1 Title: **Molecular identification of potential aquaculture pathogens adherent to cnidarian zooplankton.**

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27

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Abstract:

Cnidarian jellyfish are pest species of marine aquaculture, with their acute impacts well documented in farmed fish, particularly affecting the delicate gill tissue. Less is known about subsequent consequences of exposure, including their association with secondary bacterial infections. The aim of this study was to identify whether potentially pathogenic bacteria were present as part of the adherent microbial populations of three medusozoan jellyfish species; *Obelia geniculata*, *Neoturris pileata* and the Lion's Mane jellyfish *Cyanea capillata*. A number of

potential pathogens of commercial aquaculture were identified, including *Aeromonas salmonicida*, *Vibrio splendidus* and *Vibrio alginolyticus*. These findings suggest that jellyfish must be considered not just agents of direct trauma to fish in aquaculture, but also potential reservoirs and vectors of bacterial disease. Since jellyfish may be increasing in the coastal waters where marine aquaculture occurs, the role of jellyfish in bacterial outbreaks has implications for marine aquaculture globally.

Highlights:

- This work investigates the adherent microbial community of cnidarians, focusing on pathogens of finfish.
- Potential pathogens of aquaculture are identified adherent to jellyfish common in temperate coastal waters.
- Cnidarian tissue can host a variety of bacterial species, including *Aeromonas salmonicida*, *Vibrio splendidus* and *Vibrio alginolyticus*, all bacteria previously associated with disease in fish.

1. Introduction:

Bacteria are commonly implicated in the infection of moribund fish or fish suffering from complex gill pathologies in aquaculture (Herrero et al., 2018). Whilst many species are present without apparent harm, bacterial diseases such as Vibriosis and Tenacibaculosis are of concern in the marine production stage of salmonid production (Bruno et al., 2013; Mitchell and Rodger, 2011), and prevention of Furunculosis remains of critical importance (Meyers et al., 2008). Exclusion of pathogens from the open marine pen environment is problematic due to the free exchange of water, which can contain bacteria and other organisms which might cause harm to fish.

82 Pelagic animals of the phylum Cnidaria (commonly referred to as jellyfish) are one such harmful organism
83 common in the marine environment. Jellyfish are a well-documented pest species of aquaculture, negatively
84 impacting fish welfare, production and survival (Rodger et al., 2011). Strong currents can break large
85 jellyfish against nets, while smaller jellyfish simply pass through the mesh, so fragments of gut and tentacles
86 or entire small jellyfish are inhaled by fish, with nematocyte stings triggered to cause gill and even
87 gastrointestinal trauma (Bruno and Ellis, 1985; Cronin et al., 2004; Lotan et al., 1996). Discharge of stings
88 involves extrusion of a collagen barb and envenomation of tissue with a mixture of proteinaceous
89 compounds, resulting in tissue trauma, particularly to the delicate gill epithelium (Bosch-Belmar et al.,
90 2016b; Helmholtz et al., 2010; Hessinger and Lenhoff, 1998; Östman, 2000; Powell et al., 2018). Sessile
91 cnidarian life stages can also impact fish health through biofouling of the cage environment, since hydroid
92 polyps also possess stinging nematocytes that can discharge when animals are dislodged into the pen by net
93 washing (Baxter et al., 2012b; Guenther et al., 2010). Damage to and occlusion of gills by fragments of
94 gelatinous material impairs osmoregulation and reduces respiratory function (Mitchell et al., 2011).
95 Subsequent bacterial colonization is also a common histological finding following physical disruption of the
96 gill epithelium by stinging nematocytes (Bosch-Belmar et al., 2016a; Mitchell et al., 2012)

97

98 In addition to the established physical impact on gill tissue from exposure to jellyfish, these organisms that
99 are nearly ubiquitous in marine environments may have an additional negative impact on aquaculture. The
100 surface microbiome of cnidarian species is specialised and distinct from environmental bacterial
101 populations, hosting a varied population of bacteria (Abouna et al., 2015; Cavanaugh, 1994; Schuett et al.,
102 2007; Zarubin et al., 2012). While environmental factors certainly impact bacterial presence and survival,
103 research suggests that cnidarians themselves are also capable of actively selecting and shaping their
104 microbial communities (Brown et al., 2017; Fraune and Bosch, 2007), with proposed symbiotic relationships
105 in toxin production (Schuett and Doepke, 2010; Weiland-Brauer et al., 2015; Abouna et al., 2015;
106 Cavanaugh, 1994; Schuett et al., 2007; Zarubin et al., 2012).

107

Wild fish and parasites such as sea lice are understood to be carriers of bacterial pathogens. However, the risk of jellyfish is rarely considered in transmission of pathogens (Barker et al., 2009; Belkin and Colwell, 2005; Cusack and Cone, 1986; Nylund et al., 1991). Nevertheless, *Tenacibaculum maritimum*, the causative agent of tenacibaculosis, has been isolated within the adherent microbial communities of *Phialella quadrata* and *Pelagia noctiluca*, with *P. quadrata* implicated as vector of this bacterium during an outbreak of disease in farmed Atlantic salmon (Delannoy et al., 2011; Ferguson et al., 2010). *T. maritimum* has also been detected on zooplankton distant from any farms (Fringuelli et al., 2012). Alteration and dysbiosis of the gill microbiome by exposure to jellyfish might go some way to explaining the impact of microscopic species such as *Obelia* (Kintner and Brierley, 2018). *T. maritimum* is not alone in its capacity for erosive epithelial infections in fish species, and further research is required to identify whether other potential pathogens of aquaculture production might also be present in cnidarian microbiomes. Identification of adherent bacteria on the tissue of jellyfish that might come into contact with farmed fish is therefore essential for an understanding of the role jellyfish may play in possible initiation of bacterial disease.

This study aimed to establish whether further potential pathogens of aquaculture production are present in the microbiomes of the cnidarians *Cyanea capillata*, *Neoturris pileata* and *Obelia geniculata*, since these species occur in coastal areas favoured by aquaculture production (Baxter et al., 2012a; Pikesley et al., 2014; Powell et al., 2018) and are potentially associated with pathology in fish (Guenther et al., 2010; Kintner and Brierley, 2018; Powell et al., 2018). Amplification of the highly conserved 16S rDNA sequence is the most common method for differentiation of mixed populations of bacteria, but this sequence is limited in the amount of species level resolution it provides, particularly for the genera of concern to fish health (Thompson et al., 2004; Yamamoto et al., 2000). Here we supplemented sequencing of 16S rDNA with additional loci to quickly and cost-effectively identify various jellyfish-derived bacterial isolates to species level. Of the bacterial species identified there were several potential pathogens, including *Aeromonas salmonicida*, *Vibrio splendidus*, *Vibrio alginolyticus* and *Pseudomonas fluorescens*.

2. Methods:

2.1 Cnidarian sample collection and bacterial isolate preparation

Live intact specimens of *Cyanea capillata* and *Neoturris pileata* medusae and *Obelia geniculata* hydroids were collected from four coastal locations around the mainland of Shetland (Lunna lat. 60.419004, lon. –1.105436, Redayre lat. 60.193509, lon. –1.405769, Roe Sound lat. 60.377864, lon. –1.384974 and North of Papa lat. 60.130489, lon. –1.342794), and identified by assessment of morphological characteristics. Each specimen was rinsed with sterile sea water to remove loosely associated environmental microorganisms before being suspended overnight in a purpose-built sterile tank facility with flowing UV-treated seawater (Hao et al., 2015).

Tissue sections were used for bacterial culture in broth media targeted for culture of pathogenic bacterial isolates. Samples from *C. capillata* gut were obtained by sterile swabbing, and samples from *C. capillata* fishing tentacles by removal of 1cm² tissue sections. Smaller *N. pileata* and *O. geniculata* (0.5-10mm and 8-11mm in length respectively) were halved and placed directly into the broth media. Two media were utilized for each sample - Bovine Brain-Heart Infusion (BHI) and Flexibacter Maritimus Media (FMM) broths (Pazos et al., 1993; Rosenow, 1919). Each sample was incubated for 24 hours with occasional agitation at 25°C, then streaked onto BHI and FMM agar plates using a sterile inoculation loop for incubation for a further 24 hours at 25°C. Resulting polycultures were divided for further plate culture until monocultures were achieved, as judged by morphological appearance. Colonies from these plates were then selected and cultured in corresponding broth media for amplification of bacterial quantities over a further 72 hours at 25°C. Culture conditions were tailored to encourage growth of the maximum possible marine pathogen species (Garcia Moreno and Landgraf, 1998; Starliper, 2013)

To exclude bacteria that are generally present in the environment rather than specifically associated with the jellyfish, sea water was also collected during sampling visits at each location into 1L sterile containers. Following settling, 0.5mL samples were collected from the bottom of containers and placed in separate broth media for incubation alongside cnidarian samples. 0.5mL samples were also collected from the tank

systems. Cultures obtained from water samples were subjected to an identical sequencing protocol as cnidarian samples and the results utilised for exclusion of bacteria that were not specifically adherent to cnidarian tissue from subsequent analyses.

2.2 DNA Extraction and Polymerase Chain Reaction amplification

DNA from bacterial monocultures was extracted with a crude boiling approach and stored at -80°C . Universal primers (see table 1) targeting an approximately 1500bp region of the 16S ribosomal gene were utilized to determine sample identity to genus level (Weisburg et al., 1991) using previously described PCR conditions (Cepeda et al., 2003). Following genus identification from the 16S sequences, further individual gene loci were targeted to enable species-level identification of a subset of samples.

Samples identified as being from the genus *Pseudomonas* were subjected to PCR using primers to amplify the *rpoD* gene (see table 1) (Yamamoto et al., 2000) using recommended thermocycling conditions (Mulet et al., 2011, 2009). For samples of genus *Aeromonas*, extracted DNA was subjected to PCR using primers amplifying an approximately 1100bp fragment of the *gyrB* gene using previously described PCR conditions (Yáñez et al., 2003). Samples from the genus *Vibrio* were subjected to PCR using primers targeted to the 16S-23S Intergenic-Spacer (IGS) region (see table 1) (Jensen et al., 1993; Wong and Lin, 2001) with a thermocycler protocol of 5mins 95°C , and 36 cycles of 30s 95°C , 30s 56°C and 30s 72°C , with a final extension of 5min 72°C .

All PCR reaction products were subjected to agarose gel electrophoresis in 1x Tris-Acetate EDTA buffer and the DNA fragments visualized after ethidium bromide staining with UV light. Bands of the appropriate size were cut from the gel and purified with the Thermo Scientific Isolate II gel elution kit following the manufacturer's instructions prior to sequencing.

2.3 PCR fragment sub-cloning and sequencing

189 Multiple similar length amplicons of different nucleotide sequence are obtained by PCR of the IGS region
190 from *Vibrio*. Therefore, bands were eluted separately from agarose gel and sub-cloned into plasmid vectors
191 in an effort to capture this variation. Sub-cloning of PCR fragments into pGEM-T Easy vector (Promega
192 labs) followed the manufacturer's instructions except for using only half the amount of vector and adjusting
193 the insert quantity accordingly. Plasmids were transformed and cultured in XL1-blue or XL10 blue strains of
194 *Escherichia coli* (Agilent Technologies) via standard heat shock procedures and antibiotic growth
195 conditions. Single colonies were selected for individual 50µg/ml Ampicillin LB broth culture at 37°C
196 overnight with shaking. Plasmid DNA was isolated using the Qiagen DNA miniprep kit following the
197 manufacturer's instructions.

198

199 V3.0 Big-dye terminator mix (Perkin Elmer) was used following the manufacturer's instructions for DNA
200 sequencing. For *Aeromonas* and *Pseudomonas* samples, eluted PCR bands were directly sequenced without
201 sub-cloning using forward primer GyrB3F and sequencing primer 70Fs (5'-
202 ACGACTGACCCGGTACGCATGTA-3') (Yamamoto et al., 2000) respectively. Between four and nine
203 independent colonies were sequenced for each original isolate confirmed as *Vibrio*, generating two to nine
204 unique IGS amplicons for each sample, sequenced from insert-containing plasmids using T7 sequencing
205 primers. Sequencing reactions were processed at the Department of Zoology sequencing service, University
206 of Oxford, or with the Eurofins sequencing service.

207

208 2.4 Sequence Analysis

209 Nucleotide sequences were edited using Geneious software (Geneious 9.0.5, <https://www.geneious.com>,
210 Kearse et al., 2012) to remove PCR primer-binding sites and plasmid vector sequence. Sequences were then
211 compared nucleotide to nucleotide using BLASTn against the Genbank database. Additional comparisons
212 were also performed against the curated databases Ribosomal Database Project RRID:SCR_006633 (Cole et
213 al., 2014) for 16S, and the PseudoMLSA Database (Bennasar et al., 2010) now found at
214 <http://microbiologia.uib.es/bioinformatica>) for *Pseudomonas* isolates. Multiple sequence alignments were

produced with JalView using CLUSTAL omega default settings and neighbour-joining phylogenetic tree construction was performed using CLUSTAL omega and MEGA 7.

3. Results

68 unique 16S sequences were identified from initial sequencing of independent colonies derived from the bacterial monocultures, after removal of within-source duplicates and cnidarian-derived sequences with 100% identity with environmental and aquarium cultures. Classification to genus level was possible with the majority of these partial 16S sequences. Using BLASTn and the parameters of >97% identity over 100% of the sequence against Genbank entries, 12 distinct genera were identified from the samples obtained from the three species of jellyfish. Some isolates were matched to multiple genera and, after excluding mismatches due to misclassifications or use of historical nomenclature within the database, could still only be classified to a higher taxonomic level. Overall, culturable populations were dominated by Class Gammaproteobacteria, phylum Proteobacteria.

The known pathogen *T. maritimum*, previously isolated as part of the adherent microbial community of other cnidarian species, is a member of the phylum Flavobacteria. Despite culture conditions suited to culture bacterial genera of this phylum, no Flavobacteria were identified. The dominant culturable phylum of Proteobacteria does, however, contain a number of genera associated with disease in fish. Jellyfish samples were collected around the coastline of Shetland; this coast supports over a hundred Atlantic salmon marine cages containing Atlantic salmon, ballan wrasse and lumpfish. Species level classification of jellyfish-associated bacteria therefore focused on *Aeromonas*, *Vibrio* and *Pseudomonas*, as these genera contain the causative agents of diseases considered of high importance in local aquaculture production (Bruno et al., 2013; Rodger et al., 2010). Lack of sufficient variation in the 16S gene for species-level resolution is well documented, particularly for *Pseudomonas* and *Vibrio* (Alsina et al., 1996; Yamamoto et al., 2000). Unambiguous identification of distinct species within the genera of interest was therefore achieved through sequencing of additional gene loci, summarized in Table 2.

3.1 *Aeromonas*

The samples confirmed as *Aeromonas* from 16S sequencing were identified to species level by sequencing of the *gyrB* gene. Resultant sequences were confirmed by comparison to Genbank as *Aeromonas molluscorum* and *Aeromonas salmonicida*, with their relatedness to *Aeromonas* type strains demonstrated in a Neighbour-Joining phylogenetic tree (Figure 1: *Aeromonas* GyrB Tree alignment provided as Supplementary Figure 1).

3.2 *Pseudomonas*

From sequencing of the *rpoD* gene, several *Pseudomonas* samples were identified as *Pseudomonas fluorescens* and *Pseudomonas fulva* relative to the species sequences available on Genbank, with >97% identity over 100% of the sequence length. Through construction of a phylogenetic tree using RpoD sequences of type strains obtained through the curated PseudoMLSA database (Bennasar et al., 2010), additional suspected species *Pseudomonas alkylphenolia* and *Pseudomonas guineae* could be identified from *Pseudomonas* sequences that did not meet our similarity threshold criteria in Genbank searches (Supplementary figures 2 & 3, alignment).

3.3 *Vibrio*

Species level resolution was achieved for *Vibrio* samples by utilising primers designed to target the 16S-23S intergenic spacer region (IGS). Multiple genetically distinct IGS regions were obtained from single monoculture genomes, with sequences varying both from each other and from the closest matches within the Genbank database. An exemplar of the variation is shown for *Vibrio* Sample A in supplementary material (Supplementary figure 4). In addition to amplification of the IGS region, the primer set utilized also amplified a similar length region of a DNA helicase encoding gene, which was discarded from our analyses following its identification from similarity searches to Genbank.

Genbank matches were obtained for each IGS sequence and used to obtain a consensus classification of *Vibrio* samples to species level (Supplementary table 1). Within each sample, some sequences proved to be diagnostic to species level and others did not, using the parameters of >97% identity over 100% of the sequence against the Genbank matches, highlighting the need for sequencing multiple fragments. IGS fragments that matched more than one species on Genbank using parameters of >97% identity over 100% of the sequence length or that did not fulfil these criteria were not considered sufficiently diagnostic.

Ultimately, three species of *Vibrio* were identified; *Vibrio alginolyticus*, *Vibrio splendidus* and *Vibrio crassostreae*. Ambiguous results were obtained for two samples (samples E and F, Supplementary table 1). These isolates represent possible new species or strains, as none of the IGS fragment sequences could be matched with >97% identity to NCBI database submissions. The closest matches to these unclassified isolates were to *V. splendidus* and *Vibrio alginolyticus* (Supplementary Table 1). The sequences from these novel *Vibrio* were deposited in Genbank with accession numbers MH310872- MH310876.

All samples sequenced for species classification are summarised in Table 2, providing information regarding sample source, final species designation and corresponding accession numbers, MH205967-MH205988 for 16S sequences and MH310838- MH310882 from further sequencing.

Discussion

We have used 16S DNA sequencing followed by selected additional gene sequences to identify several bacteria to the species level that are present in jellyfish microbiomes and which are potentially pathogenic to fish. Sequencing of 16S is the most commonly used method for classification of mixed bacterial populations, notably in high throughput metagenomic diversity studies. However, 16S sequencing alone cannot provide sufficient resolution of microbial populations when investigating specific species (Yamamoto et al., 2000) , and species-level identification was the desired outcome of this study. Culture

295 was employed in this study as a method of dividing polymicrobial samples into single species monocultures.
296 Following this, sequencing was applied for accurate designation of isolates, as culture of marine microbes is
297 rarely sufficiently sensitive for species-level resolution (Achtman and Wagner, 2008; Beaz-Hidalgo et al.,
298 2010; Curtis et al., 2002). Initial 16S sequencing identified samples to genus level, and further sequencing of
299 select isolates provided species level resolution. Further sequencing was conducted on all samples classified
300 to the genera of interest.

301

302 Despite the use of a potentially diversity-limiting culture step, a range of genera of interest were obtained.
303 Designation of culturable samples based on 16S sequencing was primarily to the Class
304 Gammaproteobacteria, with a minority of Firmicutes and Actinobacteria. The proportionally high presence
305 of isolates classed as Gammaproteobacteria is in agreement with available literature regarding dominant
306 microbial classes of other cnidarians (Schuett and Doepke, 2010; Tinta et al., 2012; Weiland-Brauer et al.,
307 2015). Although the culture step was tailored to facilitate growth of Flavobacteriaceae for identification of
308 *T. maritimum*, none was observed (Pazos et al., 1996). Use of culture, even targeted culture such as
309 performed here, has been shown to yield fewer bacteria than comparable high throughput molecular
310 techniques (Hiergeist et al., 2015; McDonald et al., 2017). Failure to isolate *T. maritimum*, or any other
311 pathogenic species, may then be due to a number of factors, such as low inoculation cell concentration,
312 production of inhibitory compounds by other bacteria or competition from faster growing isolates in culture.
313 Even a loss of interactions that occur between organisms in the microbiome might have precluded the
314 isolation of specific bacteria, rather than reflecting true absence of species such as *T. maritimum* (Joint et al.,
315 2010).

316

317 Of the bacteria that were isolated and sequenced, within the genus *Aeromonas* the potentially fish
318 pathogenic species *A. salmonicida* was identified. Both typical and atypical furunculosis, associated with *A.*
319 *salmonicida* infections in fish, are diseases more frequently associated with freshwater environments,
320 however marine outbreaks are not uncommon (Belkin and Colwell, 2005). This species has been suggested
321 as an obligate fish pathogen, reliant on vector transmission at sea due to its limited survival duration in salt

water (Rose et al., 1990) with past infections in the marine environment linked to carrier fish coming from freshwater. The isolation of this species from *C. capillata* suggests that in addition to wild fish, jellyfish species may also act as natural reservoirs and vectors for transmission of marine furunculosis.

Results of species-level identification from the genus *Vibrio* included species *V. splendidus* and *V. alginolyticus*, both previously associated with fish disease (Gulla et al., 2015; Hjeltne et al., 2018). *V. alginolyticus* is a pathogenic bacterium associated with vibriosis in a variety of finfish species (Balebona et al., 1998). *V. splendidus* has recently become a bacterium of concern to the Atlantic salmon production industry due to its suspected association with mortalities in the ballan wrasse and lumpfish that are used as cleaner fish (Bornø et al., 2016; Gulla et al., 2015). *V. splendidus* is closely related to another species identified in this study, *V. crassostreae*, which was only recently differentiated as a separate species (Faury et al., 2004).

Of the other species identified, in the genus *Pseudomonas*, *P. fluorescens* is rarely considered a primary pathogen, although it does cause sporadic infections in fish, often as an opportunistic secondary infection (Austin and Austin, 2012). It is worth remembering that potentially pathogenic bacteria can be identified with sufficient sequencing depth from most environments (Gibbons et al., 2013), with *P. fluorescens* being a commonly isolated environmental organism. However, due to the tissue wash step employed in this study and exclusion of concurrently culturable environmental isolates, we can confirm this isolate as a true inhabitant of the jellyfish adherent community from which it was obtained. *P. fluorescens* produces products with antimicrobial and antifungal properties as well as roles in surface attachment in biofilms (Holmström and Kjelleberg, 1999; Maddula et al., 2006; Sarniguet et al., 1995; Schnider et al., 1995) that might be advantageous in biomediation of the cnidarian microbiome. Other species identified in this study not considered a risk to fish health include *A. molluscorum* and *P. fulva*.

A relative paucity of available type strain *rpoD* sequences hindered unambiguous classification of *Pseudomonas* isolates; 79 *Pseudomonas* type strains were obtained from the PseudoMLSA database for

349 phylogenetic analysis (Figure 2), however, as many as 248 species of *Pseudomonas* are reported to exist.
350 Further resolution of sample identities might be possible with additional sequencing of *rpoD* genes beyond
351 the existing type strain species available, or sequencing of additional gene loci.

352
353 The results of this study show that potentially harmful bacteria are present on the surface of the cnidarian
354 species investigated, jellyfish which can and do come into contact with aquaculture production. Whilst
355 disease initiation is a multifactorial process and the in vivo pathogenicity of bacteria isolated is as yet
356 unconfirmed, their presence is confirmed in the adherent microbial communities of these jellyfish, in
357 sufficient densities to be culturable. Our results imply that exposure of fish to the jellyfish species studied
358 here also risks exposure to potentially pathogenic bacteria capable of proliferating in the gills. Of particular
359 concern is exposure of unvaccinated species such as the cleaner fish employed in Atlantic salmon
360 production. Bacterial disease appears to be associated with the high losses of these species that can be
361 experienced by producers, with bacterial disease one of the most common clinical findings in mortalities of
362 these fish (Nilsen et al., 2014; Bornø and Lie Linaker, 2014; Gulla et al., 2016).

363
364 A multitude of factors impact the onset and progression of bacterial infection, but jellyfish are considered a
365 strong predisposing factor of bacterial gill disease (Rodger et al., 2011). Potentially providing the perfect
366 delivery mechanism for pathogens, discharge of stinging nematocysts causes physical trauma and impairs
367 immunity of epithelial tissue. This trauma can facilitate the growth of pathogenic bacteria within wounds or
368 may even allow entry across epithelial surfaces for systemic bacterial effects such as septicemia (Dror et
369 al., 2006; Gomez et al., 2013; Handler et al., 1997). The diseases furunculosis and vibriosis are both
370 promoted by removal of the mucus layer and tissue trauma (Balebona et al., 1998; Dror et al., 2006) such as
371 occurs during jellyfish exposure. These diseases cause erosive tissue damage similar to *T. maritimum*, the
372 proteolytic fish pathogen already linked to vector transmission by jellyfish (Delannoy et al., 2011; Ferguson
373 et al., 2010).

Sample size and limited geographical area of collection preclude conclusions regarding presence of these bacteria in the core microbiome of the jellyfish species investigated. However, this study does demonstrate the ability of jellyfish to host bacteria with disease-causing potential within their microbiomes. With that in mind, we suggest there may be appreciable risk to fish following exposure to the three common cnidarian species studied here, which the aquaculture industry should bear in mind as it moves towards improved treatment and prevention of bacterial disease. Outbreaks of bacterial disease in marine aquaculture production units preceded by jellyfish blooms may well be due to vector transmission of infective bacteria, however, current under-reporting and lack of routine monitoring of jellyfish populations limits linking outbreaks of clinical bacterial disease in farmed fish to jellyfish exposure.

Figure legends:

Figure 1

Phylogenetic tree demonstrating the relationships of jellyfish adherent bacteria *Aeromonas gyrB* sequences (highlighted in bold) alongside all partial *gyrB* type strain *Aeromonas* sequences available in the Genbank database (species associated with fish disease are underlined (Beaz-Hidalgo et al., 2010; Godoy et al., 2010; Kozińska, 2007)). The sequence alignments were performed using CLUSTAL omega and the tree constructed in MEGA 7 using the neighbor-joining method with maximum likelihood distances. Numbers represent bootstrap values for each node based on 1500 replications and the tree is rooted with the outgroup of *Vibrio splendidus*, *Pseudoalteromonas marina* and *Photobacterium damsela*. Sequences marked with a dagger symbol (†) were obtained from NCBI taxonomic samples not confirmed as type strains.

Figure 2

Phylogenetic tree demonstrating the relationships of *Pseudomonas rpoD* sequences derived from samples in this study (highlighted in bold) alongside all partial *Pseudomonas rpoD* sequences available from the PseudoMLSA curated list of type strains in Genbank. Species associated with fish disease are underlined.

402 Some groups of sequences have been collapsed to improve legibility (full tree can be observed in
403 supplementary data, Figure 2). The sequence alignments were performed using CLUSTAL omega and the
404 tree constructed in MEGA 7 using the neighbor-joining method with maximum likelihood distances.
405 Numbers represent bootstrap support values for each node based on 1500 replications and the tree is rooted
406 with the outgroup of *Acinetobacter baumannii*.

407

408 **Supplementary Figure 1**

409 *Aeromonas* phylogenetic tree alignment. This alignment was used to construct the phylogenetic tree in
410 Figure 1.

411

412 **Supplementary Figure 2**

413 Full *Pseudomonas rpoD* phylogenetic tree. Sequences condensed into Groups 1-11 in Fig. 2 are identified.

414

415 **Supplementary Figure 3**

416 Alignment for construction of *Pseudomonas rpoD* phylogenetic tree

417

418 **Supplementary Figure 4**

419 Multiple sequence alignment demonstrating the variation in IGS regions obtained from the bacterial
420 monoculture Sample A. Partial 16S and 23S flanking sequences are left uncoloured at the 5-prime and 3-
421 prime ends respectively, and regions encoding tRNA genes are highlighted using boxes.

422

423 **Table Legends:**

424

425 **Table 1**

426 Table of primers utilized for genus and species-level resolution of samples obtained from jellyfish tissue.

427

428 **Table 2**

Summary of all sequencing data produced in this study with sample sources as well as corresponding accession numbers.

Table 3

Intergenic Spacer (IGS) sequences obtained in this study with *Vibrio* species-level classification against Genbank with BLASTn. Positively identified sequences (based on the parameters of 100% coverage and 97% or higher identity) are highlighted in bold. Where multiple matches are considered significant or matches do not meet the minimum criteria of 100% coverage and 97% identity, no positive identification was determined. Sufficient coverage was not obtained for sequences C_IGS4 and F_IGS3 (in grey) and so these are also not included in the classification decision.

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AIG56_Oyen/1-597 1 TAGCCCTAGGGGAACCTGGGGTGGATCACTCCTTATACGAAGATA...CCAAGATGAGTGTCCACACAGATTGATTAGGTTTAGA...AAGTAAACGAGACGAT 100
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 AIG59_Oyen/1-589 128 GGACACGGCCCTTTACCGGCGGTAAACAGGGGTTCCAGTCCCTACGGGATACCACTCTTTAAGTATCTCTCTCAGAGATTAAAAATGGTCT 221
 AIG54_Oyen/1-488 95CCAGAG...CTTTAATTAAACGTT...AAGTTATTGATTAAAGCTT... 136
 AIG55_Oyen/1-488 95CCAGAG...CTTTAATTAAACGTT...AAGTTATTGATTAAAGCTT... 136
 AIG51_Oyen/1-410 95CCAGAG...CTTTAATTAAACGTT...AAGTTATTGATTAAAGCTT... 135
 AIG53_Oyen/1-412 95CCAGAG...CTTTAATTAAACGTT...AAGTTATTGATTAAAGCTT... 135
 AIG57_Oyen/1-412 95CCAGAG...CTTTAATTAAACGTT...AAGTTATTGATTAAAGCTT... 135
 AIG58_Oyen/1-412 95CCAGAG...CTTTAATTAAACGTT...AAGTTATTGATTAAAGCTT... 135
 AIG56_Oyen/1-597 316TTCCGAAAGAACTAGCTAGCTTTGAAAGCTGAGCTGATTGA...TTACTTACGAGTAAATCAATCAAAATTTAAAGTTCTCAATGTTTATCTT 412
 AIG59_Oyen/1-589 222 ATTAGTTTG...AATCAAGCTCTTTAAAGCTTTGAAAGCTGAGCTGATTGA...TTACTTACGAGTAAATCAATCAAAATTTAAAGTTCTCAATGATTATCTT 318
 AIG54_Oyen/1-488 136TTTG...CTTTATGCTTTAAAGCTTTGAAAGCTGAGCTGATTGA...TTACTTACGAGTAAATCAATCAAAATTTAAAGTTCTCAATGTTTATCTT 227
 AIG55_Oyen/1-488 136TTTG...CTTTATGCTTTAAAGCTTTGAAAGCTGAGCTGATTGA...TTACTTACGAGTAAATCAATCAAAATTTAAAGTTCTCAATGTTTATCTT 227
 AIG51_Oyen/1-410 136TTTG...CTTTATGCTTTAAAGCTTTGAAAGCTGAGCTGATTGA...TTACTTACGAGTAAATCAATCAAAATTTAAAGTTCTCAATGTTTATCTT 228
 AIG53_Oyen/1-412 136TTTG...CTTTATGCTTTAAAGCTTTGAAAGCTGAGCTGATTGA...TTACTTACGAGTAAATCAATCAAAATTTAAAGTTCTCAATGTTTATCTT 228
 AIG57_Oyen/1-412 136TTTG...CTTTATGCTTTAAAGCTTTGAAAGCTGAGCTGATTGA...TTACTTACGAGTAAATCAATCAAAATTTAAAGTTCTCAATGTTTATCTT 228
 AIG58_Oyen/1-412 136TTTG...CTTTATGCTTTAAAGCTTTGAAAGCTGAGCTGATTGA...TTACTTACGAGTAAATCAATCAAAATTTAAAGTTCTCAATGTTTATCTT 228
 AIG56_Oyen/1-597 413 TCATTAGATAAACCAACCAACACACATTCAAGTGTCTTGTTATTCGAA...TTCAATGTTTACATTGATTCAAC... 479
 AIG59_Oyen/1-589 319 TCATTAGATAAACCAACCAACACACATTCAAGTGTCTTGTTATTCGAA...TTCAATGTTTACATTGATTCAATGTTTAAAGTTCTCAATGTTTATCTT 421
 AIG54_Oyen/1-488 228 TCATTAGATAAACCAACCAACACACATTCAAGTGTCTTGTTATTCGAA...TTCAATGTTTACATTGATTCAATGTTTAAAGTTCTCAATGTTTATCTT 430
 AIG55_Oyen/1-488 228 TCATTAGATAAACCAACCAACACACATTCAAGTGTCTTGTTATTCGAA...TTCAATGTTTACATTGATTCAATGTTTAAAGTTCTCAATGTTTATCTT 430
 AIG51_Oyen/1-410 229 TCATTAGATAAACCAACCAACACACATTCAAGTGTCTTGTTATTCGAA...TTCAATGTTTACATTGATTCAATGTTTAAAGTTCTCAATGTTTATCTT 430
 AIG53_Oyen/1-412 229 TCATTAGATAAACCAACCAACACACATTCAAGTGTCTTGTTATTCGAA...TTCAATGTTTACATTGATTCAATGTTTAAAGTTCTCAATGTTTATCTT 430
 AIG57_Oyen/1-412 229 TCATTAGATAAACCAACCAACACACATTCAAGTGTCTTGTTATTCGAA...TTCAATGTTTACATTGATTCAATGTTTAAAGTTCTCAATGTTTATCTT 430
 AIG58_Oyen/1-412 229 TCATTAGATAAACCAACCAACACACATTCAAGTGTCTTGTTATTCGAA...TTCAATGTTTACATTGATTCAATGTTTAAAGTTCTCAATGTTTATCTT 430
 AIG56_Oyen/1-597 480AATTGATTCGGGCAACACAGTTATCAAGAA...TTAACCCCTTCTTGATGACAAACCAAAACCTTGGTTAGTTGCCATACGTT... 567
 AIG59_Oyen/1-589 422 AAGTAAATGATTCGGGCAACACAGTTATCAAGAA...TTAACCCCTTCTTGATGACAAACCAAAACCTTGGTTAGTTGCCATACGTT... 524
 AIG54_Oyen/1-488 331 AAGTAAATGATTCGGGCAACACAGTTATCAAGAA...TTAACCCCTTCTTGATGACAAACCAAAACCTTGGTTAGTTGCCATACGTT... 524
 AIG55_Oyen/1-488 331 AAGTAAATGATTCGGGCAACACAGTTATCAAGAA...TTAACCCCTTCTTGATGACAAACCAAAACCTTGGTTAGTTGCCATACGTT... 524
 AIG51_Oyen/1-410 295AATTGATTCGGGCAACACAGTTATCAAGAA...TTAACCCCTTCTTGATGACAAACCAAAACCTTGGTTAGTTGCCATACGTT... 372
 AIG53_Oyen/1-412 295AATTGATTCGGGCAACACAGTTATCAAGAA...TTAACCCCTTCTTGATGACAAACCAAAACCTTGGTTAGTTGCCATACGTT... 372
 AIG57_Oyen/1-412 295AATTGATTCGGGCAACACAGTTATCAAGAA...TTAACCCCTTCTTGATGACAAACCAAAACCTTGGTTAGTTGCCATACGTT... 372
 AIG58_Oyen/1-412 295AATTGATTCGGGCAACACAGTTATCAAGAA...TTAACCCCTTCTTGATGACAAACCAAAACCTTGGTTAGTTGCCATACGTT... 372
 AIG56_Oyen/1-597 558AAGACCCCTTCGGGTTGATGGTTAAGTGACTAAGCGTAC... 597
 AIG59_Oyen/1-589 525 AAGTGAAGCAATAGAAACCTTCGGGTTGATGGTTAAGTGACTAAGCGTACCTAAGCGGTAC 589
 AIG54_Oyen/1-488 434 AAGTGAAGCAATAGAAACCTTCGGGTTGATGGTTAAGTGACTAAGCGTAC... 488
 AIG55_Oyen/1-488 434 AAGTGAAGCAATAGAAACCTTCGGGTTGATGGTTAAGTGACTAAGCGTAC... 488
 AIG51_Oyen/1-410 373AAGACCCCTTCGGGTTGATGGTTAAGTGACTAAGCGT... 410
 AIG53_Oyen/1-412 373AAGACCCCTTCGGGTTGATGGTTAAGTGACTAAGCGTAC... 412
 AIG57_Oyen/1-412 373AAGACCCCTTCGGGTTGATGGTTAAGTGACTAAGCGTAC... 412
 AIG58_Oyen/1-412 373AAGACCCCTTCGGGTTGATGGTTAAGTGACTAAGCGTAC... 412

Gene target	Application	Primer	Sequence	Reference
16S	All bacteria	20F	5'-AGAGTTTGATCATGGCTCAG-3'	1
16S	All bacteria	1500R	5'-GGTTAC-CTTCTTACGACTT-3'	1
<i>rpoD</i>	<i>Pseudomonas</i>	70F	5'- ACGACTGACCCGGTACGCATGTAY ATGMGNGARATGGGNACNGT-3'	2
<i>rpoD</i>	<i>Pseudomonas</i>	70R	5'- ATAGAAATAACCAGACGTAAGTTN GCYTCNACCATYTCYTTYTT-3'	2
<i>gyrB</i>	<i>Aeromonas</i>	GyrB3F	5'-TCCGGCGGTCTGCACGGCGT-3'	3
<i>gyrB</i>	<i>Aeromonas</i>	GyrB14 R	5'-TTGTCCGGGTGTACTCGTC-3'	3
IGS	<i>Vibrio</i>	G1F	5'-GAAGTCGTAACAAGG-3'	4,5
IGS	<i>Vibrio</i>	L1R	5'-CAA GGCATCCACCGT-3'	4,5

Sample Identifier	Origin	Genus level identification	Accession of 16S sequence	Species level classification	Accession of further sequencing
Ae1CcapG	<i>C. capillata</i> , gut	<i>Aeromonas</i>	MH205967	<i>A. molluscorum</i>	MH310838
Ae2CcapT	<i>C. capillata</i> , tentacle		MH205968	<i>A. salmonicida</i>	MH310839
A9Ogen	<i>O. geniculata</i>	<i>Vibrio</i>	MH205969	<i>V. splendidus</i>	MH310852
					MH310853
					MH310854
					MH310855
					MH310856
					MH310857
					MH310858
					MH310859
B5Ogen	<i>O. geniculata</i>		MH205970	<i>V. splendidus</i>	MH310860
					MH310861
C4Npil	<i>N. pileata</i>		MH205971	<i>V. alginolyticus</i>	MH310862
					MH310863
					MH310864
D7Npil	<i>N. pileata</i>		MH205972	<i>V. splendidus</i>	MH310865
					MH310866
					MH310867
					MH310868
					MH310869
					MH310870
E2Npil	<i>N. pileata</i>		MH205973	Novel strain	MH310871
					MH310872
F3CcapG	<i>C. capillata</i> , gut		MH205974	Novel strain	MH310873
					MH310874
					MH310875
G3Ogen	<i>O. geniculata</i>		MH205975	<i>V. crassostreae</i>	MH310876
					MH310877
					MH310878
H3CcapG	<i>C. capillata</i> , gut		MH205976	<i>V. splendidus</i>	MH310879
		MH310880			
		MH310881			
P3Ogen	<i>O. geniculata</i>	<i>Pseudomonas</i>	MH205979	<i>P. fulva</i>	MH310882

P7CcapG	<i>C. capillata</i> , gut		MH205983	<i>P. fluorescens</i>	MH310846
P8CcapT	<i>C. capillata</i> , tentacle		MH205984	<i>P. fulva</i>	MH310847
P9Npil	<i>N. pileata</i>		MH205985	<i>P. fulva</i>	MH310848
P1CcapT	<i>C. capillata</i> , tentacle		MH205977	<i>Pseudomonas</i> sp.	MH310840
P2CcapT	<i>C. capillata</i> , tentacle		MH205978		MH310841
P4Ogen	<i>O. geniculate</i>		MH205980		MH310843
P5CcapT	<i>C. capillata</i> , tentacle		MH205981		MH310844
P6CcapG	<i>C. capillata</i> , gut		MH205982		MH310845
P10Ogen	<i>O. geniculate</i>		MH205986		MH310849
P11Ogen	<i>O. geniculate</i>		MH205987		MH310850
P12Ogen	<i>O. geniculata</i>		MH205988		MH310851

Sample	Sequence	Cover	Identity	E value	Match	Accession	Consensus
AOgen	AIGS1	100%	98%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	<i>Vibrio splendidus</i>
		100%	79%	2.00E-63	<i>Vibrio tapetis</i> subsp. <i>tapetis</i> isolate <i>Vibrio tapetis</i> CECT4600 genome assembly, chromosome: A	LT960611.1	
	AIGS3	100%	98%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
		100%	79%	2.00E-64	<i>Vibrio tapetis</i> subsp. <i>tapetis</i> isolate <i>Vibrio tapetis</i> CECT4600 genome assembly, chromosome: A	LT960611.1	
	AIGS4	89%	96%	0	<i>Vibrio splendidus</i> strain ATCC 33125 16S-23S ribosomal RNA intergenic spacer, partial sequence	AF413024.1	
		87%	92%	6.00E-134	<i>Vibrio splendidus</i> LGP32 chromosome 2	FM954973.2	
	AIGS5	89%	96%	0	<i>Vibrio splendidus</i> strain ATCC 33125 16S-23S ribosomal RNA intergenic spacer, partial sequence	AF413024.1	
		87%	92%	6.00E-134	<i>Vibrio splendidus</i> LGP32 chromosome 2	FM954973.2	
	AIGS6	100%	98%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
		100%	92%	0	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
		100%	83%	1.00E-101	<i>Vibrio vulnificus</i> strain VV2014DJH chromosome 1, complete sequence	CP019320.1	
		100%	80%	1.00E-101	<i>Vibrio vulnificus</i> strain 93U204 chromosome I, complete sequence	CP009261.1	
		100%	79%	1.00E-97	<i>Vibrio vulnificus</i> strain FORC_037 chromosome I, complete sequence	CP016321.1	
	AIGS7	100%	98%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	

		100%	79%	2.00E-64	<i>Vibrio tapetis</i> subsp. <i>tapetis</i> isolate <i>Vibrio tapetis</i> CECT4600 genome assembly, chromosome: A	LT960611.1	
	AIGS8	100%	98%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
		100%	79%	3.00E-61	<i>Vibrio tapetis</i> subsp. <i>tapetis</i> isolate <i>Vibrio tapetis</i> CECT4600 genome assembly, chromosome: A	LT960611.1	
	AIGS9	100%	87%	2.00E-178	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
BOgen	BIGS3	100%	99%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	<i>Vibrio splendidus</i>
	BIGS4	100%	96%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
CNpil	CIGS1	100%	99%	0	<i>Vibrio alginolyticus</i> strain K08M4 chromosome 1, complete sequence	CP017916.1	<i>Vibrio alginolyticus</i>
		100%	96%	0	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
	CIGS3	100%	94%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
		100%	92%	0	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	

	CIGS4	84%	98%	0	<i>Vibrio splendidus</i> strain ATCC 33125 16S-23S ribosomal RNA intergenic spacer, partial sequence	AF413024.1	
		79%	92%	4.00E-91	Uncultured <i>Shewanellaceae</i> bacterium clone I3K-356ITS 16S-23S ribosomal RNA intergenic spacer, partial sequence	AY933360.1	
		79%	88%	2.00E-74	Uncultured <i>Pseudoalteromonas</i> sp. clone I50-488ITS 16S-23S ribosomal RNA intergenic spacer, partial sequence	AY932999.1	
DNpil	DIGS1	100%	97%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	<i>Vibrio splendidus</i>
		100%	98%	5.00E-158	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
		100%	90%	1.00E-108	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
		100%	85%	2.00E-83	<i>Vibrio splendidus</i> LGP32 chromosome 2	FM954973.2	
	DIGS3	100%	99%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
	DIGS4	100%	100%	1.00E-123	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
		100%	96%	2.00E-105	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
		100%	93%	2.00E-95	Uncultured <i>Shewanellaceae</i> bacterium clone I3K-356ITS 16S-23S ribosomal RNA intergenic spacer, partial sequence	AY933360.1	
	DIGS5	100%	99%	0.00E+00	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
	DIGS6	100%	99%	0.00E+00	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	

	DIGS7	100%	99%	0.00E+00	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
ENpil	EIGS1	100%	93%	0	<i>Vibrio alginolyticus</i> strain K08M4 chromosome 1, complete sequence	CP017916.1	Novel <i>Vibrio</i>
		100%	90%	1.00E-165	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
	EIGS2	100%	96%	0	<i>Vibrio alginolyticus</i> strain K08M4 chromosome 1, complete sequence	CP017916.1	
		100%	93%	0	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
FCcapG	FIGS1	100%	95%	2.00E-177	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	Novel <i>Vibrio</i>
	FIGS2	100%	95%	3.00E-156	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
		100%	93%	3.00E-146	Uncultured <i>Shewanellaceae</i> bacterium clone I3K-356ITS 16S-23S ribosomal RNA intergenic spacer, partial sequence	AY933360.1	
	FIGS3	99%	95%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
		92%	92%	5.00E-154	Uncultured <i>Shewanellaceae</i> bacterium clone I3K-356ITS 16S-23S ribosomal RNA intergenic spacer, partial sequence	AY933360.1	
GOgen	GIGS1	100%	98%	0	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	<i>Vibrio crassostreae</i>
		100%	96%	0	<i>Vibrio alginolyticus</i> strain K08M4 chromosome 1, complete sequence	CP017916.1	
	GIGS2	100%	99%	0	<i>Vibrio alginolyticus</i> strain K08M4 chromosome 1, complete sequence	CP017916.1	
		100%	97%	0	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
	G_IGS3	100%	99%	0	<i>Vibrio alginolyticus</i> strain K08M4 chromosome 1, complete sequence	CP017916.1	

		100%	98%	0	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
HCcapG	H_IGS1	100%	99%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	<i>Vibrio splendidus</i>
		100%	97%	0	<i>Vibrio alginolyticus</i> strain K08M4 chromosome 1, complete sequence	CP017916.1	
		100%	91%	1.00E-165	<i>Vibrio crassostreae</i> 9CS106 chromosome 1, complete sequence	CP016228.1	
		100%	83%	7.00E-108	<i>Aliivibrio salmonicida</i> LFI1238 chromosome 1 complete genome	FM178379.1	
		100%	82%	4.00E-100	<i>Vibrio fischeri</i> ES114 chromosome I, complete sequence	CP000020.2	
		100%	82%	2.00E-94	<i>Vibrio fischeri</i> MJ11 chromosome I sequence	CP001139.1	
	H_IGS2	100%	99%	0.00E+00	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	
	H_IGS3	100%	99%	0	<i>Vibrio splendidus</i> LGP32 chromosome 1	FM954972.2	

Declaration of interests

☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: