



REVIEW

Solar UV radiation modulates animal health and pathogen prevalence in coastal habitats—knowledge gaps and implications for bivalve aquaculture

Gary F. Kett^{1,*}, Sarah C. Culloty^{1,2}, Sharon A. Lynch¹, Marcel A. K. Jansen¹

¹Aquaculture & Fisheries Development Centre, School of Biological, Earth & Environmental Sciences & Environmental Research Institute, University College Cork, North Mall, Cork T23 XA50, Ireland

²MaREI Centre, Environmental Research Institute University College Cork, Cork P43 C573, Ireland

ABSTRACT: Ultraviolet radiation (UVR) is an important environmental factor that can have an impact directly, or indirectly, on the health of organisms. UVR also has the potential to inactivate pathogens in surface waters. As a result, UVR can alter host–pathogen relationships. Bivalve species are threatened by various pathogens. Here, we assessed the impacts of UVR on (i) bivalves, (ii) bivalve pathogens and (iii) the bivalve host–pathogen relationship. UVR consistently impedes pathogens. However, the effect of UVR on marine animals is variable, with both positive and negative impacts. The limited available data allude to the potential to exploit natural UVR for disease management in aquaculture, but also highlight a striking knowledge gap and uncertainty relating to climate change.

KEY WORDS: UV radiation · Bivalve · Pathogen · Host–pathogen dynamics · Aquaculture · Solar disinfection

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1. INTRODUCTION

The United Nations Environmental Effects Assessment Panel (EEAP) has identified the paucity of data surrounding solar disinfection, and its effects on animals and humans, as a major knowledge gap, and that filling this gap is crucial in maintaining health and water security into the future (EEAP 2019). Solar disinfection is the ultraviolet radiation (UVR)-mediated inactivation of pathogens resulting from the impact of UVR on cell structures, such as DNA, lipids and membranes (Kohn et al. 2016, Williamson et al. 2017). Solar radiation is widely recognised as a significant germicide in surface waters (Burkhardt et al. 2000, Lytle & Sagripanti 2005, Williamson et al. 2017), and

is estimated to be responsible for the inactivation of between one-quarter and two-thirds of virus particles in seawater (Noble & Fuhrman 1997). Global bivalve aquaculture has a net worth of over 16 billion USD (FAO 2018); however, in recent years, disease outbreaks and mass mortality events have been increasing at coastal bivalve production sites globally (Samain & McCombie 2008, Lynch et al. 2012, Dubert et al. 2017). Disease outbreaks and mass mortality events have significant economic and social impacts on revenue and local communities (Guilloreau et al. 2017, Krause et al. 2019). Given the important role of bivalve molluscs in sustainable food production and ecosystem functioning (FAO 2018, van der Schatte Olivier et al. 2018), and the recog-

*Corresponding author: g.kett@umail.ucc.ie

nised potential of UVR for pathogen control, it is pertinent to explore the potential impacts of UV on bivalve health and bivalve host–parasite relationships.

The ultraviolet (UV) part of the solar spectrum comprises highly reactive radiation that can be categorised according to the wavelengths as UV-A ($\lambda = 315\text{--}400\text{ nm}$), UV-B ($\lambda = 280\text{--}315\text{ nm}$) and UV-C ($\lambda = 180\text{--}280\text{ nm}$) (EEAP 2019). Only solar UV-A and longer UV-B wavelengths penetrate into the biosphere, although shorter UV-B wavelengths and UV-C are commonly generated by artificial light sources for applications such as disinfection (Acra et al. 1990). Despite the reactive characteristics of all UV wavelengths, such radiation can have both beneficial and detrimental impacts on human, animal, plant and microbial life (EEAP 2019). Examples of positive impacts of UV include immunomodulation and vitamin D synthesis in humans (Grant et al. 2003, Hart et al. 2011). Another beneficial UV effect relates to UV vision, present in many animal species, and its impact on animal–plant relationships, foraging, communication, navigation and mate selection (Hunt et al. 2001, Kevan et al. 2001, Honkavaara et al. 2002, Dyer & Chittka 2004). Negative impacts of UV exposure in humans and animals include mutagenesis, skin cancers, photodermatoses, eye diseases and immune system suppression. In some cases, UV can induce activation of latent herpes simplex virus and human papillomavirus (Norval et al. 2007). Yet, UV is also widely known as a disinfectant of bacterial, viral, fungal and protozoan pathogens (Morris 1972, Chang et al. 1985, Acra et al. 1990).

Penetration of UVR through the water column depends on absorption and scattering, primarily caused by coloured dissolved organic matter (CDOM) and suspended particulate matter, respectively. The latter includes both biotic, e.g. phytoplankton, and abiotic matter (Scully & Lean 1994, Nelson & Guarda 1995, Aphalo & Albert 2012). In turn, optical properties of water are dependent on climate characteristics such as temperature, acidification, and local circulation and mixing patterns, which can all affect the levels and distribution of organic matter in the water column (Behrenfeld et al. 2006, Brewin et al. 2015). UV penetration depth is also dependent on the UV wavelength as shorter wavelengths are attenuated more rapidly, thus UV-A travels further through the water column than UV-B, which is usually attenuated in the upper photic layer (Smyth 2011). Tedetti & Sempéré (2006) provide a review on UV penetration depths in a range of marine habitats. Coastal waters have relatively low UV penetration compared with open oceans. The $Z_d(10\%)$ value, i.e. the depth at

which the surface irradiance is reduced to 10%, ranges from 0.2 to 13 m and 0.08 to 6 m, for UV-A (340 nm) and UV-B (305 nm), respectively, for coastal waters of Northern Europe. In comparison, in the open Atlantic Ocean, the $Z_d(10\%)$ for UV-A and UV-B can be as much as 38 and 17 m, respectively (Tedetti & Sempéré 2006).

Bivalve molluscs, such as mussels, clams, scallops, cockles, abalone and oysters, are calcifying, filter-feeding, intertidal organisms. Bivalve consumption has grown by almost 3% annually since 2000, and bivalves have been identified as an important food source to meet the growing demands of a rapidly expanding world population (FAO 2018). Bivalves are also of great ecological significance, providing a range of ecosystem services such as water filtration, denitrification and carbon sequestration (Gallardi 2014, van der Schatte Olivier et al. 2018). Maintaining healthy bivalve populations is key to their ecosystem function, and central to sustainable culturing (FAO 2018). At present, natural and farmed bivalve populations are challenged by a wide variety of water-borne pathogens and parasites. Bivalve molluscs can easily accumulate water-borne pathogens due to the filtration of large volumes of water (Ben-Horin et al. 2015, Song et al. 2016). Bivalve molluscs, like other organisms, have mechanisms of defence against UV radiation. The exterior calcium carbonate shell, which is coloured with pigments such as melanin, carotenoids and tetrapyrroles, protects the soft internal tissues from the external environment, including UVR (Williams 2017). Internally, bivalves contain photoprotective compounds such as mycosporine-like amino acids (MAAs) and carotenoids (Goto-Inoue et al. 2020).

Primary pathogens of interest to bivalve aquaculture in Europe are the Osterid herpesvirus (OsHV-1) and its variants (OsHV-1 μ Var) as well as bacterial species of the genus *Vibrio*, e.g. *V. aestuarianus* and *V. splendidus*. These pathogens have been linked to recurring episodes of mass mortalities in Pacific oysters *Crassostrea gigas* throughout Europe (Samain & McCombie 2008, Lynch et al. 2012, Pernet et al. 2014, Barbosa-Solomieu et al. 2015, EFSA 2015). Other *Vibrio* species that have been linked to disease and mortality in bivalves include *V. anguillarum*, *V. tubiashii* and *V. tapetis* (Ben-Horin et al. 2015, Travers et al. 2015). Other common bacterial pathogens include species of the genera *Pseudomonas*, *Aeromonas* and *Nocardia*. Common viral diseases are caused by *Iridoviridae* species including gill necrosis virus (GNV), haemocyte infection virus (HIV) and oyster velar virus (OVV) (Zannella et al. 2017). Noroviruses

(NoV), belonging to the *Calciviridae*, are particularly problematic as they can be transferred from bivalve molluscs to humans upon ingestion, leading to outbreaks of viral gastroenteritis (Bartsch et al. 2016, Razafimahefa et al. 2020). Furthermore, UV depuration of bivalves, which effectively reduces most bacterial contamination, is not capable of reducing NoV loads below infectious doses (McLeod et al. 2017). Protozoans have also caused great damage to bivalve production sites. Oysters and clams have experienced outbreaks of diseases caused by species belonging to the genera *Bonamia*, *Marteilia*, *Haplosporidium* and *Perkinsus* (Culloty & Mulcahy 2007, Engelsma et al. 2014, Zannella et al. 2017). The losses associated with these outbreaks pose a significant threat to the global mollusc aquaculture industry, which had an estimated worth of 30 billion USD in 2016 (FAO 2018). Outbreaks of bivalve diseases are expected to increase in coming years due to changing marine environments (Callaway et al. 2012, Rowley et al. 2014).

In the present review, the relationship between marine bivalves, pathogens and UV radiation was explored (Fig. 1). A search of published literature was undertaken, using a combination of pertinent terms: ultraviolet, UV, UV-A, UV-B, UV-C, solar radiation, health, immuno-suppression, immuno-modulation, disease, pathogen, parasite, bivalve and host-parasite interaction. Databases searched include: ScienceDirect, Web of Science, JSTOR, Scopus, Wiley Online Library and Google Scholar. The aim of the analysis presented in this paper is to (1) capture existing knowledge on the effects of UVR on bivalves, their water-borne pathogens and parasites, and the relationship between them, and (2) to explore the potential future role of solar UV-A and UV-B in the biosecurity of commercial bivalve aquaculture.

2. EFFECTS OF UVR ON ORGANISMS AND SYSTEMS

2.1. UV and marine macrobiota

A large number of reviews and meta-analyses have been produced in recent years encapsulating the current research regarding the effects of UVR on aquatic biota. Here, these reviews are discussed with reference to the findings of over 7000 studies. There has been considerable research into the effects of UVR on marine organisms such as zooplankton (Williamson et al. 1994), crustaceans (Rautio & Tarrantotti 2010), echinoderms (Lamare, et al. 2011), gas-

tropods (Davis et al. 2013), fish (Blazer et al. 1997) and cetaceans (Martinez-Levasseur et al. 2013). However, effects of UVR on bivalve species have not been studied to the same extent as for other animal groups. This is a knowledge gap that needs to be addressed to enhance food production and to better understand ecosystem interactions. Dahms & Lee (2010) reviewed the literature surrounding UVR impacts on marine ectotherms and concluded that UVR is a threat to natural populations as reproductive health is impaired by UVR, although defence mechanisms, avoidance or repair can offset damage. Lamare et al. (2011) reviewed 65 publications regarding UVR and echinoderms and found that UV induced strong avoidance responses while also boosting protective damage repair mechanisms. Their review discusses different types of damage including inhibited development, fertilization and motility in sperm, and increased mortality and DNA damage. Llabrés et al. (2013) reviewed 1784 experiments involving UV-B and marine biota including cnidarians, crustaceans, echinoderms, tunicates, fish

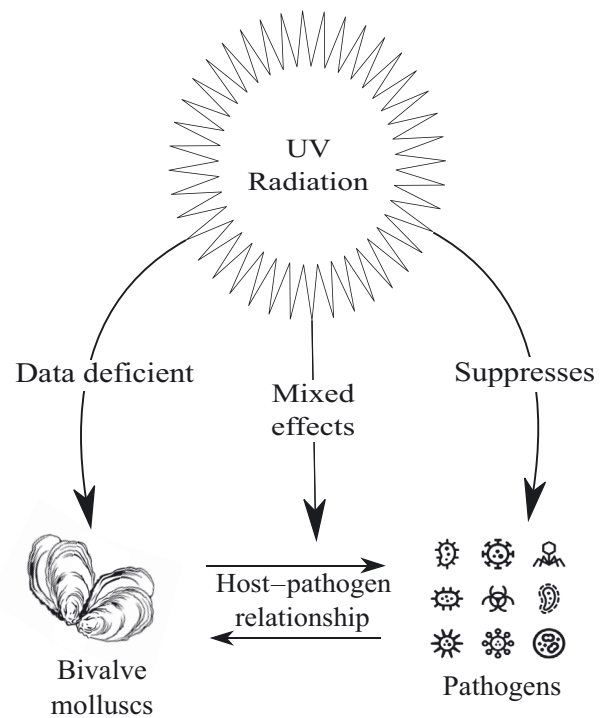


Fig. 1. Schematic depicting the potential effects of ultraviolet radiation (UVR) on host-pathogen relationships. UVR can suppress pathogens mainly through deleterious effects on DNA. UVR can also impact on molluscs, although the literature is poorly developed. Finally, UVR can modulate the immune system of the mollusc, altering host-pathogen relationships. The net UV effect on host-pathogen relationships is highly variable and can include antagonistic, additive or synergistic effects

and molluscs, amongst others. The most common finding was increased mortality following exposure to UV-B. More recently, Jin et al. (2017) analysed results of 4995 studies on the responses of marine and freshwater algal species to UV. Mortality was the most common response to increased UV-B, followed by molecular and cellular alterations. Peng et al. (2017) analysed 146 studies on 127 species of freshwater plankton, fish and amphibians and concluded that UV-B had a significant negative effect on metabolism, behaviour, growth and reproduction, cellular-molecular responses and survival. The literature contains ample evidence of detrimental UV effects on marine organisms. Yet, no reference to bivalve molluscs was found in any of the aforementioned studies.

One further area where literature is lacking is in the responses of different life stages to UVR. This gap in knowledge is particularly relevant where larval, juvenile or adult life stages display different physiological, biochemical and/or behavioural traits. Macroalgal spores are more susceptible to UV damage than sporophytic and gametophytic structures (Roleda et al. 2007, Jin et al. 2017). Similarly, early life stages, i.e. gametes and larvae, of many heterotrophs and ectotherms are more vulnerable to UV-induced damage than juveniles or adults, as described in multi-species meta-analyses (Bancroft et al. 2007, Dahms et al. 2011, Llabrés et al. 2013). However, UV sensitivity of early life stages is not universal, and some studies have shown the opposite (Jokinen et al. 2008, Peng et al. 2017). It is important to be aware of variations in sensitivity and tolerance, as different life stages may inhabit different spatio-temporal niches characterised by different UVR intensities (Dahms et al. 2011, Alves & Agustí 2020). For example, the larval stage of some species is planktonic and inhabits the upper photic layer, where UV exposure is most relevant, especially under certain environmental conditions, e.g. low phytoplankton and nutrient levels, clear cloudless skies and low ozone areas (Dahms et al. 2011).

Effects of UV-B exposure on marine biota may be direct, as described above, or indirect, mediated through trophic chains. For instance, UV-B exposure can decrease the polyunsaturated fatty acid (PUFA) content in phytoplankton (Wang & Chai 1994, Skerratt et al. 1998), with subsequent effects on consumers. Primary producers are the main source of PUFAs in the marine environment (Guschina & Harwood 2009, Zhukova 2019). PUFAs are important dietary elements in vertebrates and invertebrates alike, and are essential for cell membrane function, acting as precursors to hormones and modulating

immune systems (Brett & Müller-Navarra 1997, Zhukova 2019). PUFAs can support immune function in shellfish (Delaporte et al. 2003), fish (Arts & Kohler 2009) and other vertebrates, including humans (Wu & Meydani 1998, Calder 2014, Venugopal & Gopakumar 2017). High PUFA diets for bivalve molluscs such as Manila clams *Ruditapes philippinarum* and Pacific oysters *Crassostrea gigas* can modulate immune function through increases in total haemocyte count (THC), percentage of granulocytes, phagocytic rate and oxidative activity (Delaporte et al. 2003). Moreover, haemocytes of *C. gigas* supplemented with the PUFA arachidonic acid (ArA) display lower susceptibility to the common bacterial pathogen *Vibrio aestuarianus* (Delaporte et al. 2006).

2.2. UV in pathogens and parasites

Parasitism is often perceived as a negative biotic stress for host organisms. Yet, parasites also play an important role in regulating host populations by influencing behaviour, growth and reproductive success, as well as affecting community structure and trophic interactions (Marcogliese 2004, 2008). Nevertheless, due to the threat posed by aquatic microbes to humans, wildlife and commercial species, the level of UV required to inactivate bacterial, viral, protozoan and fungal pathogens has been researched in considerable detail. Studies predominately show an inhibitory effect, i.e. disinfection of pathogens by UV radiation, although the extent of disinfection depends on many factors such as wavelength, dose and pathogen biology (Morris 1972, Chang et al. 1985, Acra et al. 1990, Liltved et al. 1995, Williamson et al. 2017). Shortwave UV-C (~254 nm; generated using artificial UV lamps) is frequently used to inactivate pathogens in water, food products, crops and equipment, and aquaculture products (Gray, 2014). However, longer-wave, solar UV-B and UV-A radiation may also affect parasitism either through direct or indirect exposure effects (Häder et al. 2015). The antimicrobial properties of solar UVR have been utilised to create cheap and effective water purification treatment (Acra et al. 1990, Wegelin et al. 1994, Dejung et al. 2007, Davies et al. 2009). UV treatment, particularly using UV-C, is effective in inactivating various classes of pathogens including bacteria, viruses, protozoans and fungi (Hijnen et al. 2006). The mechanisms behind UV-induced damage and repair of DNA, proteins and lipids are beyond the scope of this review, but comprehensive information on these topics can be

found in Sinha & Häder (2002), Buma et al. (2003), Hijnen et al. (2006) and Rastogi et al. (2010).

3. EFFECTS OF UVR ON BIVALVES, THEIR PATHOGENS AND HOST-PATHOGEN RELATIONSHIPS

3.1. Effects of UVR on bivalve molluscs

A total of 8 published studies on the effects of UVR on bivalve molluscs were found in the literature (Table 1). Some studies (4) explicitly identified a role of UV-B; otherwise, studies showed the combined effects of UV-B, UV-A and/or photosynthetically active radiation (PAR) or the combined influence of UVR, temperature and light. UV can reduce the diversity and biomass of the biofouling community, including *Mytilus edulis*, yet these effects can be transitory (Wahl et al. 2004). In that study, UV-A had a greater effect on decreasing biomass and diversity of shallow fouling communities than UV-B, although both together had the strongest effect. Similarly, UV exposure can reduce the surface cover of the green mussel *Perna viridis* and the horse mussel *Modiolus comptus* compared to a no-UV treatment (Dobretsov et al. 2005). Conversely, *M. edulis* density and recruitment can be positively correlated with UV-B and broadband UV, respectively (Lotze et al. 2002, Molis et al. 2003). With regard to dispersal and survival, Hoyer et al. (2014) found no negative effect of UV on the larvae of the Asian clam *Corbicula fluminea*. At the molecular level, Regoli et al. (2000), measured the total oxidant scavenging capacity of scallops from polar (*Adamussium colbecki*, *Chlamys islandicus*) and temperate (*Pecten jacobaeus*) regions. It was found that the Antarctic scallop *A. colbecki* had significantly higher total oxidant scavenging capacity compared to the temperate and northern species. It is hypothesised that this difference is due to exposure to higher UV doses in clear Antarctic waters. The authors discussed the implications of this finding in the sense that UVR can induce photolysis of dissolved organic matter to produce H_2O_2 , thus exposing aquatic biota to increased reactive oxygen species (Abele et al. 1998), while also altering the ability of animals to respond to external stressors. Thus, published studies reveal a wide range of positive effects, e.g. increased recruitment and density (Lotze et al. 2002, Molis et al. 2003), negative effects, e.g. reduced biomass and surface cover (Wahl et al. 2004, Dobretsov et al. 2005), and neutral effects (Hoyer et al. 2014) of UVR on various aspects of bivalve biol-

ogy. Species from different geographic regions exhibit varying capabilities to respond to UV, although UV-tolerant species can still be affected by sudden increases in UV exposure (Regoli et al. 2000).

3.2. Effects of UV on mollusc pathogens

Table 2 displays the studies found which investigated the use of UV to inactivate pathogens commonly found in bivalves. Liltved et al. (1995) examined the inactivation of bacterial and viral pathogens, problematic to aquaculture, under UVR. It was found that ubiquitous *Vibrio* bacteria, pathogenic to many bivalve species, were sensitive to UV-C irradiation. *Vibrio anguillarum* and *V. salmonicida* required exposure of 1.8 and 1.5 mWs cm^{-1} UV-C, respectively, to achieve 99.9% inactivation. In comparison, the bacterium *Yersinia ruckeri*, primarily a fish pathogen but recently identified in bivalve species (Chistyulin et al. 2017), is more resistant and required exposure of 2.7 mWs cm^{-1} UV-C to achieve 99.99% inactivation. Joux et al. (1999) investigated the effects of UV-B (0.23 mW cm^{-1}) on various bacterial species associated with disease outbreaks in bivalve aquaculture e.g. *Vibrio natriegens* and *Pseudomonas* spp. These bacteria have been linked to summer mortality syndrome and bacillary necrosis at bivalve production sites (Paillard et al. 2004, Garnier et al. 2007, Zannella et al. 2017). It was found that *V. natriegens* was the most sensitive to UV-B, yet also exhibited a 'very effective' UV-A-mediated photoreactivation pathway that repaired UV-B-induced DNA damage. Fernández Zenoff et al. (2006) measured the resistance of bacterial species collected from different altitudes to UV-B radiation (intensity: 0.33 mW cm^{-1} , dose: 3.931 kJ m^{-2}). Many of the bacteria examined are known to be pathogenic to bivalve species. For example, *Actinobacteria* are a group which contains *Nocardia crassostreae* and *Cytophaga* sp., species that are aetiological agents of 'nocardiosis' and 'hinge ligament erosion' diseases in oysters, respectively (Travers et al. 2015, Zannella et al. 2017). Fernández Zenoff et al. (2006) found that bacterial survival was dependent on strain origin. For example, *Pseudomonas* sp. from the marine environment showed the lowest resistance to the UV-B dose, compared to the high-altitude-originated *Pseudomonas* sp. The authors also measured the recovery of the bacteria studied and found significant variation between recovery strategies independent of habitat of origin. The highest accumulation of cyclobutane

Table 1. Impact of ultraviolet radiation (UVR) on bivalve species. Experiment types are as follows: SUP: supplementary, i.e. experiment was carried out using supplementary UV-emitting bulbs; EXCL: exclusion, i.e. experiment utilised UV-blocking filters to compare effect of natural light against specific wavelength-excluded light; MAT: mathematical model utilised to study impact of stressor, i.e. no manipulation experiment carried out

Study organism	Treatment	Experiment type	Experiment description	Result	Role of UV in result	Reference
Eastern oyster <i>Crassostrea virginica</i>	UV (unspecified)	Unspecified	<i>C. virginica</i> transplanted to polluted dock and larvae of these were exposed to UVR	Growth rates reduced in larvae	Not identified	Peachey (2003)
Giant clam: <i>Tridacna gigas</i> & dinoflagellates	UV-A & B	EXCL	Clams with symbiotic algae kept in aquaria exposed to natural sunlight. Objective of experiment was to study effect on algae	Results focused primarily on <i>Zooxanthellae</i> population. No biological parameters of clams investigated	Not identified	Buck et al. (2002)
Asian clam: <i>Corbicula fluminea</i>	Full spectrum UVR	MAT	Modelling experiment to determine the drivers of larvae dispersal of invasive bivalve	UV radiation is not a main driver of larvae dispersal or mortality	Not identified	Hoyer et al. (2014)
Clam spp.: <i>Arca</i> spp.	10 % above ambient	SUP	Mylar filters and solar simulators used. Only recorded mortality	No reduction in mortality observed.	Not identified	Reaka-Kudla et al. (1993)
Blue mussel: <i>Mytilus edulis</i> & macrobenthic flora/fauna	0.258–0.384 W m ⁻¹ UV-B	SUP	Aquatic settlement panels with UV lamps to investigate impact on community structure, density and biomass	Mussel density positively correlated with UV-B. Effect was not long lived and may have been due to shading algae	Identified species composition & diversity	Molis et al. (2003)
Blue mussel <i>Mytilus edulis</i> & (UV-A, UV-B and PAR) algal species	Solar radiation (UV-A, UV-B and PAR) 0.04 W m ⁻¹ UV-B	EXCL	Floating raft with wavelength exclusion filters to examine impact of UV on community structure	High UV (August) positively related with mussel recruitment	Identified settlement/community structure	Lotze et al. (2002)
Blue mussel: <i>Mytilus edulis</i> & macrobenthic flora/fauna	Solar radiation (30 W m ⁻¹) UV-B & UV-A	EXCL	Floating raft with wavelength exclusion filters to examine impact of UV on community structure	UV-B reduced diversity and biomass but not as much as UV-A and effects were short-lived	Identified Community structure	Wahl et al. (2004)
Green mussel: <i>Perna viridis</i> & Horse mussel: <i>Modiolus comptus</i>	Solar radiation UV-B & UV-A	EXCL	Floating raft with wavelength exclusion filters to examine impact of UV on community structure	Exposure to UVR reduced the % cover of bivalve species	Not identified	Dobretsov et al. (2005)
Antarctic scallop: <i>Adamussium colbecki</i>	1.8 W UV-B & 1.0 W UV-A radiation (60 h)	SUP	Experiment designed to measure total oxyradical scavenging capacity (TOSC) in polar and temperate scallop species	Exposure to UV-A and UV-B significantly reduced antioxidant capabilities in scallops	Identified UV-A & B reduced TOSC by 25 – 35 % UV-A only was less effective at 15 – 20 %	Regoli et al. (2000)

Table 2. Impact of UVR on marine pathogens. Experiment types are as follows: SUP: supplementary, i.e. experiment was carried out using supplementary UV-emitting bulbs; EXCL: exclusion, i.e. experiment utilised UV-blocking filters to compare effect of natural light against specific wavelength-excluded light. CPD: cyclobutane pyrimidine dimer

Study organism	Host species	Treatment	Experiment type ^a	Experimental design	Result	Role of UV-B in result	Reference
Bacterial pathogens							
<i>Vibrio natriegens</i> , <i>Sphingomonas</i> sp., <i>Pseudalteromonas haloplanktis</i> , <i>Deleya aquamarina</i> , <i>Pseudomonas stutzeri</i>	Fish and shellfish	950 –1500 J m ⁻¹ UV-B	SUP	Bacteria exposed to UV-B bulbs and left to recover in UV-A; measured resulting CPDs and sensitivity to UV-B	<i>V. natriegens</i> is very sensitive to UV-B; photorepair mechanism evident	Identified inactivation of bacteria	Joux et al. (1999)
<i>Actinobacteria</i> sp., <i>Pseudomonas</i> sp., <i>Cytophaga</i> sp., <i>Serratia</i> sp.	Fish and shellfish	3.9 kJ m ⁻¹ UV-B	SUP	Measured bacterial survival, resistance, dimerization and photo-repair rates under UVR	Inactivated 63 % of bacteria; survival, resistance, CPD formulation and repair occurred in all species but responses varied	Identified responsible for all results	Fernández Zenoff et al. (2006)
<i>Vibrio anguillarum</i> <i>Vibrio salmonicida</i> <i>Yersinia ruckeri</i>	Fish and shellfish	UV-C (254 nm)	SUP	Measured inactivation of pathogens under short-wave UV	UV Inactivated 99.9 % of bacteria with 1.5 – 2.8 mWs cm ⁻¹	Identified inactivation of bacteria	Lilved et al. (1995)
Viral pathogens							
Norovirus (NoV) GI, GII, F-specific RNA (FRNA) bacteriophage	Bivalve molluscs and humans	Simulated solar radiation	SUP	Measured inactivation of viral pathogens under full spectrum solar UV	Summer UV conditions reduced detection of NoV and FRNA significantly faster than winter UV conditions	Identified inactivation of virus and bacteriophage	Flannery et al. (2013)
OsHV-1 μ Var	Bivalve molluscs	UV-C 1.08 mW cm ² at 254 nm	SUP	Oyster tissue homogenates containing OsHV-1 μ Var were exposed to UV-C and then injected into healthy oyster tissue	UV irradiation of filtered tissue homogenates was successful in removing viral DNA. Healthy oysters injected with UV treated homogenate did not experience mortality	Identified inactivation of virus	Schikorski et al. (2011)
Range of viruses & bacteriophages	Unspecified	Natural solar radiation	EXCL	Investigated rates of decay and infectivity of virus particles under UV	All viruses decayed significantly faster under UV light	Identified decay of bacteriophages	Noble & Fuhrman (1997)
Viral species LMG1-P4, PWH3a-P1, LBIVL-P1b	Unspecified	Natural solar radiation	EXCL	Examined mechanisms and radiation rates of viral decay from solar radiation	All viruses highly sensitive to solar radiation; decay rates ranged from 2 – 10 times higher than dark controls	Identified decay of viruses	Suttle & Chen (1992)
Protozoan parasite							
<i>Cryptosporidium parvum</i>	Mammals	0, 32 and 66 kJ m ⁻¹ UV-B	SUP & EXCL	Both lab and field experiments using UV-B lamps and UV-blocking filters to determine whether oocyst infectivity into human cells was affected by UV-B	Artificial doses of 32 and 66 kJ m ⁻¹ reduced infectivity by 58 and 98 %; natural exposure doses or half or full solar intensity reduced infectivity by 67 and >99 %	Identified reduced oocyst infectivity	Connelly et al. (2007)

pyrimidine dimer (CPD) photoproducts, and the most efficient recovery, under both light and dark treatments, were exhibited in *Acinetobacter johnsonii* and *Cytophaga* sp., whereas *Pseudomonas* strains had low survival after UV-B exposure and demonstrated low capacity to recover through photoreactivation.

The infectious pancreatic necrosis virus (IPNV) is pathogenic in fish and has been isolated in bivalves (Mortensen et al. 1992, Renault & Novoa 2004). IPNV has much higher resistance to UV-C than bacteria within the same study (122 mWs cm⁻¹ for 99.9% inactivation) compared to the aforementioned bacterial species *V. anguillarum* and *V. salmonicida* (1.8 and 1.5 mWs cm⁻¹ for 99.9% inactivation) (Liltved et al. 1995). UV-C can also inactivate ostreid herpesvirus 1 (OsHV-1) (Schikorski et al. 2011). In the latter study, oyster tissue homogenate containing OsHV-1 DNA was exposed to UV-C (254 nm, 1.08 mW cm⁻¹) and subsequently injected into healthy oysters, yet no mortality was observed. In comparison, when oysters were injected with OsHV-1 DNA that had not been exposed to UV-C, mortality was recorded. Norovirus, which is harboured in bivalves and is the aetiological agent of many gastroenteritis outbreaks in humans, can be deactivated by UV-C radiation. Flannery et al. (2013) used full-spectrum solar radiation to reduce detection of Norovirus (NoV) via RT-qPCR by 90% under conditions set to replicate summer (23.5 mW cm⁻¹, 1.8 kJ cm⁻¹ for 21 h) and winter (5.6 mW cm⁻¹, 0.5 kJ cm⁻¹, 89 h) in Ireland. Flannery et al. (2013) found that natural solar UV, rather than temperature, within the summer conditions, was a greater driver of NoV inactivation, and the difference in time required to inactivate 90% of NoV was a direct function of increased irradiance of summer compared to winter. These data suggest that although bacterial, viral and protozoan pathogens react negatively to UV exposure, the tolerance and recovery capabilities of different pathogens varies between taxa and geographic origin.

3.3. Effects of UV on host–pathogen relationships

Studies investigating the impact of UVR on non-bivalve host–pathogen relationships have led to variable conclusions regarding the overall net effect on parasitism (Table 3). Ruelas et al. (2009) examined the effect of UV-B on the freshwater molluscan gastropod *Biomphalaria glabrata* and the parasitic relationship with the miracidia of the trematode *Schistosoma mansoni*. It was found that UV-B exposure caused harm to the host, expressed as reduced survival, without af-

fecting the parasite. A variation on this scenario is where exposure to UVR negatively affects both parasite and host. An example was observed by Studer et al. (2012), who noted that UVR reduced the survival of parasitic trematode cercariae *Maritrema novaezealandensis*, but also increased host susceptibility in the amphipod *Paracalliope novizealandiae*. In this example, the most prominent effect observed was reduced parasite survival, but this may be compensated by reduced host fitness. Overall, the authors note that the net effect of this scenario is likely to be neutral; however, interactive compounding environmental variables would likely affect this interaction *in situ*. Alternatively, UVR can reduce parasitism without seemingly affecting the host, as is the case for of the crustacean host *Daphnia dentifera* and its fungal pathogen *Metschnikowia bicuspidata* (Overholt et al. 2012). In the study by Overholt et al. (2012), fungal spores were damaged by all wavelengths examined, ranging from shortwave UV-B to longwave UV-A and even PAR. In contrast, the host organism *D. dentifera* did not exhibit decreased survival unless an extremely high UV dose of 32 kJ m⁻¹ was administered, compared to the 0.7 kJ m⁻¹ required to reduce infectivity of the fungal spores. The authors note that the difference in UV tolerance between the fungal parasite and the crustacean host is primarily due to the presence of photoenzymatic DNA repair in the host. In other studies, it was found that exposure to both UVR and pathogens can synergistically increase negative impacts on hosts. For example, this was observed by Kiesecker & Blaustein (1995), who showed that amphibian embryos experienced higher mortality when simultaneously exposed to UVR and a fungal pathogen. Evidently, UVR affects host–pathogen relationships with varied net effects.

Just a single study has included UVR as a factor when studying host–pathogen relationships of bivalves. Bettencourt et al. (2013) studied the relationship between the Palourde clam and *Escherichia coli*. The authors found that *E. coli* infection was affected by seasonality, i.e. infection was lowest during summer months associated with high solar UVR, high temperature and low rainfall. However, the data do not conclusively show a specific UV effect.

4. DISCUSSION

Empirical research, reviews and meta-analyses have shown that aquatic invertebrates and vertebrates respond to UV with a mixture of negative (decreased survival, impaired metabolism, growth and reproduction) and neutral or positive (behavioural avoidance

Table 3. Impact of UVR on host–parasite interactions. Experiment types are as follows: SUP: supplementary, i.e. experiment was carried out using supplementary UV-emitting bulbs; EXCL: exclusion, i.e. experiment utilised UV-blocking filters to compare effect of natural light against specific wavelength-excluded light

Study organism	Treatment	Experiment type	Experiment design	Result	Role of UV-B in result	Reference
AQUATIC INVERTEBRATES						
Host: Palourde clam <i>Ruditapes decussatus</i> Parasite: Bacteria: <i>Escherichia coli</i>	Natural solar radiation	n/a	Clams collected from field throughout year and screened for <i>E. coli</i>	Correlation between high temperature/solar radiation with low <i>E. coli</i> infection	Not identified	Bettencourt et al. (2013)
Host: Freshwater snail <i>Biomphalaria glabrata</i> Parasite: Trematode: <i>Schistosoma mansoni</i>	500, 625, 750, 825 and 1000 J m ⁻¹ UV-B	SUP	Examined effect of UV-B on survival of infected snails and susceptibility and resistance of snails to infection	UV-B lowered survival in infected snails; UV-B had no effect on susceptibility or resistance to infection	Identified survival of infected snails	Ruelas et al. (2009)
Host: Crustacean <i>Daphnia</i> spp. Parasite: Fungal: <i>Metschnikowia bicuspidata</i>	9.5 – 15 kJ m ⁻¹ UV-B	SUP	Lab and field experiments to determine susceptibility of host and infectivity of parasite under UVR	UV-B reduced infectivity of parasite but did not alter susceptibility of host to infection	Not identified	Overholt et al. (2012)
AQUATIC VERTEBRATES						
Host: Wistar rats <i>Rattus norvegicus</i> Parasite: Nematode: <i>Trichinella spiralis</i>	800 mJ (45% UV-B)	SUP	Rats infected with <i>T. spiralis</i> exposed to UVR to investigate impact of radiation on infection & immunosuppression	UV-B suppresses resistance to parasitic infection; radiation suppresses cellular immune response	Identified immuno-suppression	Goettsch et al. (1994)
Host: Amphibian species <i>Bufo boreas</i> , <i>Hyla regilla</i> , <i>Rana cascadae</i> Parasite: Fungal: <i>Batrachochytrium dendrobatidis</i>	17.9 µW cm ⁻¹ UV-B	EXCL	Investigated combined effect of fungal pathogen & UV-B; measured frog mortality	No effect was found from UV-B alone nor synergistic with fungus	Not identified	Garcia et al. (2006)
Host: Amphibian embryos: <i>Bufo boreas</i> , <i>Hyla regilla</i> , <i>Rana cascadae</i> Parasite: Fungal: <i>Saprolegnia ferax</i>	Natural solar UV-B	EXCL	Field experiment to test synergism between exposure to UV-B and fungal pathogen	Results showed synergistic effect of UV-B and pathogen which caused mortality higher than stressor alone	Identified induced mortality in pathogen & host	Kiesecker & Blaustein (1995)
Host: Snail: <i>Zeacumantus subcarinatus</i> Amphipod: <i>Paracalliope novizealandiae</i> Parasite: Trematode: <i>Maritrema novaezealandensis</i>	PAR + UV-A + UV-B, 5.84 kJ m ⁻¹ UV-B (> 300 nm)	EXCL, SUP	Experiment aimed to investigate effect of UVR on trematode transmission through life stages	UVR had negative effect on both survival and infectivity of cercariae—net effect neutral	Not identified (results discussed as UVR)	Studer et al. (2012)
Host: Fish: <i>Gambusia holbrooki</i> Parasite: Protozoan: Whitespot <i>Ichthyophthirius multifiliis</i>	0.23 W m ⁻¹ and 0.47 W m ⁻¹ UV-B, UV-A and PAR present	SUP	Experiment designed to test effect of temperature and UV-B on the energy consumption and disease susceptibility	Synergistic effect of high UV-B and high temperature which caused large rise in infection intensity	Identified UV-B and temperature suppressed metabolism and exacerbated infection	Cramp et al. (2014)

and/or defence, and upregulation of molecular defence and/or repair mechanisms) responses. Some evidence exists for UV impacting negatively on bivalve growth (Peachey 2003), antioxidant capacity (Regoli et al. 2000) and surface cover (Wahl et al. 2004, Dobretsov et al. 2005). In contrast, positive effects of UV exposure included increased density (Molis et al. 2003) and recruitment (Lotze et al. 2002). No studies could be found which investigated the impact of UV on bivalve health including immune response or pathogen prevalence. There is evidently a noticeable shortage of data on the UV biology of bivalve molluscs, which hinders our comprehension of the effects of such radiation on coastal ecosystems. It is important to understand the effects of environmental conditions on organisms in order to maintain their ecological and economic functions. Furthermore, a better understanding of the impacts of current environmental conditions such as UVR is required to better predict animal health in future scenarios of a rapidly changing climate.

Bivalve molluscs face threats from various pathogens and parasites (Walker 2004, FAO 2018). Thus, any factor modulating organismal health and immune responses is relevant, especially in the context of the economic and ecological value of bivalve molluscs. Generally, UVR has diverse impacts on host–pathogen relationships. The literature contains case studies of UV-induced increases in infection, generally due to reduced host health or immunosuppression (Ruelas et al. 2009), as well as cases of net decreases in parasitism (Overholt et al. 2012). Additionally, UVR may have negative effects on both host and parasite, which can render the net effect on parasite transmission neutral (Studer et al. 2012). While these observations are far from conclusive, they allude to the potential to exploit natural UVR solar disinfection for disease management in the aquaculture industry through optimised management and handling practices. Specific information related to the biology of hosts and parasites is needed to predict outcomes of UVR on systems in question, and these should be addressed on a case-by-case basis to avoid making generalisations. Improved understanding of the effects of UV on bivalve–pathogen relationships is required to ascertain whether natural UV can be exploited as a tool for modulating bivalve host–pathogen interactions in shellfish aquaculture.

A clear pattern of pathogen responses to UV exposure emerges from the literature reviewed. A negative ‘inactivation’ or ‘decay’ response from bacterial, viral, bacteriophage and protozoan species is widely reported, reducing the overall pathogen presence or

infectability. UV exposure has been shown to be detrimental to the survival of common bivalve pathogens such as *Vibrio* spp., OsHV-1, NoV and *Cryptosporidium*. This finding was expected given the widespread commercial application of UV-C in disinfection and sterilisation. However, the data presented show that UV sensitivity, for example of *Vibrio natriegens* (Joux et al. 1999), extends into the UV-B wavelengths, indicating the potential for natural solar radiation to decrease the risk of water-borne pathogens. It is important to note the variation in dosages used in these experiments, ranging from 0.9 kJ m⁻¹ UV-B as used to inactivate *Vibrio* spp. (Joux et al. 1999) to 3.9 kJ m⁻¹ UV-B as used by Fernández Zenoff et al. (2006) to inactivate *Pseudomonas* spp., up to 66 kJ m⁻¹ UV-B as used by Connelly et al. (2007) to reduce infectivity of protozoan oocysts. In 2019, the daily UV-B levels received at the Irish Meteorological Service station in the southwest of Ireland ranged from 0.03 to 4.32 kJ m⁻¹ (Met Eireann, unpubl. data). A better understanding of pathogen inactivation under natural solar UVR is required in order to apply this process to coastal aquaculture.

A common scenario of UV-modulated changes in host–pathogen relationships relates to UV-mediated changes in pathogenicity. However, it is worth noting that an inverse relationship also exists where parasitism modulates UV exposure in bivalves. For example, parasitized cockles *Cerastoderma* spp. and Manila clams *Ruditapes philippinarum* are more often found closer to the sediment surface, where UV levels are higher, compared to healthier counterparts (Thomas & Poulin 1998, Blanchet et al. 2003, Nam et al. 2018). In another instance, oysters *Crassostrea virginica* and *Ostrea edulis* infected with a surface-coating *Vibrio* infection had under-calcified, fragile shells compared to healthy oysters (Elston et al. 1982). Such, parasite-related changes to host biology may leave these animals more vulnerable to a range of environmental factors, and potentially result in exposure to higher UVR doses. These observations show the complexity of the interactions between bivalves, pathogens and UVR.

Full understanding of the effects of UVR on organisms requires knowledge of both dose–response curves and wavelength–response curves (Paul & Gwynn-Jones 2003). As is the case with much of the photo-ecology literature, a strong bias exists in favour of research based on the use of high UV doses, i.e. research focused on assessing the impacts of high UV doses associated with stratospheric ozone depletion (Paul & Gwynn-Jones 2003, Jansen & Bornman 2012). It is only in some areas of research that the

perception of the biological impacts of UVR has shifted to the environmental role of low doses of natural UV. These low doses may act as a regulator of specific processes and/or as an environmental cue rather than an 'abiotic stressor' (Jansen & Bornman 2012). In the field of plant science research, UV is known as a regulator of biochemical pathways by inducing transcriptional responses and signalling pathways (Pontin et al. 2010, Jansen & Bornman 2012, Krasylenko et al. 2012). However, in zoological studies, the potential of UV to act as an intrinsic biochemical modulator and/or immunoregulator has not been fully investigated.

5. FUTURE OUTLOOK

Manipulation of host–pathogen relationships can enhance biosecurity and support sustainable production in the aquaculture sector. UVR is a natural factor that can potentially be exploited to alter host–pathogen relationships. However, the current knowledge base is too narrow to fully comprehend the potential impacts of UVR. More high-quality research is needed with a strong emphasis on accurate reporting of experimental conditions, and especially UV doses and spectra. It is important to use ecologically relevant UV doses, i.e. wavelength, intensity and exposure duration, when investigating potential impacts on host–pathogen relationships *in situ*. Due to bell-shaped dose–response curves, low-intensity UVR effects may be the opposite of those observed under high-intensity UVR (Aphalo & Albert 2012). Experiments should also be designed to collate data on sub-lethal effects of UVR, including immunomodulation and indirect trophic-level effects such as PUFA availability. It would be advisable to include multiple developmental stages in future studies to compare and contrast vulnerabilities and coping mechanisms in different life stages. Furthermore, future studies should look to explore the complex relationship between environment and parasitism in a bi-directional manner. This would allow for better understanding of not only how parasitism is influenced by an animals' environment, but also how parasitism affects the environment to which an animal is exposed. If it is shown that UVR consistently impacts host–pathogen relationships in a predictable manner, then this knowledge can be exploited through optimised management and handling practices. Practical measures to alter UV exposure *in situ* can be achieved by changing the spatial design of bivalve farms, e.g. by altering the position of stock

along the intertidal gradient; by altering structural design of lantern cages, mussel socks or hanging long-lines; or by the use of mesh bags with specific optical properties. In subtidal cultivation, the depth at which animals are kept could be changed in order to optimise UV exposure. Finally, the timing of processes such as laying out new seed may be altered to increase or decrease UV exposure. Thus, were UV to emerge as a significant environmental factor in modulating the host–pathogen relationships of bivalves, practical measures would be available to exploit this finding in a commercial setting. With this, efforts can be focused on addressing and advancing biosecurity in shellfish aquaculture and meeting sustainable food security goals for a rapidly growing human population.

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*Editorial responsibility: Jean-Sébastien Lauzon-Guay,
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