Received: 31 October 2019 | Revised: 20 December 2019 | Accepted: 20 December 2019

DOI: 10.1111/jfd.13134



ORIGINAL ARTICLE

Journal of Fish Diseases | WILEY

# Infection dynamics of *Bonamia exitiosa* on intertidal *Ostrea angasi* farms

Jessica Jamuna Buss[1,2] | Kathryn Helen Wiltshire[2] | James Owen Harris[1,2] | Jason Elliot Tanner[2] | Marty Robert Deveney[1,2]

[1]College of Science and Engineering, Flinders University, Adelaide, SA, Australia

[2]South Australian Research and Development Institute (SARDI), Aquatic Sciences Centre and Marine Innovation Southern Australia, West Beach, SA, Australia

**Correspondence**
Jessica Jamuna Buss, College of Science and Engineering, Flinders University, Adelaide, SA 5001, Australia.
Email: Buss0017@flinders.edu.au

**Funding information**
South Australian Research and Development Institute; Fisheries Research and Development Corporation, Grant/Award Number: 2015-001; Flinders University; Australian Government Department of Agriculture

## Abstract

*Bonamia* spp. cause epizootics in oysters worldwide. In southern Australia, *Bonamia exitiosa* Hine, Cochennac and Berthe, 2001 threatens aquaculture of *Ostrea angasi* Sowerby, 1871. *Bonamia* spp. infections can display strong seasonality, but seasonal dynamics of *B. exitiosa*–*O. angasi* are unknown. *Ostrea angasi* naïve to *B. exitiosa* infection were stocked onto farms in three growing regions, and *B. exitiosa* was monitored seasonally for one year. Environmental parameters we measured did not correlate with *B. exitiosa* prevalence or infection intensities. Extreme temperatures suggest *O. angasi* culture systems need development. *Bonamia exitiosa* prevalence increased over time. After three months, *O. angasi* had *B. exitiosa* prevalence of 0.08–0.4, and after one year, the prevalence was 0.57–0.88. At some sites, *O. angasi* had >0.5 *B. exitiosa* prevalence in >6 months, but at other sites, >9 months passed before prevalence was >0.5. *Bonamia exitiosa* infection intensities were low with no seasonal pattern but were affected by the interaction of site, season and oyster meat:shell ratio. Understanding infection and initiating a breeding programme for resistance would provide benefits for *O. angasi* industry expansion.

**KEYWORDS**

*Bonamia exitiosa*, farm trial, *Ostrea angasi*, South Australia

## 1 | INTRODUCTION

Mollusc aquaculture provides a substantial supply of food; global mollusc production in 2016 was 17.1 million tonnes (FAO, 2018). Since the 1970s, diseases caused by the intracellular protozoa *Bonamia* spp. have negatively affected oyster industries in Europe, North America, South America, North Africa, New Zealand and Australia (Arzul et al., 2006; Hill et al., 2014).

A *Bonamia* sp. was identified in Australia in the early 1990s in farmed and wild populations of the Native Oyster (*Ostrea angasi*, Sowerby, 1871) (see Hine & Jones, 1994). Extensive investigations including genome sequencing have identified all southern Australian *Bonamia* isolates as *Bonamia exitiosa* Hine, Cochennac and Berthe, 2001 (see Bradley, 2019; Buss, Harris, Tanner, Wiltshire, & Deveney, 2019a). Handlinger et al. (1999) reported that histological surveys of wild *O. angasi* across SA in 1992–93 did not detect *Bonamia*. Surveys of farmed Pacific oysters (*Crassostrea gigas* Thunberg, 1793) in SA in 2002, however, reported *Bonamia*-like cells (Diggles, 2003), but no confirmatory diagnosis was made. If these cells were *B. exitiosa*, these data support that *C. gigas* is a host of *Bonamia* spp. as proposed by Lynch et al. (2010). It is therefore likely that *B. exitiosa* was introduced or became widespread in SA between 1993 and 2002.

*Bonamia* spp. transmit directly between hosts (Arzul & Carnegie, 2015). Large farmed oyster populations may have facilitated the proliferation of *B. exitiosa* in SA, leading to the high prevalence observed by Buss, Wiltshire, Prowse, Harris, and Deveney (2019b). Although the origin of SA *B. exitiosa* is unknown, it likely arrived via an anthropogenic route. Transmission of *Bonamia ostreae* Pichot, Comps, Tigé, Grizel and

  

Rabouin, 1980 is linked to vessel biofouling (Howard, 1994), translocation of stock (Hudson & Hill, 1991; Peeler, Oidtmann, Midtlyng, Miossec, & Gozlan, 2011) and the seafood trade (Feng et al., 2013). Given that *B. exitiosa* is now established across southern Australia, aquaculture operators and reef restoration proponents need to understand and take the pathogen into account in their planning.

Environmental conditions affect infection dynamics of *Bonamia* spp.–host systems. High salinity (>20 psu) is associated with higher *B. exitiosa* prevalence and/or infection intensities in *Crassostrea ariakensis* Fujita, 1913 (see Audemard, Carnegie, Bishop, Peterson, & Burreson, 2008; Audemard, Carnegie, Hill, Peterson, & Burreson, 2014; Audemard, Carnegie, Stokes, et al., 2008; Bishop, Carnegie, Stokes, Peterson, & Burreson, 2006); higher *B. exitiosa* prevalence and infection intensities in *Ostrea chilensis* Philippi, 1844 (see Hine, Diggles, Parsons, Pringle, & Bull, 2002); and increased survival of *B. ostreae* cells (Arzul et al., 2009). *Bonamia* spp. in different hosts have a range of seasonal patterns of infection. In *B. exitiosa*-*C. ariakensis*, higher *B. exitiosa*-associated prevalence and mortality occurs in spring, summer and early autumn, but *B. exitiosa* was undetectable in *C. ariakensis* at <25°C in late autumn and winter (Carnegie et al., 2008). For *B. exitiosa*–*O. chilensis*, the prevalence peaks in autumn and winter (Hine, 1991). In *B. ostreae*–*Ostrea edulis* Linnaeus, 1758 transmission occurs throughout the year, but higher *B. ostreae* prevalence is observed in winter (Arzul et al., 2006; Culloty & Mulcahy, 1996) and spring (Culloty & Mulcahy, 1996; Engelsma et al., 2010).

Field infection dynamics and *B. exitiosa* seasonality are undescribed in *O. angasi*. This study aimed to assess seasonal changes in *B. exitiosa* prevalence and infection intensities in intertidally cultured *O. angasi* over a year. Understanding *B. exitiosa*–*O. angasi* infection dynamics will inform farm management decisions and aid development of the *O. angasi* aquaculture industry.

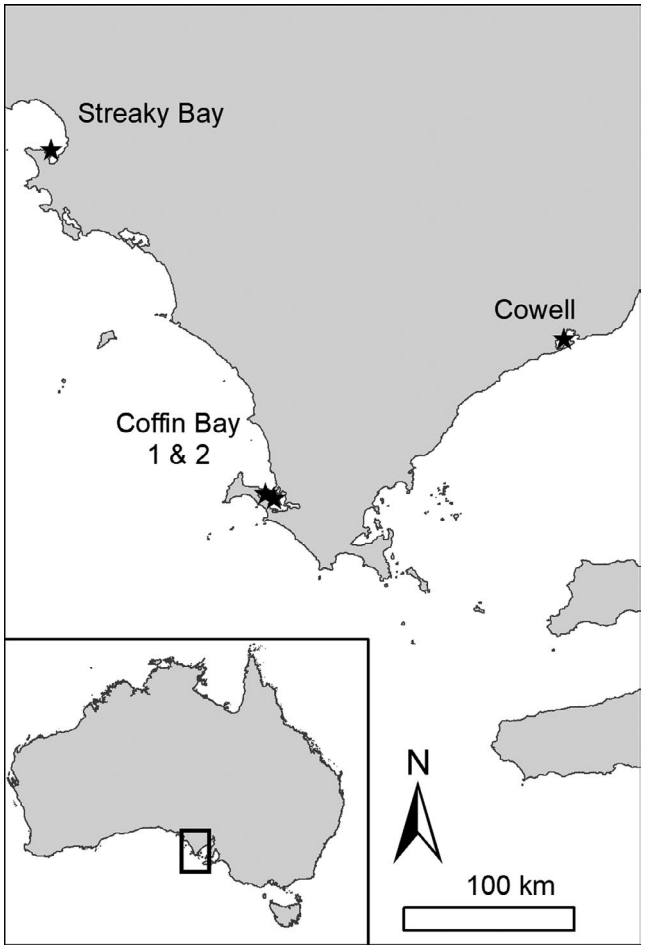


**FIGURE 1** *Ostrea angasi* farm stocking locations in the Eyre Peninsula, South Australia. Each star shape represents one farm

## 2 | METHODS

### 2.1 | Experimental animals

Common names used are consistent with Australian Fish Names Standard AS 5300-2015 (Standards Australia, 2015).

Fourteen-month-old (7–10 mm) *O. angasi* that had not been used for any experiments were sourced from the South Australian Research and Development Institute (SARDI) Aquatic Sciences Centre (SAASC) Mollusc Hatchery (West Beach, Adelaide, South Australia). Testing by real-time PCR (Corbeil et al., 2006) ($n$ = 150) and histology ($n$ = 150) did not detect *Bonamia* (mean Bayesian estimated prevalence, credible intervals: 0.017, 0.000–0.05; Buss et al., 2019b).

### 2.2 | Farm stocking and location

Four oyster farms on the Eyre Peninsula (South Australia) were chosen as experimental sites: Coffin Bay 1, Coffin Bay 2, Cowell and Streaky Bay (Figure 1). Approximately 600 juvenile *O. angasi* (total $n$ = 1,780) were stocked in three replicate baskets (15 L, SEAPA) and deployed at each of the four sites. At Coffin Bay and Cowell, oysters were deployed in 3-mm mesh size baskets, and at Streaky Bay, oysters were deployed in 6-mm mesh size baskets. All oysters were chosen from the same cohort and transported to farms within 48 hr of leaving the hatchery.

Coffin Bay 1 is in western Coffin Bay. It has a moderate-energy environment, is sheltered from prevailing winds and is characterized by a sandy seafloor and high biofouling, comprising mostly barnacles and mussels. Coffin Bay 2 is in the central channel of Coffin Bay and experiences large tidal fluctuations. It is a high energy, deep-water site, with a sandy substrate and high biofouling, comprising barnacles and mussels. Cowell is in southern Franklin Harbour, adjacent to a mangrove (*Avicennia marina* (Forssk.) Vierh.) forest. It is a shallow and low-energy environment with a fine sediment substrate and dense *Posidonia australis* Hook. f. beds. The Cowell site has high turbidity and extreme barnacle biofouling with settlement predominantly in summer. Streaky Bay is in southern Streaky Bay and is a shallow, exposed site with high wave and wind energy. This site is characterized by a sandy benthos with *P. australis* and *Amphibolis antarctica* (Labill.) Asch. beds and a *Pinna bicolor* Gmelin, 1791 population. All sites are intertidal; oysters were periodically exposed to air and then submerged under water. In summer during tidal maxima,

**TABLE 1** Sampling timeline of *Ostrea angasi* from four South Australian farms over four seasons[a]

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | S | S | A | A | A | W | W | W | Sp | Sp | Sp | S |
| 2017 | | St | | | X1 | | | X2 | | | X3 | |
| 2018 | | X4 | | | | | | | | | | |

[a]"St" denotes date of stocking, "X" denotes sampling date, and the number corresponds to the number of sampling trips since stocking. "S" is summer, "A" is autumn, "W" is winter, and "Sp" is spring.

the substrate at Cowell and Streaky Bay sites was completely exposed. Sites were stocked in the Austral summer in late February 2017 (Table 1).

## 2.3 | Experimental design: oyster sampling

To assess the dynamics of *B. exitiosa* in *O. angasi*, the cohort of oysters was monitored seasonally over a year (Table 1). Every three months at the end of each Austral season, all baskets were inspected and a sample of 20 oysters per replicate basket ($n$ = 60) were removed from the baskets following a randomization plan, placed in an ice box, transported ashore and sampled. Oysters were weighed (OHAUS, Scout General (SPX) Portable Balance Scales, Model # SPX223), and shell length was measured with a digital calliper (Craftright 150-mm Stainless Steel Digital Vernier Caliper) along the longest shell axis (hinge to top of shell). Oyster meat was removed, the empty shell was weighed, and the meat-to-shell ratio was calculated (meat weight (g)/shell weight (g) × 100). At the end of the trial, all oysters were removed and survival was estimated.

## 2.4 | Diagnostic sampling: heart smears and terminology

Heart smears were used to determine the prevalence and infection intensities of *B. exitiosa* in *O. angasi*. Within 24 hr of sampling, heart smears from sample oysters were made on slides, dried, fixed and stained as per Buss et al. (2019b). Heart smears were viewed under a compound light microscope (Brightfield Olympus BX53), and *B. exitiosa* infection intensities were graded using a semi-quantitative score following Buss et al. (2019b). Parasitology terminology used for *B. exitiosa* prevalence and infection intensity is consistent with Bush, Lafferty, Lotz, and Shostak (1997).

## 2.5 | Experimental design: environmental parameters

Two temperature loggers (HOBO Pendant® Temperature/Light Data Logger 64K-UA-002–64, accuracy ± 0.47°C at 25°C) were used per site, with one placed at the same height as the oyster baskets (the above probe) to measure the temperature oysters were experiencing, and one placed directly below (the below probe) on the benthos to monitor the water temperature. A conductivity logger (Odyssey Conductivity and Temperature Logger, 80 mS/cm, accuracy 3% of reading) was also used at each site to assess conductivity. Each conductivity logger was placed on the benthos below the oysters. Every 3 months, environmental data were retrieved and collated. Phytoplankton data per season and site were provided by the South Australian Shellfish Quality Assurance Program (SASQAP).

## 2.6 | Statistical analyses

Infection intensity data were compared using the Quantitative Parasitology 3.0 (Reiczigel, Marozzi, Fábián, & Rózsa, 2019), using Sterne's exact confidence intervals for 95% bootstrap confidence intervals for mean infection intensities (with 5,000 replications). Mean infection intensities were considered significantly different when confidence intervals did not overlap.

A Bayesian Latent Class Model (LCM) was built and used to calculate estimated prevalence with credible intervals using JAGS code modified from the prevalence R package (Devleesschauwer et al., 2015). This model used uninformative beta (1, 1) priors for prevalence estimates. Priors for DSe (diagnostic sensitivity) and DSp (diagnostic specificity) of heart smear were informed by outputs from the analysis of Buss et al. (2019b). These beta priors reflected 95% confidence that heart smear DSe and DSp fall within the credible interval with the mean specified in Table 2. The Markov chain Monte Carlo (MCMC) simulations were obtained by running the model in JAGS v. 4.3.0 (Plummer, 2017) using three chains for 10,000 iterations, thinned at a rate of 10, following 2,000 iterations for adaptation and 10,000 iterations for burn-in. JAGS was run using the R2jags package (Su & Yajima, 2015) in R (R Core Team, 2017). The convergence was assessed using the Gelman–Rubin convergence statistic and confirmed by visual inspection of trace, density and autocorrelation plots generated using the MCMCvis package (Youngflesh, 2018). Estimated prevalence values were assessed as being different when credible intervals did not overlap.

A generalized linear model (GLM) was used to assess *B. exitiosa* infection intensities in oysters across site and season. A negative binomial distribution was used for infection intensity analysis due to the overdispersion of data relative to a Poisson distribution. Negative binomial GLMs were conducted in R using the MASS package (Venables & Ripley, 2002). *Bonamia exitiosa* infection intensity plots for each site and season were created using the R package ggplot2 (Wickham, 2016).

**TABLE 2** The beta priors, associated mean and 95% credible intervals for diagnostic sensitivity (DSe) and diagnostic specificity (DSp) for heart smear, used to calculate estimated prevalence, plus the posterior predictions for DSe and DSp of heart smear[a]

| Test | DSp or DSe | Beta priors | Mean, 95% credible intervals | Posterior predication (mean, credible intervals) |
|---|---|---|---|---|
| Heart smear | DSe | (113, 72) | 0.61 (0.54–0.68) | 0.66 (0.61–0.70) |
| Heart smear | DSp | (27, 18) | 0.60 (0.45–0.73) | 0.71 (0.64–0.78) |

[a]Heart smear priors were derived from Buss et al. (2019b).

## 3 | RESULTS

### 3.1 | Prevalence

Estimated *B. exitiosa* prevalence from heart smears increased over time; estimated prevalence ranged from 0.08–0.40 after 3 months to 0.57–0.88 after 12 months (Table 3). *Ostrea angasi* from Coffin Bay sites 1 and 2 exceeded 0.5 *B. exitiosa* prevalence after six months, whereas those from Cowell and Streaky Bay took nine months for *B. exitiosa* prevalence to exceed 0.5. *Ostrea angasi* collected at the end of winter from Coffin Bay 2 that had higher estimated *B. exitiosa* prevalence than *O. angasi* from Cowell, but credible intervals for other sites overlapped (Table 3). At the end of spring, there were no differences in estimated *B. exitiosa* prevalence in *O. angasi* (Table 3).

The posterior predicted means of DSe and DSp for heart smear were higher than the prior means from Buss et al. (2019b) (Table 2), but the 95% credible intervals of the posterior predictions overlapped those of the priors.

### 3.2 | Infection intensity

Mean *B. exitiosa* infection intensities did not differ at each site between seasons (Table 3). There were no differences between sites within each season except for winter, when *O. angasi* from Cowell and Streaky Bay had lower mean infection intensities than *O. angasi* from Coffin Bay 2 (Table 3).

GLM showed a significant three-way interaction between site, season and meat:shell ratio (LRT: $\chi^2(9) = 26.12$, $p = 1.95e^{-3}$). *Ostrea angasi* from Coffin Bay 2 and Streaky Bay had higher infection intensities associated with higher meat:shell ratio in summer and spring, but in autumn and winter, higher infection intensities were associated with lower meat:shell ratio (Figure 2). This pattern was not consistent between sites (Figure 2).

### 3.3 | Survival and size data

The final proportion of survivors at all sites varied between 17.01% and 32.77% (Table 4). The lowest proportion of surviving oysters was at Streaky Bay.

After 1 year, Cowell had larger oysters (20 g mean weight) than other sites (<9 g mean weight (Table 3).

### 3.4 | Environmental parameters

Initial data exploration using a correlation matrix showed infection intensities, and the prevalence did not correlate with any measured environmental parameter. Cowell experienced the greatest temperature difference: maximum temperature: 48.7°C, and minimum temperature: 5.8°C (Table 5).

In summer, temperature at Coffin Bay 1 had a maximum of 35°C, but only December data were available because the probe malfunctioned. At Coffin Bay 2, temperature exceeded 40°C once. At Cowell, the temperature exceeded 35°C 19 times and five of these events exceeded 40°C. Streaky Bay exceeded 35°C 11 times, and five of these events exceeded 40°C.

## 4 | DISCUSSION

We observed the clear patterns of prevalence for *B. exitiosa* in farmed *O. angasi*. *Bonamia exitiosa* was detected in *O. angasi* at all four farm sites within three months of stocking. *Bonamia exitiosa* prevalence increased in *O. angasi* at all sites over time, with highest prevalence (>0.57) after one year, but *B. exitiosa* infection intensities in *O. angasi* were not different between autumn and summer. Our findings are consistent with Buss et al. (2019b) who found *B. exitiosa* estimated prevalence of >0.59 and infection intensities of <4.36 in *O. angasi* on SA farms. At Cowell and Streaky Bay, *B. exitiosa* prevalence in *O. angasi* took nine months to exceed 0.5, whereas Coffin Bay sites exceeded 0.5 infection prevalence within six months of deployment. Sites with slower increase in prevalence may be more suitable for farming *O. angasi*. In warmer water, *O. angasi* grows more rapidly (Dix, 1980), and higher temperatures at Cowell could explain why oysters stocked in that area were larger than oysters from other sites. These data indicate that *B. exitiosa*–*O. angasi* infections are site-dependent as described for *B. ostreae* in *O. edulis* in Europe (Culloty, Cronin, & Mulcahy, 2004). These data therefore can inform decisions about the suitability of sites for oyster aquaculture (Culloty et al., 2004).

Diagnostic tests and their accuracy are well described for *B. exitiosa* in farmed *O. angasi* populations (Buss et al., 2019b). Understanding DSe and DSp of each test means that cost- and time-effective tests such as heart smear (Diggles, Cochennec-Laureau, & Hine, 2003) can be used and provide more accurate prevalence estimates than for less well-characterized tests and provide better interpretation of infection dynamics (Buss et al., 2019b; McDonald & Hodgson, 2018). The posterior predictions of

**TABLE 3** Size data (mean ± standard deviation), Bayesian estimated prevalence and mean infection intensity (calculated through quantitative parasitology) of *Bonamia exitiosa* in *Ostrea angasi* from heart smears over four seasons in South Australia[†,‡]

| | | Oyster data | | | | *Bonamia exitiosa* data | |
|---|---|---|---|---|---|---|---|
| Season | Site | Weight (g) (mean ± *SD*) | Shell length (mm) (mean ± *SD*) | Meat:shell ratio (%) (mean ± *SD*) | *n* | Estimated prevalence (Bayesian credible intervals) | Mean infection intensity, cell count (confidence intervals) |
| Autumn | Coffin Bay 1 | 6.02 ± 2.04 | 39.77 ± 4.78 | 45.20 ± 8.07 | 60 | 0.40 (0.07–0.76)$^{ab}$ | 3.65 (2.62–5.04)$^{b}$ |
| | Coffin Bay 2 | 6.66 ± 2.13 | 38.91 ± 4.28 | 38.63 ± 7.39 | 60 | 0.33 (0.03–0.65)$^{ab}$ | 4.38 (2.88–7.74)$^{ab}$ |
| | Cowell | 10.17 ± 6.46 | 45.31 ± 13.52 | 46.10 ± 11.47 | 60 | 0.09 (0.00–0.31)$^{b}$ | 3.64 (2.07–5.64)$^{ab}$ |
| | Streaky Bay | 3.05 ± 1.15 | 29.70 ± 4.12 | 44.65 ± 6.27 | 60 | 0.08 (0.00–0.26)$^{b}$ | 4.00 (2.50–7.15)$^{ab}$ |
| Winter | Coffin Bay 1 | 7.79 ± 4.36 | 40.74 ± 6.66 | 41.92 ± 5.84 | 60 | 0.53 (0.16–0.88)$^{ab}$ | 4.61 (3.56–5.82)$^{ab}$ |
| | Coffin Bay 2 | 5.22 ± 2.78 | 32.76 ± 5.98 | 37.84 ± 5.90 | 59 | 0.88 (0.62–1.00)$^{a}$ | 7.02 (5.28–9.67)$^{a}$ |
| | Cowell | 9.62 ± 4.42 | 44.46 ± 7.52 | 49.42 ± 10.85 | 60 | 0.20 (0.01–0.50)$^{b}$ | 3.10 (2.30–4.50)$^{b}$ |
| | Streaky Bay | 3.80 ± 1.44 | 29.61 ± 4.08 | 40.48 ± 5.07 | 60 | 0.44 (0.10–0.79)$^{ab}$ | 3.78 (2.74–5.22)$^{b}$ |
| Spring | Coffin Bay 1 | 6.36 ± 2.91 | 38.14 ± 5.51 | 40.51 ± 5.89 | 60 | 0.89 (0.66–1.00)$^{a}$ | 4.67 (3.64–6.93)$^{ab}$ |
| | Coffin Bay 2 | 6.39 ± 4.17 | 33.05 ± 6.91 | 35.86 ± 7.13 | 59 | 0.80 (0.49–0.99)$^{a}$ | 4.31 (3.50–5.29)$^{ab}$ |
| | Cowell | 9.34 ± 5.44 | 45.63 ± 8.93 | 53.06 ± 10.25 | 60 | 0.53 (0.16–0.87)$^{ab}$ | 3.03 (2.34–3.83)$^{b}$ |
| | Streaky Bay | 5.37 ± 2.68 | 33.71 ± 7.18 | 38.67 ± 4.58 | 59 | 0.63 (0.26–0.94)$^{ab}$ | 4.03 (2.87–7.56)$^{ab}$ |
| Summer | Coffin Bay 1 | 7.70 ± 4.21 | 38.07 ± 5.71 | 35.92 ± 8.38 | 60 | 0.88 (0.65–1.00)$^{a}$ | 5.51 (4.12–8.36)$^{ab}$ |
| | Coffin Bay 2 | 8.44 ± 3.79 | 37.97 ± 7.57 | 28.94 ± 6.99 | 60 | 0.87 (0.61–1.00)$^{a}$ | 5.22 (4.12–7.48)$^{ab}$ |
| | Cowell | 20.69 ± 10.64 | 53.90 ± 10.56 | 36.34 ± 7.94 | 60 | 0.57 (0.20–0.91)$^{ab}$ | 3.37 (2.77–4.20)$^{b}$ |
| | Streaky Bay | 9.24 ± 3.28 | 42.49 ± 4.98 | 41.91 ± 4.96 | 60 | 0.78 (0.46–0.98)$^{ab}$ | 3.36 (2.73–4.11)$^{b}$ |

[†]Different superscripts denote differences at a 5% level, with [a] representing the highest value.

[‡]*SD*: standard deviation; *n*: sample size per site.

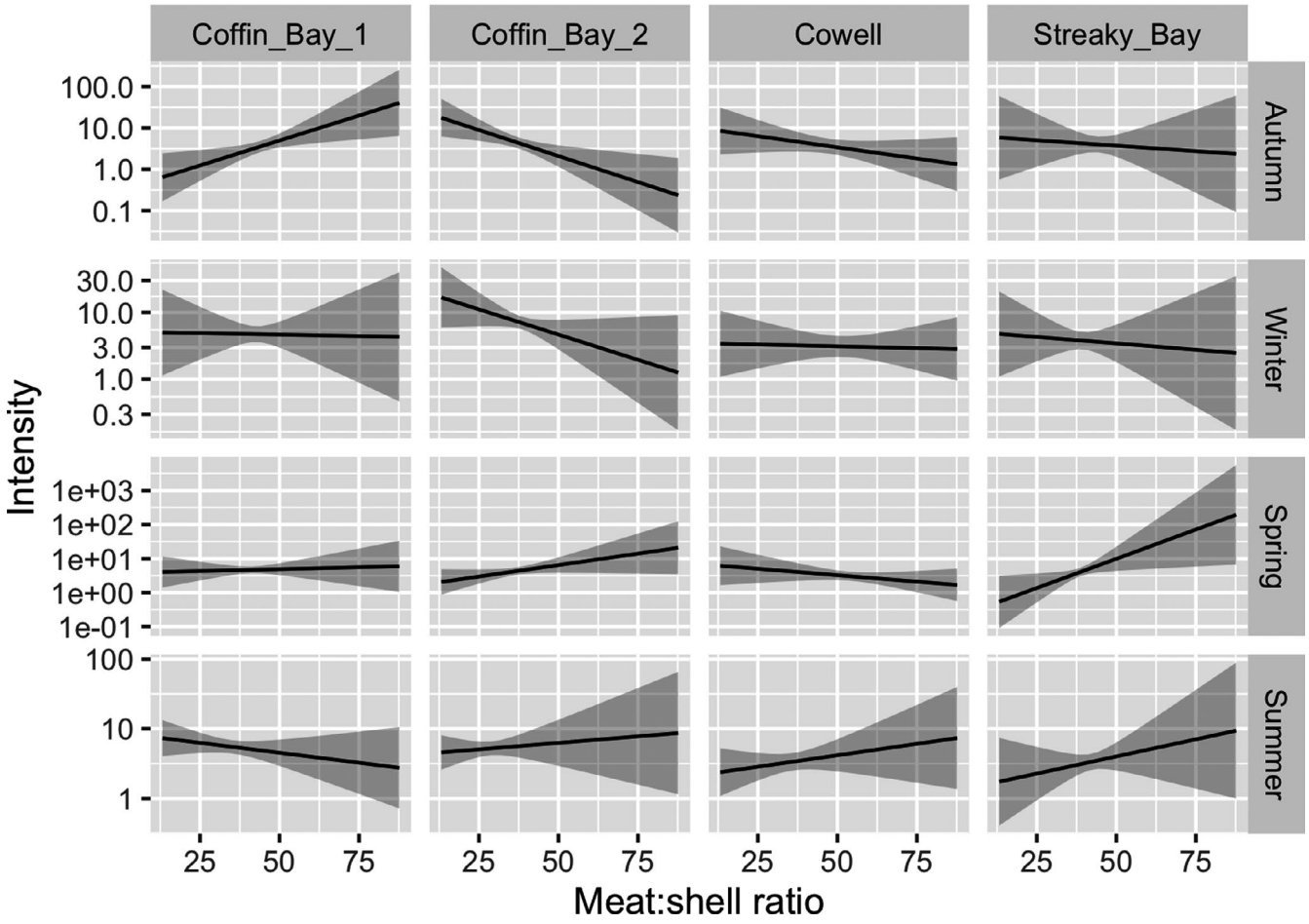


**FIGURE 2** *Bonamia exitiosa* mean infection intensity in *Ostrea angasi* per site (Coffin Bay sites 1 and 2, Cowell and Streaky Bay), per season (autumn, winter, spring and summer) and the relation to meat:shell ratio

prevalence from heart smears had overlapping credible intervals with the heart smear priors, indicating that the data in this study are consistent with priors in Buss et al. (2019b). This similarity increases confidence in the estimated prevalence in this study. Understanding test accuracy improves the certainty of results from field trials and surveillance programmes.

Sites with different environments were included in this study, but the environmental parameters we measured did not influence the prevalence or infection intensities of *B. exitiosa*. It is likely that parameters we did not measure, including proximity and density of oysters (Arzul & Carnegie, 2015; Lallias et al., 2008) such as farmed and wild populations of *O. angasi* and possibly *C. gigas*, had greater influence than environmental parameters. *Crassostrea gigas* is the predominant oyster farmed in SA (Nell, 2001) and a likely host of *Bonamia* spp. (see Diggles, 2003; Lynch et al., 2010). Coffin Bay is the best known and largest oyster farming region in SA with 145 leases (184 ha), followed by Streaky Bay (38 leases, 172 ha) and Cowell (37 leases, 115 ha) (PIRSA, 2017). Populations of farmed *C. gigas* and *O. angasi* in Coffin Bay are larger than in the other regions, which may drive the higher *B. exitiosa* prevalence in *O. angasi*, but estimates of total farmed oyster population sizes were not available to us. The first record of wild *C. gigas* in SA was in 1990 (Hone, 1993), and feral oyster numbers in growing regions can be substantial but are subject to control (EPA, 2005; Wear,

**TABLE 4** Count data of *Ostrea angasi* from four South Australia farms after four seasons

| Site | Initial count at stocking | Final total counts (dead and alive)[a] | Final counts (live) | Proportion live oysters remaining at end of trial (%) |
|---|---|---|---|---|
| Coffin Bay 1 | 1,785 | 685 | 585 | 32.77 |
| Coffin Bay 2 | 1,785 | 399 | 386 | 21.62 |
| Cowell | 1,785 | 438 | 414 | 23.19 |
| Streaky Bay | 1,775 | 181 | 302 | 17.01 |

[a]Final live counts included oysters that were removed for sampling per season.

**TABLE 5** Mean seasonal (Au = autumn, Wi = winter, Sp = spring, Su = summer) water conductivity and temperature data from four South Australian oyster farms (CB1 = Coffin Bay 1, CB2 = Coffin Bay 2, CW = Cowell, SB = Streaky Bay)

| | Water conductivity (mS/cm) (mean ± *SE*)[a] | | | | Water temperature: top probe (°C) (mean ± *SE*)[a] | | | | Water temperature: bottom probe (°C) (mean ± *SE*)[a] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | CB1 | CB2 | CW | SB | CB1 | CB2 | CW | SB | CB1 | CB2 | CW | SB |
| Au | 54.03 ± 0.16 | 51.04 ± 0.52 | 55.65 ± 0.11 | 54.53 ± 0.16 | 18.63 ± 0.03 (13.85–25.71) | 18.75 ± 0.03 (14.90–31.17) | 19.34 ± 0.04 (10.94–31.47) | 19.19 ± 0.04 (7.88–40.07) | 20.77 ± 0.03 (16.71–25.22) | 18.67 ± 0.02 (14.71–23.97) | 19.28 ± 0.03 (11.82–29.75) | 19.34 ± 0.03 (11.14–27.27) |
| Wi | 58.49 ± 0.09 | 52.44 ± 0.79 | 55.13 ± 0.20 | 43.01 ± 0.91 | 13.18 ± 0.01 (9.47–18.52) | 13.53 ± 0.07 (7.98–25.03) | 12.82 ± 0.01 (5.76–16.62) | 13.49 ± 0.01 (7.58–22.05) | 13.20 ± 0.01 (9.47–17.00) | 13.35 ± 0.01 (10.75–15.76) | 12.76 ± 0.01 (6.06–15.95) | 13.53 ± 0.01 (9.87–18.71) |
| Sp | 48.81 ± 0.54 | 48.06 ± 0.65 | 60.33 ± 0.16 | 42.48 ± 0.71 | 17.68 ± 0.21 (12.21–35.0) | 17.34 ± 0.04 (10.75–41.23) | 17.88 ± 0.04 (9.37–35.01) | 15.74 ± 0.07 (9.77–28.56) | 17.28 ± 0.03 (12.11–24.93) | 17.07 ± 0.03 (11.43–23.20) | 17.98 ± 0.03 (10.26–27.17) | 18.23 ± 0.03 (10.16–34.80) |
| Su | 42.84 ± 1.40 | 59.14 ± 0.26 | 63.13 ± 0.15 | 44.23 ± 2.30 | 21.64 ± 0.07 (14.80–32.60) | 22.74 ± 0.02 (15.28–40.07) | 24.21 ± 0.04 (15.66–48.69) | 23.73 ± 0.03 (14.33–48.16) | 22.69 ± 0.02 (17.19–26.68) | 22.64 ± 0.02 (17.38–28.26) | 23.58 ± 0.02 (17.57–32.81) | 23.29 ± 0.02 (14.71–34.90) |

*Note:* Numbers in parentheses list the minimum and maximum temperature for that site and season.

Abbreviation: *SE*, standard error.

[a]Conductivity probes were positioned at the bottom of the oyster farm post. The temperature probes included one at the top and one at the bottom of the oyster farm post.

Theil, Bryars, Tanner, & de Jong, 2004). *Ostrea angasi* populations are not monitored. The size of wild populations of *O. angasi* and *C. gigas* at each site is therefore unknown. Other bivalve species could also be hosts; Coffin Bay has large and growing populations of blue mussel (*Mytilus galloprovincialis* Lamarck, 1819) (unpublished data). Northern Hemisphere *M. galloprovincialis* held on a *B. ostreae*-affected oyster farm for 2 years were not infected when assessed by histology (Figueras & Robledo, 1994), but it is unknown whether *M. galloprovincialis* can become infected with *B. exitiosa*. Coffin Bay also has a large, commercially fished population of Vongoles (*Katelysia* spp.; see Dent, Mayfield, & Carroll, 2016). Streaky Bay has large populations of *P. bicolor* on the substrate of the oyster leases, and *P. bicolor* shells are a favoured habitat for *O. angasi* settlement (Crawford, 2016). Further investigation of the capacity of other bivalves to act as hosts or reservoirs for *B. exitiosa* could better inform the risk profile for farms.

Contaminants are associated with increased prevalence, mortality and disease in molluscs for a variety of pathogens (Morley, 2010). Mangrove systems capture and retain wastewater-borne contaminants and pollutants (Maiti & Chowdhury, 2013; Tam & Wong, 1995). Environmental contaminants were not measured in this study, but lower prevalence near mangroves in Cowell may be linked to lower environmental contamination at this site.

There were no differences in *B. exitiosa* infection intensities in *O. angasi* over one year; infection intensities of *O. angasi* varied seasonally but with the pattern differing between sites and meat:shell ratio. Higher infection intensities in *O. angasi* at Coffin Bay 2 and Streaky Bay were associated with higher meat:shell ratios in spring and summer, but with lower meat:shell ratios in autumn and winter. Hine (1991) found that *O. chilensis* in New Zealand had light *B. exitiosa* infections in spring and summer and heavy *B. exitiosa* infections in autumn. Buss et al. (2019b) found higher *B. exitiosa* infection intensities were associated with lower meat:shell ratios for harvest size 20- to 22-month-old *O. angasi* in winter. Meat:shell ratio is driven by complex oceanographic and climatic factors that vary seasonally between sites (Grangeré, Ménesguen, Lefebvre, Bacher, & Pouvreau, 2009; Rahman, Henderson, Miller-Ezzy, Li, & Qin, 2020). Oyster populations undergoing mortality caused by *Bonamia* spp. have poor condition including *O. angasi* (see Corbeil, Handlinger, & Crane, 2009) and *O. edulis* (see Rogan, Culloty, Cross, & Mulcahy, 1991). Meat:shell ratio may therefore be an indicator of *B. exitiosa* infection severity; poor condition may occur when oysters have advanced infection, and better condition may occur when oysters have earlier stages of *B. exitiosa* infection. Data from this study show oysters from some sites in autumn and winter were prone to lower condition and more advanced stages of *B. exitiosa* infection, but in spring and summer, oysters in better condition were associated with earlier stages of *B. exitiosa* infection. A longer study or a study with more sites may clarify these differences and reveal whether the variability is driven more by season or site.

Hine (1991) also found that prevalence and infection intensity of *B. exitiosa* infection in the gonad increased after spawning in

summer. *Ostrea angasi* spawn between mid-spring and early autumn (O'Sullivan, 1980) when they are over two years of age (Crawford, 2016) and brood larvae only when they are over 68-mm shell length (O'Sullivan, 1980). Oysters in this study were not old enough to be sexually mature and were not incubating larvae. Seasonal patterns in *B. exitiosa* infections may be more pronounced and consistent in mature *O. angasi* than in the juvenile animals in our experiment.

We found that temperature did not influence *B. exitiosa* prevalence or infection intensities in *O. angasi*. In other *Bonamia* sp.–host systems, the effect of temperature varies; higher water temperature (>20°C) is associated with increased *B. exitiosa* prevalence and infection intensities in *C. ariakensis* (see Audemard et al., 2014; Carnegie et al., 2008), but *B. ostreae* prevalence increased in *O. edulis* at lower water temperatures (10°C) (see Cochennec-Laureau & Auffret, 2002). The environment, parasite and host influence infection (Scholthof, 2007), but observational understanding of *B. exitiosa–O. angasi* infection dynamics is more useful for management than understanding the effects of individual environmental parameters. Infection dynamics could be better understood by monitoring *B. exitiosa* infection in *O. angasi* in several year classes over multiple years and would aid farm management decisions including timing of stocking, stocking density, site management and husbandry and timing harvest of *O. angasi*.

Survival assessment at the end of the experiment showed that survival after one year was low (17%–33%). *Bonamia exitiosa* infection intensities were lower (3.01–7.02 cells/heart smear) than described for *O. angasi* experiencing clinical *B. exitiosa* disease and mortality (15.40–24.20 cells/heart smear) by Buss et al. (2019a). It is therefore unlikely that oysters were dying from clinical *B. exitiosa* infection in this study. Buss et al. (2019b) surveyed farmed *O. angasi* and also found low infection intensity (heart smear intensity <4.36 cells/slide). Low *O. angasi* survival was not associated with *B. exitiosa* prevalence or infection intensity and was probably caused by suboptimal management of the oysters. Streaky Bay had lower *O. angasi* survival than other sites, but oysters at this site were cultured in baskets with larger mesh size (6 mm vs. 3 mm), and the grower noted loss of oysters within the first season. *Ostrea angasi* can have high survival (52%–92%) when grown subtidally (Mitchell, Crawford, & Rushton, 2000) and also intertidally (>99%) (Li, Miller-Ezzy, Crawford, Gardner, & Deveney, 2019), but optimized approaches to maximizing survival in farmed *O. angasi* have not been identified.

In SA, *O. angasi* are mostly cultivated on intertidal leases in adjustable long-line systems designed for *C. gigas* (Nell, 2001; Wear et al., 2004). These systems are different to benthic, rack or hanging rope systems used to farm *O. edulis* in Europe (Héral & Deslous-Paoli, 1991). Our temperature data demonstrate that oysters experience extreme conditions in intertidal systems. *Crassostrea gigas* is tolerant to elevated water temperature (Rahman, Henderson, Miller-Ezzy, Li, & Qin, 2019) and can survive acute exposures of up to 34°C (Holliday, 1995), but 42°C water temperature for 1 hr caused 100% acute mortality (Rajagopal et al., 2005). Information on the thermal tolerance of *O. angasi* is limited; temperatures above 31°C increase mortality in *O. angasi* larvae (O'Connor, 2015), but optimal and lethal temperatures for other *O. angasi* life stages have not been assessed. *Ostrea angasi* is a subtidal species (Edgar, 2008) and is likely to have a lower upper temperature tolerance than intertidal adapted *C. gigas*. Intertidal oyster farms are more prone to impacts of climate change, and a breeding programme could select traits that facilitate better production in challenging climates (Leith & Haward, 2010).

*Ostrea angasi* reefs are being restored across southern Australia (Gillies, Crawford, & Hancock, 2017) and are also at risk of *B. exitiosa* infection. *Bonamia exitiosa* transmission between oyster farms and restored reefs could create mutual disease risk. To date, however, Australian sites for reef restoration have been approved based on oceanographic modelling and ecosystem-based development principles to avoid increasing pathogen and biosecurity risks. *Ostrea angasi* farming and reef restoration could also co-expand if careful management is applied. Susceptible-infected parasite models (Bidegain et al., 2017) simulating *Perkinsus marinus* (Mackin, Owen, & Collier) Levine, 1978 infection dynamics between wild and farmed *Crassostrea virginica* Gmelin, 1791 show that farmed *C. virginica* could act as a pathogen sink by removing parasites if the farmed population was harvested before onset of clinical disease and shedding of parasites (Ben-Horin et al., 2018). Timing harvests may therefore provide an alternate management strategy and facilitate expansion of both *O. angasi* aquaculture and reef restoration, but an understanding of parasite uptake and shedding prior to onset of clinical signs and optimal harvest times would need to be established to develop practically implementable farm management.

Aquaculture and reef restoration could benefit from a programme to breed for resistance against *B. exitiosa*. In Rossmore, Ireland, an *O. edulis* breeding programme produces *B. ostreae*-resistant *O. edulis*. *Bonamia ostreae* prevalence decreased from 90% to <15% with negligible mortality in selected stock. This programme, however, was based on mass selection and breeding from survivors and took 30 years to achieve substantial *B. ostreae* resistance (Lynch, Flannery, Hugh-Jones, Hugh-Jones, & Culloty, 2014). If the Australian oyster industry chose to expand *O. angasi* production, a breeding programme incorporating an infection model to test susceptibility and molecular methods to identify markers of resistance could decrease time to achieving resistant stock. Such a programme would be expensive, and cost–benefits would need to be examined to justify the expense.

This is the first analysis of *B. exitiosa* infection dynamics in *O. angasi*. *Bonamia exitiosa* occurred at all our study sites, and although *O. angasi* from some sites had slower increases in *B. exitiosa* prevalence and may be more suited to *O. angasi* cultivation, *O. angasi* at all sites had >0.5 prevalence after one year. Intensification of *O. angasi* farming at Cowell and Streaky Bay may, however, change infection dynamics. Reef restoration projects also need to continue to be well planned to ensure that they are not developed where they can negatively interact with oyster farms. Pairing site-specific information with a programme to breed for resistance against *B. exitiosa* would aid expansion of *O. angasi* aquaculture.

## ACKNOWLEDGEMENTS

This work was funded by the Fisheries Research and Development Corporation (FRDC) project "2015-001 Bonamiasis in farmed Native Oysters (*Ostrea angasi*)" on behalf of the Australian Government and its Department of Agriculture, with additional support from Flinders University and the South Australian Research and Development Institute (SARDI). We thank all participating oyster farmers, the South Australian Oyster Growers Association (SAOGA) and Prof. Xiaoxu Li (SARDI, Aquatic Sciences) for their cooperation and supply of oyster stock. We are grateful to Dr. Brian Jones and Dr. Henry Lane (Ministry for Primary Industries, New Zealand Animal Health Laboratory, Wallaceville), who demonstrated specific diagnostic techniques for *Bonamia*. Thanks are due to Dr. Mark Crane, Dr. Nick Moody and Dr. David Cummins (from the Australian Animal Health Laboratory) who provided training in qPCR diagnostics and Dr. Tracey Bradley (Department of Economic Development, Jobs, Transport and Resources, Victoria) who provided Victorian *Bonamia* identification material. Yvette Hannig and Pat Vilimas at the Flinders Microscopy Suite at Flinders University assisted with further microscope training and access.

## CONFLICT OF INTEREST

The authors have no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## ORCID

*Jessica Jamuna Buss* https://orcid.org/0000-0001-6220-0989

## REFERENCES

Arzul, I., & Carnegie, R. B. (2015). New perspective on the haplosporidian parasites of molluscs. *Journal of Invertebrate Pathology*, *131*, 32–42. https://doi.org/10.1016/j.jip.2015.07.014

Arzul, I., Gagnaire, B., Bond, C., Chollet, B., Morga, B., Ferrand, S., … Renault, T. (2009). Effects of temperature and salinity on the survival of *Bonamia ostreae*, a parasite infecting flat oysters *Ostrea edulis*. *Diseases of Aquatic Organisms*, *85*, 67–75. https://doi.org/10.3354/dao02047

Arzul, I., Miossec, L., Blanchet, E., Garcia, C., François, C., & Joly, J.-P. (2006). *Bonamia ostreae* and *Ostrea edulis*: A stable host-parasite system in France? In *Proceedings of the XI international symposium for veterinary epidemiology and economics conference*, *Cairns*, *Australia*, *6–11 August 2006* (p. 5).

Audemard, C., Carnegie, R. B., Bishop, M. J., Peterson, C. H., & Burreson, E. M. (2008). Interacting effects of temperature and salinity on *Bonamia* sp. parasitism in the Asian oyster *Crassostrea ariakensis*. *Journal of Invertebrate Pathology*, *98*, 344–350. https://doi.org/10.1016/j.jip.2008.03.010

Audemard, C., Carnegie, R. B., Hill, K. M., Peterson, C. H., & Burreson, E. M. (2014). *Bonamia exitiosa* transmission among and incidence in, Asian oyster *Crassostrea ariakensis* under warm euhaline conditions. *Diseases of Aquatic Organisms*, *110*, 143–150. https://doi.org/10.3354/dao02648

Audemard, C., Carnegie, R. B., Stokes, N. A., Bishop, M. J., Peterson, C. H., & Burreson, E. M. (2008). Effects of salinity on *Bonamia* sp. survival in the Asian oyster *Crassostrea ariakensis*. *Journal of Shellfish Research*, *27*, 535–540. https://doi.org/10.2983/0730-8000(2008)27[535:EOSOBS]2.0.CO;2

Ben-Horin, T., Burge, C. A., Bushek, D., Groner, M. L., Proestou, D. A., Huey, L. I., … Carnegie, R. B. (2018). Intensive oyster aquaculture can reduce disease impacts on sympatric wild oysters. *Aquaculture Environment Interactions*, *10*, 557–567. https://doi.org/10.3354/aei00290

Bidegain, G., Powell, E. N., Klinck, J. M., Hofmann, E. E., Ben-Horin, T., Bushek, D., … Guo, X. (2017). Modeling the transmission of *Perkinsus marinus* in the Eastern oyster *Crassostrea virginica*. *Fisheries Research*, *186*, 82–93. https://doi.org/10.1016/j.fishres.2016.08.006

Bishop, M. J., Carnegie, R. B., Stokes, N. A., Peterson, C. H., & Burreson, E. M. (2006). Complications of a non-native oyster introduction: Facilitation of a local parasite. *Marine Ecology Progress Series*, *325*, 145–152. https://doi.org/10.3354/meps325145

T. Bradley (Ed.) (2019). *Agriculture Victoria. Aquatic animal health subprogram: Bonamiasis in farmed native oysters* (Ostrea angasi). Final report. FRDC project 2015-001, Attwood, Victoria May 2019.

Bush, A. O., Lafferty, K. D., Lotz, J. M., Shostak, A. (1997). Parasitology meets ecology on its own terms: Margolis et al revisited. *The Journal of Parasitology*, *83*(4), 575–583. https://doi.org/10.2307/3284227

Buss, J. J., Harris, J. O., Tanner, J. E., Wiltshire, K. H., & Deveney, M. (2019a). Rapid transmission of *Bonamia exitiosa* by cohabitation causes mortality in *Ostrea angasi*. *Journal of Fish Diseases*. https://doi.org/10.1111/jfd.13116, in press.

Buss, J. J., Wiltshire, K. H., Prowse, T. A. A., Harris, J. O., & Deveney, M. (2019b). *Bonamia* in *Ostrea angasi*: Diagnostic performance, field prevalence and intensity. *Journal of Fish Diseases*, *42*, 63–74. https://doi.org/10.1111/jfd.12906

Carnegie, R. B., Stokes, N. A., Audemard, C., Bishop, M. J., Wilbur, A. E., Alphin, T. D., … Burreson, E. M. (2008). Strong seasonality of *Bonamia* sp. infection and induced *Crassostrea ariakensis* mortality in Bogue and Masonboro Sounds, North Carolina, USA. *Journal of Invertebrate Pathology*, *98*, 335–343. https://doi.org/10.1016/j.jip.2008.03.009

Cochennec-Laureau, N., & Auffret, M. (2002). *Experimental effects of temperature on the Bonamiasis model. European project FAIR-CT98-4120*. Environmental Factors and Shellfish Diseases, Final Report, 15/05/2002.

Corbeil, S., Arzul, I., Diggles, B. K., Heasman, M., Chollet, B., Berthe, F. C. J., & Crane, M. S. J. (2006). Development of a TaqMan PCR assay for the detection of *Bonamia* species. *Diseases of Aquatic Organisms*, *71*, 75–80. https://doi.org/10.3354/dao071075

Corbeil, S., Handlinger, J., & Crane, M. S. J. (2009). *Bonamiasis in Australian* Ostrea angasi. *Australian and New Zealand standard diagnostic procedure* (pp. 1–22). Sub-committee of Animal Health Laboratory Standards.

Crawford, C. (2016). *National review of* Ostrea angasi *aquaculture: Historical culture, current methods and future priorities*. Hobart, Australia: Institute of Marine and Antarctic Studies.

Culloty, S. C., Cronin, M. A., & Mulcahy, M. F. (2004). Potential resistance of a number of populations of the oyster *Ostrea edulis* to the parasite *Bonamia ostreae*. *Aquaculture*, *237*, 41–58. https://doi.org/10.1016/j.aquaculture.2004.04.007

Culloty, S. C., & Mulcahy, M. F. (1996). Season-, age-, and sex-related variation in the prevalence of *bonamia*sis in flat oysters (*Ostrea edulis* L.) on the south coast of Ireland. *Aquaculture*, *144*, 53–63. https://doi.org/10.1016/S0044-8486(96)01290-2

Dent, J., Mayfield, S., & Carroll, J. (2016). *Harvestable biomass of* Katelysia *spp. in the South Australian commercial mud cockle fishery*. Adelaide, Australia: South Australian Research and Development Institute (Aquatic Sciences). SARDI publication No. F2014/000191-2.

Devleesschauwer, B., Torgerson, P., Charlier, J., Levecke, B., Praet, N., Roelandt, S., … Speybroeck, N. (2015). *prevalence: Tools for prevalence assessment studies. R package version 0.4.0*. Retrieved from http://cran.r-project.org/package=prevalence

Diggles, B. K. (2003). *Shellfish disease surveillance programme - Final report June 2003* (pp. 1–24). NIWA Client Report AUS2002-018, June 2003, NIWA Project NAU03911, Prepared for Primary Industries and Resources South Australia (PIRSA).

Diggles, B. K., Cochennec-Laureau, N., & Hine, P. M. (2003). Comparison of diagnostic techniques for *Bonamia exitiosus* for flat oysters *Ostrea chilensis* in New Zealand. *Aquaculture*, *220*, 145–156. https://doi.org/10.1016/S0044-8486(02)00635-X

Dix, T. G. (1980). Growth of the Native oysters *Ostrea angasi* using raft culture in Tasmania, Australia. *Aquaculture*, *19*, 109–115. https://doi.org/10.1016/0044-8486(80)90012-5

Edgar, G. J. (2008). *Australian marine life: The plants and animals of temperate waters* (2nd ed.). Chatswood, Australia: New Holland Publishers.

Engelsma, M. Y., Kerkhoff, S., Roozenburg, I., Haenen, O. L. M., van Gool, A., Sistermans, W., … Hummel, H. (2010). Epidemiology of *Bonamia ostreae* infecting European flat oysters *Ostrea edulis* from Lake Grevelingen, The Netherlands. *Marine Ecology Progress Series*, *409*, 131–142. https://doi.org/10.3354/meps08594

Environment Protection Authority (EPA) (2005). *Code of practice for the environmental management of the South Australian oyster farming industry*. Adelaide, Australia: EPA.

Feng, C., Lin, X., Wang, F., Zhang, Y., Lv, J., Wang, C., … Li, H. (2013). Detection and characterisation of *Bonamia ostreae* in *Ostrea edulis* imported to China. *Diseases of Aquatic Organisms*, *106*, 85–91. https://doi.org/10.3354/dao02631

Figueras, A., & Robledo, J. A. F. (1994). *Bonamia ostreae* present in flat oysters (*Ostrea edulis*) does not infect mussels (*Mytilus galloprovincialis*). *Bulletin of the European Association of Fish Pathologists*, *3*, 98–100.

Food and Agriculture Organization of the United Nations (FAO) (2018). *The state of world fisheries and aquaculture 2018 - Meeting the sustainable development goals*. Rome, Italy: FAO.

Gillies, C. L., Crawford, C., & Hancock, B. (2017). Restoring *Angasi oyster* reefs: What is the endpoint ecosystem we are aiming for and how do we get there? *Ecological Management and Restoration*, *18*, 214–222. https://doi.org/10.1111/emr.12278

Grangeré, K., Ménesguen, A., Lefebvre, S., Bacher, C., & Pouvreau, S. (2009). Modelling the influence of environmental factors on the physiological status of the Pacific oyster *Crassostrea gigas* in an estuarine embayment; The Baie des Veys (France). *Journal of Sea Research*, *62*, 147–158. https://doi.org/10.1016/j.seares.2009.02.002

Handlinger, J. H., Rawlin, G., Wilson, J., Johnston, H., Condron, R., O'Donoghue, P., & Phillips, P. (1999). Bonamiasis in Australia. In *Annual international conference and exposition of the world aquaculture society, Sydney, New South Wales, 26 April–2 May, 1999*.

Héral, M., & Deslous-Paoli, J. M. (1991). Oyster culture in European countries. In W. Menzel (Ed.), *Estuarine and marine bivalve mollusk culture* (Chapter 13, pp. 154–190). Boca Raton, FL: CRC Press.

Hill, K. M., Stokes, N. A., Webb, S. C., Hine, P. M., Kroeck, M. A., Moore, J. D., … Carnegie, R. B. (2014). Phylogenetics of *Bonamia* parasites based on small subunit and internal transcribed spacer region ribosomal DNA sequence data. *Diseases of Aquatic Organisms*, *110*, 33–54. https://doi.org/10.3354/dao02738

Hine, P. M. (1991). The annual pattern of infection by *Bonamia* sp. in New Zealand flat oysters, *Tiostrea chilensis*. *Aquaculture*, *93*, 241–251. https://doi.org/10.1016/0044-8486(91)90236-Z

Hine, P. M., Diggles, B. K., Parsons, M. J. D., Pringle, A., & Bull, B. (2002). The effects of stressors on the dynamics of *Bonamia exitosus* Hine, Cochennec-Laureau and Berthe, infections in flat oysters *Ostrea chilensis* (Philippi). *Journal of Fish Diseases*, *25*, 545–554. https://doi.org/10.1046/j.1365-2761.2002.00410.x

Hine, P. M., & Jones, J. B. (1994). *Bonamia* and other aquatic parasites of importance to New Zealand. *New Zealand Journal of Zoology*, *21*, 49–56. https://doi.org/10.1080/03014223.1994.9517975

Holliday, J. E. (1995). *Nursery culture of Sydney rock oysters*, Saccostrea commercialis *(Iredale & Roughley, 1933) and Pacific oysters*, Crassostrea gigas *(Thunberg, 1793)*. PhD Thesis. University of Tasmania, Australia.

Hone, P. (1993). *Introduction of* Crassostrea gigas *(Pacific oyster) in South Australia*. Shellfish Environmental Monitoring Program. Adelaide, Australia: Department of Primary Industries.

Howard, A. E. (1994). The possibility of long distance transmission of *Bonamia* by fouling on boat hulls. *Bulletin of the European Association of Fish Pathologists*, *14*, 211–212.

Hudson, E. B., & Hill, B. J. (1991). Impact and spread of bonamiasis in the UK. *Aquaculture*, *93*, 279–285. https://doi.org/10.1016/0044-8486(91)90240-8

Lallias, D., Arzul, I., Heurtebise, S., Ferrand, S., Chollet, B., Robert, M., … Lapègue, S. (2008). *Bonamia ostreae*-induced mortalities in one-year old European flat oysters *Ostrea edulis*: Experimental infection by cohabitation challenge. *Aquatic Living Resources*, *21*, 423–439. https://doi.org/10.1051/alr:2008053

Leith, P. B., & Haward, M. (2010). *Climate change adaptation in the Australian edible oyster industry: An analysis of policy and practice*. Hobart, Tasmania, Australia: University of Tasmania.

Li, X., Miller-Ezzy, P. A., Crawford, C., Gardner, D., & Deveney, M. (2019). *Future oysters CRC-P: Species diversification to provide alternatives for commercial production*. Adelaide, South Australia, Australia: South Australian Research and Development Institute – Aquatic Science Centre.

Lynch, S. A., Abollo, E., Ramilo, A., Cao, A., Culloty, S. C., & Villalba, A. (2010). Observations raise the question if the Pacific oyster, *Crassostrea gigas*, can act as either a carrier or a reservoir for *Bonamia ostreae* or *Bonamia exitiosa*. *Parasitology*, *137*, 1515–1526. https://doi.org/10.1017/S0031182010000326

Lynch, S. A., Flannery, G., Hugh-Jones, T., Hugh-Jones, D., & Culloty, S. C. (2014). Thirty-year history of Irish (Rossmore) *Ostrea edulis* selectively bred for disease resistance to *Bonamia ostreae*. *Diseases of Aquatic Organisms*, *110*, 113–121. https://doi.org/10.3354/dao02734

Maiti, S. K., & Chowdhury, A. (2013). Effects of anthropogenic pollution on mangrove biodiversity: A review. *Journal of Environmental Protection*, *4*, 1428–1434. https://doi.org/10.4236/jep.2013.412163

McDonald, J. L., & Hodgson, D. J. (2018). Prior precision, prior accuracy, and the estimation of disease prevalence using imperfect diagnostic tests. *Frontiers in Veterinary Science*, *5*, 83. https://doi.org/10.3389/fvets.2018.00083

Mitchell, I. M., Crawford, C. M., & Rushton, M. J. (2000). Flat oyster (*Ostrea angasi*) growth and survival rates at Georges Bay, Tasmania (Australia). *Aquaculture*, *191*, 309–321. https://doi.org/10.1016/S0044-8486(00)00441-5

Morley, N. J. (2010). Interactive effects of infectious diseases and pollution in aquatic molluscs. *Aquatic Toxicology*, *96*, 27–36. https://doi.org/10.1016/j.aquatox.2009.09.017

Nell, J. A. (2001). The history of oyster farming in Australia. *Marine Fisheries Review*, *63*, 14–25.

O'Connor, S. J. (2015). *Factors effecting reproduction and larval development of* Ostrea angasi *(Sowerby 1871): Advancing hatchery production*. PhD Thesis. University of Tasmania, Australia.

O'Sullivan, B. W. (1980). The fertility of the Port Lincoln oyster (*Ostrea angasi*, Sowerby) from West Lakes, South Australia. *Aquaculture*, *19*, 1–11. https://doi.org/10.1016/0044-8486(80)90002-2

Peeler, E. J., Oidtmann, B. C., Midtlyng, P. J., Miossec, L., & Gozlan, R. E. (2011). Non-native aquatic animals introductions have driven disease emergence in Europe. *Biological Invasions*, *13*, 1291–1303. https://doi.org/10.1007/s10530-010-9890-9

Plummer, M. (2017). *JAGS Version 4.3.0 user manual*. Retrieved from https://web.sgh.waw.pl/~atoroj/ekonometria_bayesowska/jags_user_manual.pdf

Primary Industries and Regions SA (2017). *Aquaculture public register*. Retrieved from https://pir.sa.gov.au/aquaculture/aquaculture_public_register

R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rahman, M. A., Henderson, S., Miller-Ezzy, P., Li, X. X., & Qin, J. G. (2020). Analysis of the seasonal impact of three marine bivalves on seston particles in the water column. *Journal of Experimental Marine Biology and Ecology*, *522*,1–10. ttps://doi.org/10.1016/j.jembe.2019.151251

Rahman, M. A., Henderson, S., Miller-Ezzy, P., Li, X. X., & Qin, J. G. (2019). Immune response to temperature stress in three bivalve species: Pacific oyster *Crassostrea gigas*, Mediterranean mussel *Mytilus galloprovincialis* and mud cockle *Katelysia rhytiphora*. *Fish and Shellfish Immunology*, *86*, 868–874. https://doi.org/10.1016/j.fsi.2018.12.017

Rajagopal, S., van der Velde, G., Jansen, J., van der Gaag, M., Atsma, G., Janssen-Mommen, J. P. M., … Jenner, H. A. (2005). Thermal tolerance of the invasive oyster *Crassostrea gigas*: Feasibility of heat treatment as antifouling option. *Water Research*, *39*, 4335–4342. https://doi.org/10.1016/j.watres.2005.08.021

Reiczigel, J., Marozzi, M., Fábián, I., & Rózsa, L. (2019). Biostatistics for parasitologists – A primer to Quantitative Parasitology. *Trends in Parasitology*, *35*, 277–281. https://doi.org/10.1016/j.pt.2019.01.003

Rogan, E., Culloty, S. C., Cross, T. F., Mulcahy, M. (1991). The detection of *Bonamia ostreae* (Pichot et al 1980) in frozen oysters (*Ostrea edulis* L.) and the effect of the parasite on condition. *Aquaculture*, *97*(4), 311–315. https://doi.org/10.1016/0044-8486(91)90323-Y

Scholthof, K.-B.-G. (2007). The disease triangle: Pathogens, the environment and society. *Nature Publishing Group*, *5*, 152–156. https://doi.org/10.1038/nrmicro1596

Standards Australia (2015). *Australian fish names standard AS 5300-2015*. ACT, Australia: Fisheries Research and Development Corporation (FRDC) Fish Names Committee (FNC). ISBN 978-0-646-93768-7.

Su, Y.-S., & Yajima, M. (2015). *R2jags: Using R to Run 'JAGS'. R package version 0.5-7*. Retrieved from https://CRAN.R-project.org/package=R2jags

Tam, N. F. Y., & Wong, Y. S. (1995). Mangrove soils as sinks for wastewater-borne pollutants. *Hydrobiologia*, *295*, 231–241. https://doi.org/10.1007/BF00029130

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer. https://doi.org/10.1007/978-0-387-21706-2

Wear, R., Theil, M., Bryars, S., Tanner, J., & de Jong, S. (2004). *Environmental risk assessment of intertidal shellfish aquaculture in South Australia*. Adelaide, Australia: South Australian Research and Development Institute (Aquatic Sciences). SARDI publication No. RD04/0155.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis. R package version 3.2.1*. Retrieved from https://cran.r-project.org/web/packages/ggplot2/index.html

Youngflesh, C. (2018). MCMCvis: Tools to visualize, manipulate and summarize MCMC output. *Journal of Open Source Software*, *3*, 640. https://doi.org/10.21105/joss.00640

**How to cite this article:** Buss JJ, Wiltshire KH, Harris JO, Tanner JE, Deveney MR. Infection dynamics of *Bonamia exitiosa* on intertidal *Ostrea angasi* farms. *J Fish Dis*. 2020;00:1–11. https://doi.org/10.1111/jfd.13134