the lobsters are fished their abundance is low and one of their primary prey items, the purple urchin *Strongylocentrotus purpuratus*, is released from predatory control and increases in density to the point that it overgrazes the kelp forest where it lives and eventually breeches the density-dependent transmission threshold for a bacterial parasite - an epizootic ensues (Behrens and Lafferty, 2004; Lafferty, 2004). The situation is decidedly different within the Channel Island marine protected areas where lobsters are not fished and their predation keeps the urchin density low, the kelp forest flourishes, and the urchins do not experience boom-and-bust cycles of disease (Behrens and Lafferty, 2004). This is an exceptional example of the importance of crustaceans to an ecosystem but highlights the need for ecologically-informed fishery management.

4.5. Crustacean fishery health affects human community health

Coastal fishing communities around the globe are known for their strong dependence on the health and productivity of their fishery resources, and crustacean fisheries are no exception. When those resources are no longer available, regardless of the cause, the health of people living in those communities suffers. Steneck et al. (2011), describe the American lobster fishery in the Gulf of Maine as a “gilded trap” wherein there is such dependence on a single species (*H. americanus*) that future declines in that fishery could have profound economic and societal consequences. Loss of access to a fishery resource could be gradual, as might occur from migration of the target species poleward due to climate change, habitat destruction, or chronic overfishing. These changes should result in concomitantly gradual shifts in fishing activities or the species targeted, changes in employment, or intergenerational shifts away from fishing that can alter the structure of the community (Power et al., 2014).

Loss of access to a fishing resource can also be abrupt, as might occur from an environmental disaster, sudden fishery closure, or economic collapse. It is the abrupt and widespread unemployment caused by these types of events which appear to have the most dramatic effects on mental health in coastal communities. Harmful algal blooms are notorious for causing the temporary closure of fisheries in the interest of public health but can have detrimental effects on fishing communities. For example, on the west coast of the US in 2015 a persistent bloom of the diatom *Pseudo-nitzschia* caused the closure of the Dungeness crab fishery for an extended period and caused distress among coastal fishing communities that extended through other sectors of the local economy (Ritzman et al., 2018). Similarly, man-made disasters, such as the 2010 Deepwater Horizon oil spill that resulted in widespread closure of fisheries around the northern Gulf of Mexico, including lucrative penaeid shrimp and blue crab fisheries, had abrupt and long-lasting effects on mental health within coastal communities, such as clinical anxiety and depression (Morris et al., 2013). Beginning in January 2020, the COVID-19 pandemic caused a rapid collapse in demand for lobsters, crabs, and shrimp around the world, with disastrous economic and human health consequences for fishermen and fishing communities both large and small (Bennett et al., 2020; Knight et al., 2020). The One Health connection between crustacean fisheries, environmental health, and human health can be less direct through effects on community-wide mental health, but perhaps no less impactful than direct connections such as food security.

5. Conclusions and recommendations

Crustaceans are an integral part of the One Health triad – affecting and being affected by human and environmental health. It is critical that we fill research gaps, such as effects of microplastics and other pollutants on crustacean health and how bioaccumulation may affect human health. As a critical sector for food security and food safety, we must also encourage the use of best management practices in aquaculture and capture fisheries and better understand the current status and potential for zoonotic pathogens to emerge from crustaceans. It is clear that global change will continue to impact crustaceans, their environment, and humans that depend on them and thus we must act in a coordinated fashion, recognizing the linkages between the components to mitigate for these changes.

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