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## **Endobiotic bacteria and their pathogenic potential in cnidarian tentacles**

C. Schuett and H. Doepke

**Abstract** Endobiotic bacteria colonize the tentacles of cnidaria. This paper provides first insight into the bacterial spectrum and its potential of pathogenic activities inside four cnidarian species. Sample material originating from Scottish waters comprises the jellyfish species *Cyanea capillata* and *C. lamarckii*, hydrozoa *Tubularia indivisa* and sea anemone *Sagartia elegans*. Mixed cultures of endobiotic bacteria, pure cultures selected on basis of haemolysis, but also lyophilized samples were prepared from tentacles and used for DGGE-profiling with subsequent phylogenetic analysis of 16S rDNA fragments. Bacteria were detected in each of the cnidarian species tested. Twenty-one bacterial species including four groups of closely related organisms were found in culture material. The species within these groups could not be differentiated from each other (one group of *Pseudoalteromonas* spp., two groups of *Shewanella* spp., one group of *Vibrio* spp.). Each of the hosts exhibits specific endobacterial spectra. Solely *Cyanea lamarckii* harboured *Moritella viscosa*. Only in *Cyanea capillata* members of the *Shewanella* group #2 and the species *Pseudoalteromonas arctica*, *Shewanella violacea*, *Sulfitobacter pontiacus* and *Arcobacter butzleri* were detected. Hydrozoa *Tubularia indivisa* provided an amazingly wide spectrum of nine bacterial species. Exclusively in the sea anemone *Sagartia elegans* the bacterial species *P. aliena* was found. Overall eleven bacterial species detected were described recently as novel species. Four 16S rDNA fragments generated from lyophilized material displayed extremely low relationship to their next neighbours. These organisms are regarded as members of the endobiotic “terra incognita”. Since the origin of cnidarian toxins is unclear, the possible pathogenic activity of endobiotic bacteria has to be taken into account. Literature data show that their next neighbours display an interesting diversity of haemolytic, septicaemic and necrotic actions including the production of cytotoxins, tetrodotoxin and R-toxin. Findings of haemolysis tests support the literature data. The potential producers are *Endozoicimonas elysicola*, *Moritella viscosa*, *Photobacterium profundum*, *P. aliena*, *P. tetraodonis*, *Shewanella waksmanii*, *Vibrio splendidus*, *V. aestuarius*, *Arcobacter butzleri*.

**Keywords** Cnidaria, Tentacles, Endobiotic bacteria, Pathogenic activity, PCR, DGGE

77 **Introduction**

78 Interactions between bacteria and invertebrates are common in marine environment (Deming  
79 and Colwell 1982; Paul et al. 1986; Cary et al. 1997; Burnett and McKenzie 1997; Althoff et  
80 al. 1998; Schuett et al. 2005; Wichels et al. 2006). Yet, the bacterial mode of association  
81 (symbiosis, commensalisms or parasitism) and particular physiological functions are often  
82 unidentified. This also applies to the scarcely investigated cnidaria from cold-moderate  
83 regions. Jellyfish represent a major zooplanktonic fraction in the North Sea and the Atlantic.  
84 Among them are dangerous stingers causing painful dermal injuries after contact with  
85 humans. Similarly, the sessile cnidarian sea anemones and hydrozoan species harbour  
86 complex toxin cocktails, mostly of unknown chemical structures and functions. Currently the  
87 structures and activities of jellyfish species *Cyanea capillata* and *C. lamarckii* collected from  
88 the North Sea and the Atlantic are under investigation (Helmholz et al. 2007). However, the  
89 origin of cnidarian toxins is still open. A hypothesis favors the involvement of endobiotic  
90 bacteria as producers of cnidarian pathogenic activities. Reports of Palincsar et al. (1989) and  
91 Schuett et al. (2007) allowed first insight into the occurrence and morphology of organ-like  
92 bacterial aggregates in the intra-tentacular epidermis region of the sea anemone species  
93 *Aiptasia pallida* and *Metridium senile*.

94 This report provides an overview of cnidarian endobiotic bacteria from cold-moderate  
95 regions by phylogenetic analysis and allows information on their pathogenic potential.

96

97 **Material and Methods**

98

99 *Samples and preparation*

100

101 Individuals of *Cyanea lamarckii*, *Cyanea capillata*, *Tubularia indivisa* and *Sagartia elegans*  
102 were collected by divers during research cruises (June/July 2005-2008) from waters around  
103 the Orkney Islands. Tips of fresh tentacles were clipped off and subjected to washing  
104 procedures and CTAB treatment (Schuett et al. 2007) in order to remove potentially  
105 contaminating epibiotic bacteria. Light microscopic inspection showed no bacteria attached to  
106 the surface of fresh tentacle material. After removing seawater, one set of tentacle material  
107 was placed in three liquid medium modifications of Medium #621 (DSMZ, German Type  
108 Culture Collection; Staley, 1968), shown in Tab. 1. Each test tube containing one tentacle tip  
109 was incubated under aerobic conditions for two months at 18 °C. A second set containing the  
110 same sample material and medium ingredients has been incubated at microaerophilic

111 conditions (90% N<sub>2</sub> and 10% CO<sub>2</sub>). Additionally, cultures were tested for haemolytic activity  
112 according to Smibert and Krieg (1984) by using 5 % (v/v) sheep blood.

113 Positive haemolytic strains were tested for their cytolytic activity by agar diffusion  
114 test using cell culture L929 (protocol provided by Lindl, 2002).

115 Finally, washed tentacle material was lyophilized for further DNA extraction.

116

#### 117 *DNA extraction and PCR amplification of 16S rDNA fragments*

118

119 One milliliter aliquots of aerobic and microaerophilic mixed cultures respectively picked  
120 colonies from blood agar plates were used for nucleic acid extraction according to Anderson  
121 & McKay (1983). Primers 341fc (5'-cgc ccg ccg cgc ccc gcg ccc ggc ccg ccg ccc ccg ccc ccc  
122 tac ggg agg cag cag-3', clamp region underlined) and 907rwob (5'-ccg tca att cct ttr agt tt-3';  
123 Muyzer et al., 1995) were applied to PCR.

124 Reaction mixture (100 µl) contained 2 U of Taq DNA polymerase, 1x polymerase buffer and  
125 1x Master Enhancer (Eppendorf), 100 µM each dNTP, 0.4 µM each Primer and 1 µl DNA.  
126 After an initial denaturation step at 94°C for three minutes 20 cycles (one minute each step)  
127 followed: denaturation 94°C, annealing temperature starting at 65°C and decreasing by 0.5°C  
128 per cycle, elongation 68°C. Another 12 cycles were added this time using 55°C as annealing  
129 temperature. A final incubation at 68°C for 6 minutes was followed by 18 cycles lowering the  
130 temperature for 1°C per minute in order to avoid the formation of heteroduplexes. Negative  
131 controls were carried out omitting template DNA; Escherichia coli J53 served as positive  
132 control. DNA quantity was checked on agarose gels.

133 FastDNA Kit (Bio101) and DNeasy Blood & Tissue Kit (Qiagen) were combined for  
134 DNA extraction of lyophilized tentacles. Lysing Matrix tubes including a ¼" Ceramic Sphere  
135 and Garnet Matrix (Bio101) were supplemented by 1 ml CLS-TC solution and 100 mg  
136 lyophilized material. The tube was placed in a Fast Prep Instrument (FP120, Bio101),  
137 processed for 30 sec at speed 4 and incubated according to the manufacturer's manual. After  
138 the first centrifugation step the supernatant was transferred to a new tube and complemented  
139 by 20 µl proteinase K of the DNeasy Blood & Tissue Kit. The extraction was continued  
140 following Qiagen instructions. PCR was performed using Hot Master Taq polymerase  
141 (Eppendorf) and adapting the protocol (initial denaturation 1 min., annealing 30 sec.,  
142 elongation 65°C).

143 DGGE was performed using the DCode electrophoresis system (Biorad). Preparation  
144 of polyacrylamide gels (15-70 % resp. 25-55 % denaturant gradient) and electrophoresis

145 parameters (100 V, 15 h) were performed according to Muyzer et al. (1995). Bands were  
146 stained with SYBR-Gold (Molecular Probes) and excised. DNA was extracted from gel  
147 material and dissolved in 10 µl distilled water (Sambrook et al. 1989).

148

149 *Re-amplification of DNA fragments from DGGE bands*

150

151 In difficult cases a further purification of DNA fragments could be obtained by re-amplifying  
152 the extracted DNA using again the forward primer with clamp (341fc), checking the accurate  
153 position of the band and excising it after an additional DGGE run. The extracted DNA was re-  
154 amplified for sequencing by using the Taq DNA polymerase but this time applying the  
155 forward primer without clamp (341f) and omitting the enhancer. PCR products were purified  
156 by using the Qiaquick PCR Purification Kit (Qiagen) following the instructions of the  
157 manufacturer's protocol and eluted with 60 µl distilled water.

158

159 *DNA sequencing of PCR products and comparative sequence analysis*

160

161 Sequencing was carried out by Qiagen Sequencing Services / Hilden, Germany. Sequences  
162 were aligned by using the Align IR program and the advanced BLAST search program of the  
163 National Center of Biotechnology Information (NCBI) website <http://www.ncbi.nlm.nih.gov>  
164 /Blast) to find closely related sequences.

165

## 166 **Results**

167

168 *Phylogenetic analysis of mixed cultures*

169

170 Cultures were prepared at low concentrations of organic matter, applying aerobic and micro-  
171 aerophillic conditions. Different media were selected in order to widen the spectrum of  
172 culturable bacterial endobionts (Table 1). Bacterial cultures could be obtained from all four  
173 cnidarian species. Regarding DGGE patterns the influence of different media compositions on  
174 the bacterial spectrum was negligible.

175         Seventy-nine fragments of the 16S rDNA deriving from cultures of four cnidarian  
176 species were successfully sequenced, aligned and phylogenetically analyzed (consult Table 2).  
177 Most of the fragments displayed similarities between 98 and 100% to their next neighbours;  
178 exceptions were *Endozoicimonas elysicola* (97%), *Arcobacter butzleri* (97%) and  
179 *Mesorhizobium tianshanense* (89%). Seventeen bacterial species and four groups were found,

180 the latter containing different closely related bacterial species which could not be  
181 differentiated from each other. The four groups were: (#1) *Pseudoalteromonas tetraodonis* /  
182 *P. elyakovii* / *P. haloplanctis*, (#2) *Shewanella sairae* / *S. marinintestina*, (#3) *S. waksmanii* /  
183 *S. surugaensis* / *S. kaireiae* and (#4) *Vibrio splendidus* / *V. lentus* / *V. tasmaniensis* / *V.*  
184 *kanaloae*. In these cases the used fragment size was inappropriate to discriminate between the  
185 species forming these groups. Except for the *Bacillus subtilis* (Fermicutes), *Ilyobacter*  
186 *psychrophilus* (Fusobacterium) and *Arcobacter butzleri* ( $\epsilon$ -proteobacterium) all other of the  
187 endobacteria detected were members of  $\gamma$ -proteobacteria. The most abundant endobionts  
188 comprised the groups #4 and #1 as well as *Photobacterium profundum*.

189 Remarkably, eleven bacterial species were described recently as novel organisms,  
190 some of them also experienced several taxonomic rearrangements. There were *Cobetia*  
191 *marina* (Arahal et al. 2002), *Colwellia aestuarii* (Jung et al. 2006), *Endozoicimonas elysicola*  
192 (Kurahashi and Yokoto 2006), *Pseudoalteromonas aliena* (Ivanova et al. 2004),  
193 *Pseudoalteromonas marina* (Nam et al. 2007), *P. tetraodonis* (Ivanova et al. 2001),  
194 *Psychrobacter nivimaris* (Heuchert et al. 2004), *Shewanella livingstonensis* (Bozal et al.  
195 2002), *S. sairae* (Satomi et al. 2003), *S. surugaensis* (Miyazaki et al, 2006), *S. violacea* (Nogi  
196 et al. 1998). Their physiological traits are only partially known, yet.

197 Concluded, *Tubularia indivisa* provides the habitat for a wide spectrum of twelve  
198 bacterial species / groups, *Cyanea capillata* nine, *Sagartia elegans* eight and *Cyanea*  
199 *lamarckii* three.

200

#### 201 *Host specific bacteria*

202

203 All four of the cnidarian species tested harbored host specific bacteria. Thirteen endobiotic  
204 species and groups occurred as single bacterial tenants, which are regarded as “specialists” for  
205 their individual hosts. *Shewanella violacea*, *Sulfitobacter pontiacus*, *Arcobacter butzleri* and  
206 members of group #2 were detected exclusively in *C. capillata* and *Moritella viscosa* only in  
207 *C. lamarckii*. Remarkable similarities between the jellyfish hosts could not be detected. The  
208 hydrozoa *Tubularia indivisa* sheltered the endobacteria *Cobetia marina*, *Colwellia aestuarii*,  
209 *Endozoicimonas elysicola*, *Psychrobacter nivimaris*, *Shewanella livingstonensis*, *Vibrio*  
210 *aestuarianus*, *Bacillus subtilis* and *Ilyobacter psychrophilus*; the sea anemone *Sagartia*  
211 *elegans* had *Pseudoalteromonas aliena* as host specific tenant.

212

213

214 *Phylogenetic analysis of lyophilized material*

215

216 The phylogenetic analysis of six lyophilized samples comprising *Cyanea capillata*, *C.*  
217 *capillata* and *Tubularia indivisa* generated 10 bands. The band patterns displayed fewer bands  
218 than those of the cultures (Fig.1). *C. capillata* fragments displaying *Vibrio* species group #4  
219 were found in both samples (similarity 99%). *Endozoicimonas elysicola* (similarity 97%) was  
220 spotted in lyophilized but also in mixed culture material of *Tubularia indivisa*. This novel  
221 organism has also been detected previously in the sea anemone *Metridium senile* (Schuett et  
222 al 2007). An exciting result was the discovery of endobacteria showing an extremely low  
223 relationship to their next neighbours. Because of high sequence quality strange  
224 microorganisms detected in both of the *Cyanea* species and *Tubularia indivisa* should be  
225 interpreted as unknown new species. Among them were bacteria distant to *Aquaspirillum*  
226 *itersonii* (similarity 90%, found in *Cyanea lamarckii*), *Francisella philomiragia*, (similarity  
227 93%, both *Cyanea* species), and *Spiroplasma syrphidicola*, (89%, *Tubularia indivisa*). A  
228 definite phylogenetic allocation of these unambiguous sequence data to known bacteria is  
229 currently impossible.

230

231 *Aggregates*

232

233 *Tubularia indivisa* and *Sagartia elegans* contained organ-like bacterial aggregates in the  
234 tentacle's epidermis. The aggregates are smaller than those of *Aiptasia pallida* (Palincsar et  
235 al. 1989) and *Metridium senile* (Schuett et al. 2007). Nevertheless, each of these aggregate-  
236 bearing cnidaria harbor a different bacterial spectrum. *Cyanea* species showed only free  
237 floating endobiotic bacteria in their tentacles. A paper on aggregate visual nature and  
238 distribution by REM inspection is in preparation.

239

240 *Pathogenic activities of bacterial endobionts*

241

242 Nine bacterial species (out of 21) may possess pathogen activities and/or produce toxins  
243 (Table 3). This information has been taken from physiological literature data. It should be  
244 noted that the *Pseudoalteromonas* group #1 and the *Vibrio* group #4 contain members of  
245 pathogenic and non-pathogenic bacteria. All four cnidarian host organisms harbor potentially  
246 pathogen bacteria: *C. lamarckii* two species and *C. capillata* five, *Tubularia indivisa* and  
247 *Sagartia elegans* each five. *Vibrio splendidus* (the only pathogen species of group #4) has



248 been detected in all of the cnidaria tested. *Photobacterium profundum* and  
249 *Pseudoalteromonas tetraodonis* (group #1) have been found in *C. capillata*, *Tubularia*  
250 *indivisa* and *Sagartia elegans*.

251 Some remarkable examples in detail: Hydrozoa *Tubularia indivisa* harbors the  
252 potentially pathogen *Endozoicimonas elysicola* which is suspected to play a role in amoebic  
253 fish disease (Bowman and Nowak 2004). *Photobacterium profundum* produces ToxR genes  
254 that mediate virulence expression (Bidle and Bartlett 2001, Ivanova et al 2004).  
255 *Pseudoalteromonas tetraodonis* (group #1) is known to produce tetrodotoxin (Do et al. 1990;  
256 Ivanova et al. 2001). Metabolites of *Vibrio aestuarianus* may kill corals, oysters and turbot  
257 larvae. Extracellular toxic products of *Vibrio aestuarianus* (Labreuche et al. 2006, Garnier et  
258 al. 2007) may impair juvenile oysters. Members of *Vibrio splendidus* (group #4) can express  
259 septicaemic and necrotic activities (Sugumar et al. 1998, Thomson et al 2003, Koren and  
260 Rosenberg 2006). Yet, it is uncertain whether anaerobic *Ilyobacter psychrophilus*, member of  
261 the genus *Fusobacterium*, generates severe clinical infection.

262 Anthozoa *Sagartia elegans* harbors *Photobacterium profundum* and  
263 *Pseudoalteromonas aliena*, which produces cytotoxins and causes haemolytic activities  
264 (Ivanova et al. 2004). Additionally *Sagartia elegans* contains members of the groups #1 and  
265 #4 (activities see above).

266 Jellyfish *Cyanea lamarckii* provides the natural habitat for *Moritella viscosa*, which  
267 causes necrotic “winter ulcer” in salmon (Lunder et al. 2000, Heidarsdottir et al. 2008),  
268 additionally *Arcobacter butzleri*, a human pathogen species (Carbone et al. 2003, Gugliandolo  
269 et al. 2007), and finally members of group #4 (see above). The Lions mane jellyfish *C.*  
270 *capillata* carries the haemolytic species *Shewanella waksmanii*, a member of group #3  
271 (Ivanova et al. 2003), and pathogenic endobionts of the already described *Photobacterium*  
272 *profundum* and the putatively pathogenic species of groups #1 and #4 (see above).

273

#### 274 *Haemolysis*

275

276 Selection of mixed culture material based on haemolysis tests and subsequent phylogenetic  
277 analysis were applied to verify the pathogenic activities derived from literature data. The  
278 findings are in good correspondence with literature reports: Haemolytic positives were  
279 detected in *Cyanea capillata* (*Pseudoalteromonas* group 1, 3 isolates; *Vibrio* group 4, 5  
280 isolates), *Tubularia indivisa* (*Vibrio* group 4, 1 isolate), and in *Sagartia elegans*  
281 (*Pseudoalteromonas aliena*, 1 isolate; *Pseudoalteromonas* group 1, 2 isolates; *Vibrio* group 4,

282 4 isolates). In order to determine cytolytic activity, the agar diffusion test was applied to  
283 haemolysis positive pure cultures. In case of *Vibrio* group #4 strain, derived from tentacle  
284 material of *Cyanea capillata*, the cells were completely disintegrated and decolorized within a  
285 1 cm zone.

286

## 287 **Discussion**

288

289 The spectrum of culturable bacterial species is remarkable: Some of them can be regarded as  
290 “all rounders”; others were host specific. An unambiguous identification on species level was  
291 excellent for seventeen different fragments (i.e. 80%). Unclear allocation of sequence data at  
292 species level led to the formation of groups # 1 to # 4. Some authors reported similar findings  
293 of different bacterial species (Ivanova et al., 2003 for *Shewanella* species, Marques et al.,  
294 2005, Venkateswaran et al., 1998 for *Vibrio* species, Mc Aucliffe et al., 2003 for *Mycoplasma*  
295 species). The application of larger 16S rDNA or 23S rDNA fragments might be more  
296 appropriate in future experiments. Physiological information concerning pathogenic activities  
297 was exclusively taken from literature data and therefore insufficient as proof for pathogenic  
298 traits but also unsuitable in cases of unknown new species.

299 Eighty-one percent of the species or groups found were host specific. This is a clear  
300 sign that bacterial contamination of the tentacle surface was avoided during experiments,  
301 which was confirmed by microscopic inspection subsequently to CTAB treatment.

302 Which approach reflects the actual presence of endobionts - phylogenetic data derived  
303 from cultures or lyophilized material? The strange, unidentified endobacteria may be regarded  
304 as the authentic, dominant tenants inhabiting the “exotic” tentacles whose physico-chemical  
305 conditions are still not discovered. Yet, PCR-processing of lyophilized material cannot detect  
306 low bacterial numbers. The major disadvantage of cultures is their medium dependence; the  
307 bacteria that grow may be of less endobiotic importance. In our experiments the only bacterial  
308 species detected in both of the approaches was *Endozoicimonas elysicola*. To meet the actual  
309 growth requirements, refined culture techniques are needed.

310 The organ-like bacterial aggregates detected in *Sagartia elgans* and *Tubularia indivisa*  
311 contain hundreds of tightly packed, differently shaped endobacteria. Their different shapes  
312 suggest that these organisms may be host-specific. The development and function of the  
313 organ-like aggregates are unclear. Do we presently observe here an evolutionary step during  
314 the formation of organ-like aggregate structures? Is that comparable to the developmental  
315 steps of prokaryotic mitochondria or chloroplasts in eukaryotes?

316 Data show that a considerable number of bacterial species living as tenants in  
317 cnidarian hosts may have pathogenic activity. The applied haemolysis and cell culture tests  
318 support the indirect approach using trait data from literature based on phylogenetic  
319 classification. Further testing of acute cell toxicity should be performed after calibrating  
320 bacterial protein concentration.

321 There is substantial knowledge of tetrodotoxin TTX, which is an extremely potent  
322 neurotoxin. Its chemical structure and activities at cellular level are well documented  
323 (Thuesen and Kogure 1989; Do et al. 1990; Ritchie et al. 2000). TTX-carrying animals are  
324 known from different marine, limnic and terrestrial habitats of warmer regions. Among them  
325 were the well known puffer fish species (*Tetraodontidae*) but also starfish, toads, flatworms  
326 and even chaetognathes. Interestingly the toxin is produced by endobiotic bacteria (Simidu et  
327 al. 1990, Yu et al. 2004). One of those endobionts is *Pseudoalteromonas tetraodonis* (Ivanova  
328 et al. 2001). Supposedly these bacteria are also common partners of cnidarian species. In  
329 order to generate answers to the bacterial role in the production of cnidarian toxins the  
330 investigation of their physiological traits is indispensable.

331

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336

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Bacterial Species	Origin (literature data)	Toxic & Pathogenic Activities	Literature Data
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Medium DSMZ	Quantity	Notes	#621+M44	#621	#621- Glu
Peptone (Bacto)	0.25 g	pH 7,5 autoclaved	x	x	x
Yeast extract (Bacto)	0.25 g		x	x	x
Aged seawater	724.00 ml		x	725.00 ml	x
Distilled water	241.00 ml		x	x	251.00 ml
Mineral salt solution	19.00 ml	sterile filtered	x	x	x
Vitamin sol.(double conc.)	5.00 ml	sterile filtered	x	x	x
Metals 44 (DSMZ #590)	1.00 ml	sterile filtered	x	—	x
Glucose sol. (2,5 %)	10.00 ml	sterile filtered	x	x	—

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471 **Tab. 1** Medium DSMZ #621 and derivatives; metal composition M44 originates from  
 472 Medium #590. Both media are provided by the German Collection of Microorganisms and  
 473 Cell Cultures ([www.dsmz.de](http://www.dsmz.de)). Negative symbol indicates substitution of distilled water

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<i>Endozoicimonas elysicola</i>	nudibranch <i>Elysia ornata</i>	amoebic fish disease	Bowmann and Nowak 2004
<i>Moritella viscosa</i>	Atlantic salmon	necrotic, “winter ulcer”	Lunder et al. 2000
<i>Photobacterium profundum</i> SS9	deep sea crustaceans	ToxR-gene (mediating virulence expression)	Bidle and Bartlett 2001; Ivanova et al. 2004
<i>Pseudoalteromonas aliena</i>	seawater	cytotoxic, haemolytic	Ivanova et al. 2004
<i>Pseudoalteromonas tetraodonis</i> (group #1)	buffer-fish	produces tetrodotoxin	Simidu et al. 1990; Ivanova et al. 2001
<i>Shewanella wachsmanii</i>	marine worm <i>Phascolosoma sipuncula</i>	haemolytic	Ivanova et al. 2003
<i>Vibrio aestuarianus</i>	oyster juveniles, seawater	extracellular toxic products	Labreuche et al. 2006; Garnier et al. 2007
<i>Vibrio splendidus</i> (group #4)	mostly abundant in corals, oysters, turbot larval gut,	haemolytic, septicaemic, necrotic	Sugumar et al. 1998; Thomson et al. 2003; Koren and Rosenberg 2006
<i>Arcobacter butzleri</i>	brackish marine environment	human and animal pathogen, secretion of toxic factors	Carbone et al. 2003; Gugliandolo et al. 2007

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**Tab. 3** Pathogen potential of endobiotic bacteria detected in cnidarian tentacles. *Pseudoalteromonas* group #1 and *Vibrio* group #4 contain closely related pathogenic and non-pathogenic species