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INTRODUCTION

Disease effects on lobster fisheries, ecology, and culture: overview of DAO Special 6

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ABSTRACT: Lobsters are prized by commercial and recreational fishermen worldwide, and their populations are therefore buffeted by fishery practices. But lobsters also remain integral members of their benthic communities where predator–prey relationships, competitive interactions, and host–pathogen dynamics push and pull at their population dynamics. Although lobsters have few reported pathogens and parasites relative to other decapod crustaceans, the rise of diseases with consequences for lobster fisheries and aquaculture has spotlighted the importance of disease for lobster biology, population dynamics and ecology. Researchers, managers, and fishers thus increasingly recognize the need to understand lobster pathogens and parasites so they can be managed proactively and their impacts minimized where possible. At the 2011 International Conference and Workshop on Lobster Biology and Management a special session on lobster diseases was convened and this special issue of *Diseases of Aquatic Organisms* highlights those proceedings with a suite of articles focused on diseases discussed during that session.

KEY WORDS: *Panulirus argus* virus 1 · PaV1 · *Hematodinium* · Gaffkemia · *Aerococcus viridians* · Shell disease · ESD · *Aquimarina homaria* · Intersex · ICWL

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Lobsters support commercial fisheries worldwide with landings of nearly 280 000 t and efforts to grow and market lobsters or enhance natural lobster populations using aquaculture are growing (FAO 2012). Beyond their value as a seafood commodity, lobsters of the spiny, clawed, and slipper varieties are also some of the most abundant large benthic invertebrates in their ecosystems and often of significant ecological importance as predators and prey (Butler et al. 2006, Lavalli & Spanier 2007). Yet, in recent decades disturbing reports have surfaced describing diseased lobster populations. Disease is increasingly recognized as a prominent force driving the popula-

tion dynamics, fisheries, and ecology of many marine organisms and the apparent rise in lobster disease has brought focus to them, culminating recently in a special session on disease at the 2011 International Conference and Workshop on Lobster Biology and Management in Bergen, Norway. This special issue of *Diseases of Aquatic Organisms* (DAO) draws from that session with recent studies on several of the most consequential lobster diseases.

The literature indicates that lobsters do not face as large a number of pathogens and parasites as do other decapod crustaceans (e.g. shrimps and crabs). However, several diseases pose significant threats to

lobster populations in the wild or in post-capture holding facilities (see Shields 2011, Stentiford & Neil 2011, and Cawthorn 2011 for reviews). Parasitic dinoflagellates of the genus *Hematodinium*, the viral pathogen *Panulirus argus* Virus 1 (PaV1), the pathogenic bacteria *Aerococcus viridians* var. *homari* (gaffkaemia), and the syndromic epizootic shell disease (ESD) all occur in wild animals and have impacted holding and processing facilities to varying degrees. Other decapod pathogens have only been experimentally transmitted to lobsters, such as white spot syndrome virus (WSSV), but may have the potential to impact wild stocks. The studies in this DAO Special cover these pathogens in the context of the pressing issues that they create for lobster fisheries, patho-biology, and ecology.

Hematodinium sp. is a dinoflagellate parasite with broad host specificity, infecting more than 35 crustacean host species (Small 2012). It has had devastating impacts on crab populations worldwide (Morado 2011) and is a major source of mortality for juvenile Norway lobster *Nephrops norvegicus* around the UK. Prevalence of *Hematodinium* in *N. norvegicus* and the associated mortality of lobster around the UK have long been assumed to be seasonal, but Beevers et al. (2012, this DAO Special) challenge that notion with compelling new evidence to the contrary. They used a suite of assays over a nearly 2-yr period to show that a combination of assay insensitivity and variable parasite dynamics led to this erroneous conclusion; instead, it appears to be the intensity of infection, rather than prevalence per se, which varies among seasons (Beevers et al. 2012).

Infection with *Hematodinium* sp. imparts a bitter flavor and cooked appearance to the meat of some crab species yielding them unmarketable (Meyers et al. 1987, Taylor & Khan 1995). This condition gave rise to the term 'bitter crab disease' (BCD) commonly used to describe infections. Albalat et al. (2012, this DAO Special) used a sensory evaluation panel and biochemical analysis to test the quality and palatability of cooked *Nephrops norvegicus* patently infected with *Hematodinium* sp. They found that even after cooking, the meat was of considerably lower quality and flavor than that of non-infected lobsters, but surprisingly, it did not have the characteristic bitter taste described for some crab species (Meyer et al. 1987, Taylor & Khan 1995).

In contrast to *Hematodinium*, PaV1 has a very narrow host specificity and is only known to infect the Caribbean spiny lobster *Panulirus argus* (Butler et al. 2008) but does so throughout the Caribbean-wide range of *P. argus* (e.g. USA, Shields & Behringer

2004; Mexico, Huchin-Mian et al. 2008; and Cuba, Cruz-Quintana et al. 2011). Infections of PaV1 can cause locally high juvenile mortality of up to 60% (Behringer et al. 2011); mortality is much lower in adults. Shields & Behringer (2004) first hypothesized that lobsters infected with PaV1 died due to metabolic wasting, further supported by observations of depressed nutritional condition in infected lobsters (Behringer et al. 2008, Briones-Fourzán et al. 2009). Pascual-Jiménez et al. (2012, this DAO Special) used a more comprehensive suite of 13 variables to investigate how natural PaV1 infections alter the physiology, immune response, and perhaps the immuno-competency of Caribbean spiny lobsters. PaV1-infected lobsters had significantly different profiles in these characteristics suggesting that their immune response was activated in some respects, but potentially suppressed in others (Pascual-Jiménez et al. 2012). They also report the first PaV1 co-infection with PaV1-infected lobsters having a nearly 50% higher prevalence of gill infestation by an opportunistic ciliate (*Epystilis* sp. and *Zoothamnium* sp.) compared to lobsters without a PaV1 infection (Pascual-Jiménez et al. 2012).

PaV1 also has striking effects on the ecology of *Panulirus argus* including the avoidance of infected lobsters by normally social and healthy conspecifics (Behringer et al. 2006). This behavior has implications for trap-based fisheries that rely on lobsters' sociability to catch them (Behringer et al. 2012), but many fisheries in the Caribbean use non-confining structures termed 'casitas' (1 to 2 m²) to attract lobsters and facilitate their harvest. Candia-Zulbarán et al. (2012, this DAO Special) and Briones-Fourzán et al. (2012, this DAO Special) studied the effects of commercial-scale (>18 000 casitas) casita use on the prevalence and distribution of PaV1, and the behavior of lobsters in relation to diseased conspecifics in Bahía de la Ascensión on the Mexican Yucatan peninsula. Candia-Zulbarán et al. (2012) used the presence of clinical (i.e. visible) infections to show that PaV1 prevalence varied with season, location, and lobster size, but was unaffected by the presence of casitas. Although visible infections of PaV1 were high in juveniles they were very low in adults, as has been observed in the Florida Keys (Shields & Behringer 2004) and Cuba (Cruz-Quintana et al. 2011). However, unlike the Florida and Cuban fisheries where lobster catch has declined over the past decade (Ehrhardt et al. 2010), lobster fishery production in Bahía de la Ascensión has increased by ~25% over the same period (Sosa-Cordero et al. 2008). Briones-Fourzán et al. (2012) also found that PaV1 in-

fection did not alter the sheltering patterns of lobsters that use casitas, in contrast to observations in smaller natural shelters where uninfected lobsters will not share a den with a PaV1-infected lobster (Behringer et al. 2006, Lozano-Álvarez et al. 2008). Even at the highest levels of co-occupation within casitas, prevalence of PaV1 was low. Thus, the large size of casitas may permit sufficient separation of infected and uninfected lobsters to curtail transmission of PaV1 as compared to transmission measured in standard fishing traps (Behringer et al. 2012) and in the laboratory (Butler et al. 2008), or perhaps greater UV radiation limits water-borne transmission of PaV1 in the clear, shallow waters of the Yucatan (Briones-Fourzán et al. 2012).

The American lobster *Homarus americanus* supports one of the largest fisheries in New England (USA) and Atlantic Canada with > 115 000 t landed in 2010 (FAO 2012). Due to the collapse of many fin-fish fisheries some argue that the New England fishermen have become overly dependent on a single-species fishery, albeit one that for much of the region appears healthy with record harvests. However, in the mid 1990s lobsters with deep shell lesions, sometimes covering most of their carapace, began to appear in traps in southern New England (Castro & Angell 2000). The condition was termed 'epizootic shell disease' (ESD) (Smolowitz et al. 2005). A potential causative agent has recently been identified, the bacteria *Aquimarina homaria* (Quinn et al. 2012), although other co-infecting pathogens and conditions (environmental or physiological) confound a simple cause-effect relationship and potentially increase lobster susceptibility to ESD. At present, therefore, ESD is considered as syndromic. By 2011, the epizootic had so decimated lobster stocks in southern New England that the Atlantic States Marine Fisheries Commission deemed the southern New England fishery in collapse and recommended it be closed. Fishery models incorporating shell disease offer convincing evidence that ESD has indeed been a major factor in the decline of the stock (Wahle et al. 2009), underscoring the importance of considering disease in stock assessments and fishery management. ESD prevalence remains high off the coast of southern New England, where it varies temporally and geographically between 10 and 40% (Castro et al. 2012, this DAO Special). Castro et al. (2012) have reviewed the current state of knowledge on ESD including developments on the potential etiological agent, fishery effects, and environmental correlates and they discuss future research avenues and needs.

The American lobster fishery has had problems with disease in the past, notably gaffkaemia, a fatal disease first reported in 1947 (Snieszko & Taylor 1947) and caused by the bacteria *Aerococcus viridians*. Gaffkaemia is often reported from lobster held in impoundments prior to sale, where injuries to lobsters are common and facilitate pathogen transmission. However, several studies also document its presence in wild lobster populations along the northeast Atlantic coast (Stewart et al. 1966, Lavallée et al. 2001). *Homarus americanus* also has a close relative across the Atlantic in the European lobster *H. gammarus*, and gaffkaemia has been reported from facilities where imported American lobsters were held together with European lobsters. The introduction of novel pathogens to naïve but potentially susceptible populations is a great concern. Therefore, Stebbing et al. (2012, this DAO Special) surveyed wild populations of *H. gammarus* around the coast of England and Wales to determine if gaffkaemia is now endemic in wild stocks of European lobster. They confirmed via genetic analysis that gaffkaemia is indeed present at low prevalence (<1%) in wild *H. gammarus* in the UK and that the bacterial strain present in Europe is most likely of USA or Canadian origin.

To potentially curtail a similar introduction of an even more devastating pathogen, Bateman et al. (2012, this DAO Special) investigated the viability of white spot syndrome virus (WSSV) in supermarket commodity shrimp and its potential for spread to *Homarus gammarus*. WSSV has had catastrophic effects on the penaeid shrimp industry (reviewed in Lightner 2011 and Stentiford et al. 2012), and similar to *Hematodinium*, WSSV has a broad host affinity (Stentiford et al. 2009). The supermarket-derived shrimp sampled by Bateman et al. (2012) did indeed harbor viable viral particles that were transmissible to penaeid shrimp. WSSV was also successfully transmitted to *H. gammarus* fed infected supermarket-derived shrimp, but transmission required exposure to heavily infected shrimp. These are ominous results that highlight the threat of potential disease introductions assisted by greater international trade in crustaceans.

In addition to pathogens, pollutants and contaminants can cause mass mortality of wild crustaceans, as occurred off the coast of Rhode Island (USA) after a fuel oil spill in 1996 (Cobb et al. 1999). Other contaminants can be more insidious in their impact on decapod crustaceans. For example, endocrine-disrupting chemicals may cause abnormalities such as intersex individuals, which develop anatomical characteristics of both sexes (see Stentiford 2012 and ref-

erences therein, this DAO Special). Intersex was recently observed in *Homarus gammarus* from the English Channel, UK (Stentiford 2012). Observations such as this can yield insight into the effects that contaminants can have on marine organisms and the potential avenues through which contaminants may facilitate susceptibility to pathogens.

The studies included in this DAO Special demonstrate how profoundly pathogens and parasites can impact lobster host populations, and underscore the need to approach disease research proactively and from a multi-disciplinary perspective. Lobsters are relatively hardy organisms and their populations robust to moderate levels of exploitation and habitat alteration. However, when stressed by sufficient fishery exploitation or environmental degradation, these same populations can episodically succumb to pathogens that overwhelm their immunological and behavioral mechanisms of resistance. Understanding this complex interplay between pathobiology and ecology requires us to continue to broaden our scientific approach to include disciplines such as ecology, oceanographic modeling, and fishery stock assessment.

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