To treat or not to treat: a quantitative review of the effect of biofouling and control methods in shellfish aquaculture to evaluate the necessity of removal

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To treat or not to treat: a quantitative review of the effect of biofouling and control methods in shellfish aquaculture to evaluate the necessity of removal

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ABSTRACT

The global growth of farmed shellfish production has resulted in considerable research investigating how biofouling compromises farm productivity. Shellfish fitness can be compared between fouled stock and stock which has undergone treatment. As treatment options are often harsh, they may deleteriously affect stock. The projected impact of biofouling may therefore be confounded by the impact of treatments. Given the substantial cost of fouling removal, some have questioned the necessity of biofouling mitigation strategies. Meta-analysis revealed that biofouling typically reduces shellfish fitness. However, the fitness of treated stock was often lower or equal to fouled control stock, indicating that many common antifouling (AF) strategies are ineffective at enhancing farm productivity. Overall, caution and diligence are required to successfully implement biofouling mitigation strategies. The need remains for increased passive prevention approaches and novel AF strategies suitable for shellfish culture, such as strategic siting of bivalve farms in areas of low biofouling larval supply.

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Bivalve; mariculture; antifouling; fitness; farming; production

Introduction

Marine shellfish aquaculture has expanded substantially over the last few decades. Annual production of shellfish such as mussels, oysters, scallops, and clams reached ~14 million tonnes by 2010, representing 23.6% of all global aquaculture production (FAO 2012). A range of species, collectively known as biofouling, settle on and colonise abiotic and biotic substrates, the availability of which is increased through the greater surface area provided by both farm infrastructure and the high density of culture stock (Khalaman 2001; Guenther and De Nys 2006). The effect of biofouling on shellfish, farm productivity and profitability, and the wider ecosystem has received considerable attention, yet remains a contentious issue (reviewed by Fitridge et al. 2012; Lacoste and Gaertner-Mazouni 2015).

Biofouling increases production and management costs, while decreasing product value (Fitridge et al. 2012). Fouling communities may compete with shellfish directly for food resources (Woods et al. 2012; Sievers et al. 2013), impede the procurement of food and oxygen by reducing water flow around shellfish, or interfere with the opening of their valves (Wallace and Reinsnes 1985; Lodeiros and Himmelman 1996; Pit and Southgate 2003). Consequently, stock affected by biofouling can experience reduced growth, condition and survival, with subsequent negative impacts on farm productivity (de Sa et al. 2007; Adams et al. 2011; Sievers et al. 2013).

To combat biofouling on shellfish, multiple methods to reduce and remove fouling have been explored. The periodic removal of fouling organisms, however, can also increase production costs and reduce farm profitability (Colautti et al. 2006). The cost of biofouling control is estimated to account for between 5 and 30% of the final market price of the stock (see Adams et al. 2011), with considerable variability depending on cultured species and location. Treatments are time- and labour-intensive, and commonly involve subjecting stock and culture equipment to periods of air exposure, pressure washing, manual cleaning, or bathing in acetic acid, brine, fresh or hot water (Fitridge et al. 2012). Specific techniques are typically chosen based on the intensity and composition of fouling communities (de Nys and Ison 2008). Although frequently successful against soft-bodied organisms, they often fail to kill and remove several hard-bodied taxa, while increasing stock mortality (Carver et al.

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2003; Forrest and Blakemore 2006; LeBlanc et al. 2007). Techniques such as high-pressure washing fragment colonial organisms, with recolonisation of stock and farm infrastructure by the released fragments (Paetzold and Davidson 2010). Many biofouling species within shellfish culture are often closely related to the farmed species, and so identifying 'therapeutic windows', whereby fouling is killed or removed without harming culture stock, can be challenging (Forrest and Atalah 2017). Indeed, the benefits of fouling removal practices have been questioned, highlighting the lack of substantiated evidence for fitness increases in treated stock (eg Leblanc et al. 2003; Lacoste, Le Moullac, et al. 2014).

Although the production and financial implications of biofouling to shellfish aquaculture have been widely discussed, there is no general quantitative evaluation of the effect of fouling and cleaning practices on shellfish fitness and fouling loads. Given the cost of fouling removal can be significant, minor reductions in shellfish fitness caused by biofouling may not warrant expensive removal practices. If the treatment methods themselves affect stock fitness, their implementation could do more harm than good.

To address these knowledge gaps, a global meta-analysis to determine the effect of biofouling on stock fitness, and to characterise the impact of biofouling treatment practices on effective fouling removal and stock fitness was conducted. Quantitative data were extracted from the literature to systematically and objectively evaluate whether biofouling removal is worthwhile. Further, the need for increased passive prevention approaches was evaluated along with a summary of recent novel methods for biofouling control to update the comprehensive review by Fitridge et al. (2012).

Methods

Literature search

A literature search with no restriction on the date published was performed on 7 April 2017 using *ISI Web of Science* and the following terms: (*fouling OR epibiont*) AND (shellfish OR mussel OR scallop OR oyster OR cockle OR clam OR bivalve OR abalone). The reference lists of selected studies including related reviews were also examined for additional studies. Excluding duplicates, 2,252 potentially relevant studies were assessed for inclusion in the meta-analysis. The PRISMA flow diagram shows the procedure used for selection of studies for systematic review (Figure S1 in Supplementary Information). The flow diagram depicts the flow of information through the different phases of a systematic review. It maps out the number of records identified, included and excluded, and the reasons for exclusions.

Data extraction and classification

Four criteria determined study inclusion: (1) focused on shellfish aquaculture; (2) published original quantitative data on cultured shellfish fitness responses to biofouling or biofouling treatment methods; (3) utilised a control-impact (CI), before-after (BA) or before-after-control-impact (BACI) study design; and (4) the impacts of biofouling or removal practices had to be discernible from other manipulated factors (eg stocking density). Information was extracted from each study, including: location (continent and country), year of the study, culture species, primary fouling species, mitigation/removal strategy, the length of time stock was fouled, and the effect of the strategy on biofouling load and shellfish fitness (eg survival, growth; Table 1).

Effect size calculation

Data were extracted from impact and control groups from the text, tables or figures (using open source graphical digitiser software; Huwalt 2001) of each study, allowing the calculation of log response ratios (Hedges et al. 1999):

$$\ln[\mathrm{RR}] = \ln[I] - \ln[C]$$

where ln[RR] is the log response ratio, I is the impacted mean, and C is the control mean.

For observational studies and studies in which fouling was added to stock in a manipulative experiment, the control group was unfouled. Conversely, for studies

Table 1. Descriptions of the types of data extracted from papers for the seven measures for biofouling (one) and stock fitness (six).

Measure	Description
Biofouling	
	Percentage of stock with fouling Percentage cover Weight of fouling
Condition (CI)	
	Flesh weight ÷ shell weight* Flesh weight ÷ shell length* Cooked flesh weight ÷ total weight*
Flesh weight	
	Wet meat weight Dry meat weight Muscle mass
Growth	
	Increase in any morphometric direction Increase in mass Increase in volume
Size	
	Shell height Shell length Shell width
Survival	
	Survival Mortality (reversed)
Weight	
	Total weight Shell weight

*Weights for CI include wet, dry, cooked and ash-free dry.

investigating cleaning/removal strategies, the control was an uncleaned, and thus, fouled group. Therefore, response ratios less than zero indicate a negative fitness response to biofouling (for ‘observational’ or ‘fouling applied’ studies) or to biofouling removal strategies. When mortality estimates were provided, these values were converted to survival prior to RR calculation to allow direct comparisons between measures. When initial sizes were provided, stock size was converted into growth. When initial sizes were not provided, these data were still included as ‘size’ (Table 1).

A log response ratio cannot be defined for situations when the numerator or denominator is zero. In many cases, biofouling loads post-treatment were zero, and so for the effect of biofouling removal strategies on fouling loads a percentage change was calculated instead of a log response ratio. When possible, the RR for the impact of treatment on biofouling load was paired with the corresponding RR for the impact of treatment on stock fitness. For example, if a study tested 10 different durations of air exposure and provided separate data on both fouling and fitness for each, 10 RR pairs were extracted.

Statistical analysis

Linear mixed effects models with a unique identifier for each site nested within study fitted as a random effect were used to analyse the response ratio data. The site nested within study random effect induced a correlation among response ratio estimates within a study to account for any systematic differences due to, for example, common environmental conditions, or study-specific methodologies or biases (Mengersen, Jennions, et al. 2013). Model complexity was reduced (eg by removing the nested term) when sufficient data were not available to run full models, so that model estimates could still be extracted.

Treatment type (11 levels), stock species (seven levels) and fitness measure (nine levels) were all fit as fixed effects, and to estimate separate coefficients, intercepts were suppressed. Given the unbalanced nature of the dataset, independent analyses were conducted for each treatment method by stock species. Models were fit using restricted maximum likelihood (REML) to produce unbiased parameter estimates and 95% confidence intervals. Visual checks of residual plots were used to confirm that model residuals met assumptions of normality and heteroscedasticity. Where appropriate, competing models were fit using maximum likelihood (ML) and compared using Akaike’s information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). These values were rescaled as the difference between each model and the model with the lowest AIC_c (ΔAIC_c) for a given dataset.

To calculate the relationship between the effectiveness of the treatment and the impact it had on stock fitness, simple linear regression models were fit for each treatment method with sufficient data. All analyses were performed using the lme4 package (Bates et al. 2013) in R 3.2.2 (R Development Core Team 2015).

Weighting and non-independence

Mean estimates with smaller variances should contribute more weight to meta-analyses. The data extraction process and modelling approach, where the timing and intensity of independent treatment groups were treated as separate RRs, precluded the calculation of variance for each RR based on standard methods (see Lajeunesse 2011, 2015). In such situations, alternative weighting approaches can be used, such as one based on sample size (Mengersen, Schmidt, et al. 2013). Instead of omitting a proportion of studies/RRs or conducting unweighted analyses, weights were calculated based on the sum of sample sizes (Stanley and Doucouliagos 2015). Given there were many cases where $N_C = 1$, this weighting effectively down-weighted these estimates relative to a RR based on the average of multiple replicates, helping to reduce issues with non-independence.

Two unique identifiers were incorporated, where site was nested within study. The nested term accounts for correlations amongst observations at a given site and for common local environmental or contextual effects. The study random effect accounts for systematic differences due to common regional environmental conditions or study-specific methodologies. The model structure therefore helps account for non-independence of multiple response ratios extracted from the same study (eg Krist 2011). Models also use maximum likelihood methods, so response ratios are implicitly weighted by the uncertainty of the estimates (Mengersen, Jennions, et al. 2013).

Results

Thirty-three of the initial 2,252 papers were relevant at the full-text level (see Table S1 in Supplemental material for bibliography), and 696 response ratios were extracted from these papers. The majority of studies were conducted in North America (46%), followed by South America (15%) and Europe (15%), and then Asia (12%) and Australasia (12%). Studies investigating the effects of biofouling and biofouling removal focused on oysters (40%), mussels (31%), scallops (23%), clams (3%) and cockles (3%). Study designs were allocated into 10 key categories: air exposure, biological control, immersion/spraying treatment, combined treatments, fouling added, manual removal, culture media, observation, pressure

Table 2. Description of the treatment methods used to determine the effects of biofouling and biofouling control strategies on stock fitness and fouling loads.

Design	Description	N_{papers}	N_{RRs}
Air exposure	Exposing stock and/or lines, nets and cages to the air	3	26
Biological control	The addition of a biological control agent (eg crabs and urchins) to control biofouling	9	104
Immersion/spraying	The application of acetic acid, brine, lime or freshwater to stock	4	24
Combined	Combining multiple removal methods. Here, freshwater bath and manual removal	1	32
Fouling added	Experimentally manipulating fouling to quantify the impacts of biofouling on stock fitness	1	15
Manual removal	Physically removing biofouling by brushing, scrubbing or abrasion (excl. media)	11	124
Media	The addition of lava rock or expanded clay aggregate as a culture media to reduce biofouling	2	141
Observation	Comparing fouled and unfouled stock without applying treatment or manipulating the biofouling	3	8
Pressure wash	Using low- or high-pressure spraying to remove biofouling	3	198
Release coating	The addition of a fouling release coating (silicone-based) to lantern nets	1	24

wash (split into low- and high-pressure as determined by study authors) and release coating (Table 2; study summary information is in Table S1).

The impact of biofouling on shellfish fitness

Few studies examined the effect of biofouling on stock fitness without potentially confounding the results with the impact of the treatment method used to remove fouling. Of these studies, three were observational studies comparing fouled and unfouled stock (Baba et al. 2007; Daigle and Herbinger 2009; Fitridge and Keough 2013). These observational studies, combined with one manipulative study on the effect of fouling (Sievers et al. 2013), indicate that biofouling reduces shellfish growth, but has a limited impact on other fitness measures (Figure 1).

The impact of biofouling treatment practices

Exposing stock to air, biological control organisms, culture media, and immersion/spraying treatments all significantly reduced fouling loads (Figure 2). Both low- and high-pressure washing had no overall effect on the level of biofouling, whilst the addition of a fouling release coating resulted in a significant increase in the level of fouling.

Although a model with three-way interaction between treatment type, fitness measure and stock species was most supported (Table 3), plots indicate relatively few differences in overall averaged responses of mussels, oysters and scallops (Figure S2 in Supplemental material). In general, treated stock fitness was similar to untreated, fouled stock, with many confidence intervals overlapping zero. There was, however, substantial variability among treatments and among fitness measures (Figure 2).

Air exposure

Exposing shellfish to prolonged periods out of the water significantly reduced biofouling loads (−93 ± 51%; mean ± 95% CI) with little impact on stock fitness (Figure 2).

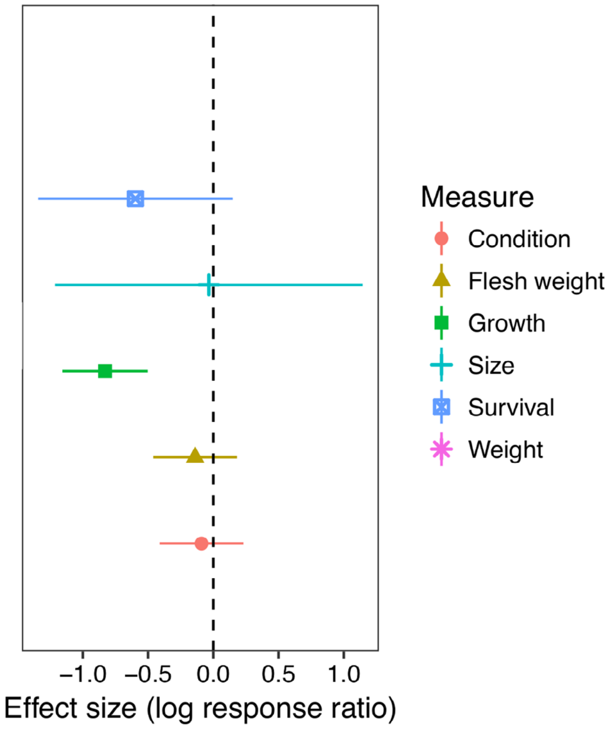

Figure 1. Forest plot of the impact of biofouling on shellfish fitness (response ratios and their 95% CIs on a log scale) from studies that are not confounded by the potential impacts of AF practices. For this and additional forest plots, linear mixed effects models with a unique identifier for each site and study fitted as a nested random effect (site within study) were used, and intercepts were suppressed to estimate separate coefficients.

Biological control

Data were available from studies using crabs, dogwhelks, isopods, periwinkles and urchins as biological control agents. Overall, biological control significantly reduced biofouling loads (−33 ± 20%), and there was evidence for increased stock growth (Figure 2). The model including the control species term was most supported (AIC_c null (k = 3): 15 *vs* AIC_c control species (k = 7): −39; ΔAIC_c : 53), with sufficient data to estimate and plot stock responses to

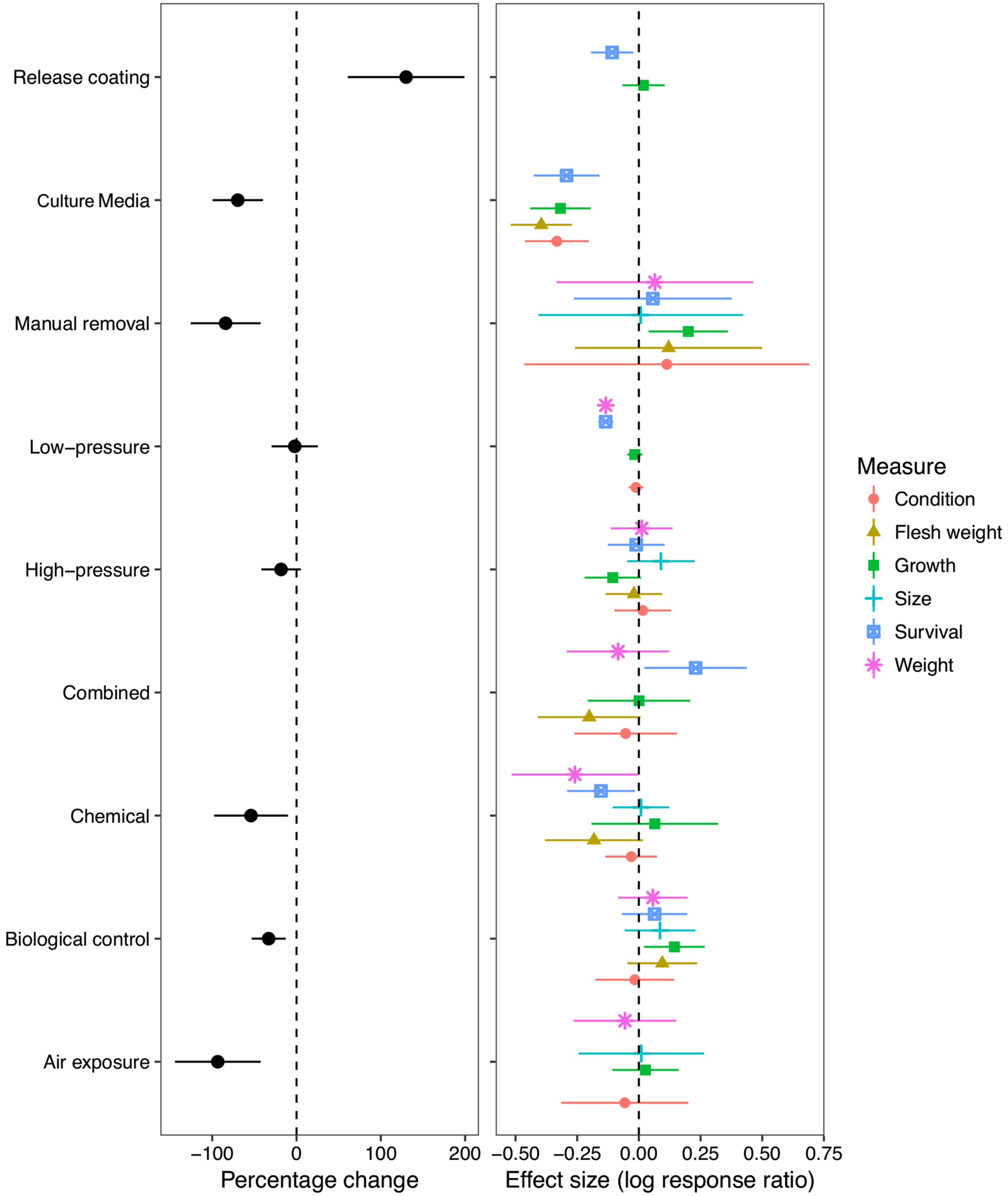

Figure 2. Forest plots showing the impact of biofouling removal strategies on (a) fouling loads (percentage changes and their 95% CIs), and (b) shellfish fitness (response ratios and their 95% CIs on log scale). A negative response indicates a reduction in fouling load or stock fitness due to the treatment.

crabs, periwinkles and urchins. Urchins had little overall effect on stock fitness, with a slight positive effect on size (Figure 3). The addition of crabs slightly reduced stock condition, but there was evidence for enhanced weight and overall size (Figure 3). Periwinkles did not affect stock survival, but did increase growth (Figure 3).

Table 3. Model selection (Akaike weights) for comparing all treatment measures (biofouling treatment), culture species (stock species), the recoded fitness proxy (fitness measure), and their interactions. Boldface values represent the most supported model (ΔAICc = 0).

	Model	*K*	AIC*c*	ΔAIC*c*	LL
All treatment methods					
	Null	4	−118	164	63
	Biofouling treatment (T)	12	−118	165	71
	Stock species (S)	8	−157	125	87
	Fitness measure (F)	10	−141	141	81
	T * S	21	−146	136	95
	F * S	33	−259	23	165
	T * F	51	−173	109	143
	T * S * F	**81**	**−282**	**0**	**235**
Manual removal					
	Null	**4**	**88**	**0**	**−40**
	F	6	91	3	−39
	S	9	89	1	−34
	F * S	18	106	18	−31
Culture medium					
	Null	4	−58	54	33
	F	6	−70	42	43
	S	7	−71	41	42
	F * S	**15**	**−112**	**0**	**73**

Note: The last two variables were also examined specifically for manual removal and the addition of culture medium. AICc, Akaike's information criterion corrected for small sample sizes; ΔAICc, difference in AIC between model and most supported model; K, number of estimated parameters; LL, log likelihood of model.

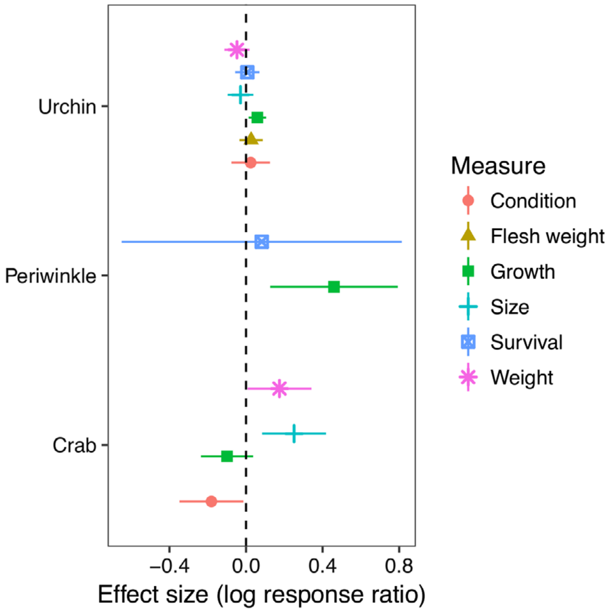

Figure 3. Forest plot of the impact of three biological control agents, urchins, periwinkles crabs, and crabs on shellfish fitness (response ratios and their 95% CIs on log scale).

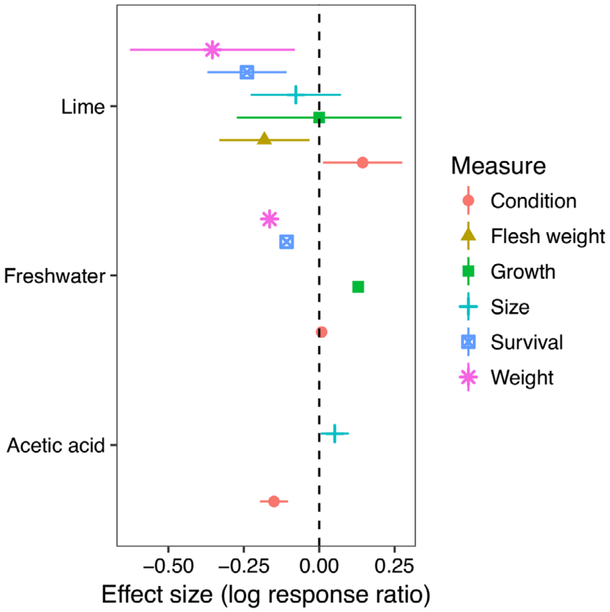

Figure 4. Forest plot of the impact of three primary immersion/spraying treatment methods – lime, freshwater and acetic acid – on shellfish fitness (response ratios and their 95% CIs on log scale). Note that for freshwater, all estimates are based on *n* = 1, so no CIs could be calculated.

Immersion/spraying treatments

Immersion/spraying treatments included the application of acetic acid, brine, freshwater and lime. Although these treatments significantly reduced biofouling loads (−54 ± 44%), stock fitness was also impacted, with weight and survival significantly reduced (Figure 2). When focusing on individual treatments, lime significantly reduced flesh weight and survival (Figure 4). Freshwater baths similarly reduced total weight and survival, but there was some evidence for superior growth in treated stock. Fewer data were available for acetic acid treatments, but there was some evidence for a compromised condition in treated stock.

Combined treatments

Data for combined treatments were from only one study, where stock were exposed to both the manual removal of fouling and freshwater bathing, which led to greater stock survival (Figure 2).

High-pressure washing

High-pressure spraying of stock did not affect biofouling loads (−18 ± 24%) and caused slight reductions in stock growth (Figure 2).

Low-pressure washing

Likewise, low-pressure spraying of stock did not affect biofouling loads (−2 ± 28%), and there was evidence for reduced stock weight and survival (Figure 2).

Manual removal

The manual removal of biofouling, typically involving brushing stock and infrastructure, significantly reduced biofouling levels (−84 ± 42%) and significantly increased the growth of treated stock (Figure 2). Increased growth was largely driven by data from scallops, but in general, all shellfish species responded similarly, with the null model most supported (Table 3).

Adding culture media

Whilst the addition of culture media significantly reduced fouling loads (−70 ± 30%), there were significant fitness impacts to culture stock (Figure 2). All fitness measures – survival, growth, flesh weight and condition – were significantly reduced following exposure to a novel culture medium. The model including the fitness measure by culture species interaction was most supported (Table 3). Whilst all three shellfish species were significantly affected by the addition of culture medium, clams exhibited the greatest fitness reductions (Figure 5).

Release coating

Fouling release coating applied to stock nets significantly increased biofouling loads (+130 ± 69%). This effect was exclusively driven by proportionally large increases of biofouling on treated stock shells. Whilst the growth of stock within treated nets was unaffected, survival was significantly reduced (Figure 2).

Relationship between effectiveness and fitness

Four treatment types had data of sufficient quality for analysis: air exposure, biological control, culture media and pressure washing. Shellfish growth when exposed to culture media increased as biofouling loads increased ($F_{1,35} = 57$, $p < 0.001$, $R^2 = 0.62$; Figure S3), whilst for all other treatments relationships between the effectiveness of the treatment and the impact it had on stock were weak (Table S2 in Supplemental material).

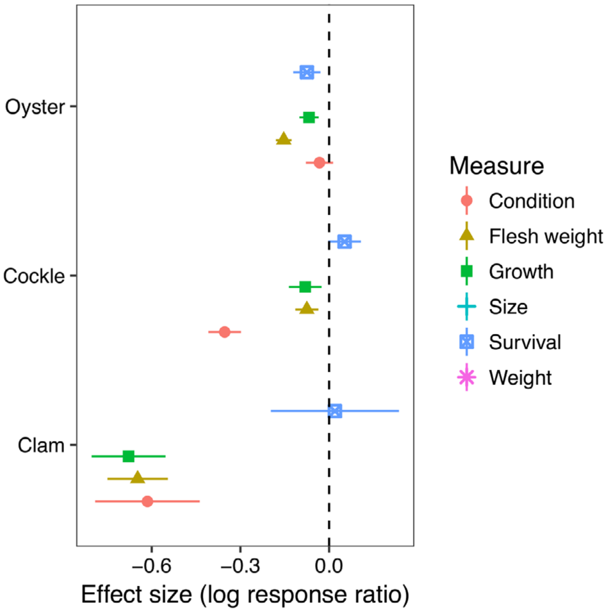

Figure 5. Forest plot of the impact of adding culture media on the fitness of oysters, cockles, and clams (response ratios and their 95% CIs on log scale).

Discussion

The meta-analysis of 33 studies from 17 countries provides a quantitative assessment of how biofouling and control methods affect cultured shellfish. While many biofouling treatment methods were effective at reducing fouling loads, they did not result in the treated stock having greater fitness than untreated stock, and instead, often reduced shellfish fitness below that of fouled, control groups. The cost associated with fouling mitigation measures may not always be justified because subsequent production is typically not enhanced. These findings highlight potential issues with common biofouling removal practices, and the need to specifically tailor approaches to maximise farm productivity and profitability.

The impact of biofouling on shellfish fitness

There is a distinct paucity of empirical data on the impact of biofouling on shellfish fitness without the impact of a treatment process potentially confounding results. This shortfall is likely due to the fact that determining the full impact of treatment practices is more important from an industry perspective. Regardless, from the available studies, there was evidence for growth reductions in fouled stock compared to unfouled stock. However, much of these data came from purely observational studies, where initial differences between fouled and unfouled stock may exist that influence biofouling loads, confounding results (eg slower growing stock may be differentially susceptible to biofouling settlement). Therefore, non-significant reductions to the other fitness measures does not necessarily translate into the complete lack of effect from biofouling.

In the one manipulative experiment, Sievers et al. (2013) added biofouling to experimental mussel ropes and monitored fitness after two months. All three experimental biofouling species significantly reduced growth rates of the Australian blue mussel *Mytilus galloprovincialis* (Lamarck 1819). Given the observed percentage reductions in growth and flesh weight, biofouling loads at the levels examined (considered low to medium) would likely have reduced overall farm productivity. Therefore, biofouling does have the capacity to reduce shellfish fitness, warranting investigation into the impact and benefit of its removal.

The impact of biofouling treatment practices

There are several possible reasons why treated stock may suffer reduced fitness relative to untreated, and thus fouled, stock. These effects may be a direct result of treatments, which impact shellfish physiology, or indirect, whereby conditions in the immediate vicinity of shellfish become degraded.

Stock fitness was most notably reduced following the immersion or spraying of shellfish with various substances, and following the addition of culture media. The three primary immersion/spraying treatments – acetic acid, freshwater and lime – reduced at least one measure of fitness that logically could impact farm profitability. Despite effectively reducing biofouling, lime baths in particular appeared to be a largely inappropriate method, as flesh weight and survival were reduced relative to untreated stock (see del Carmen Gallo-Garcia et al. 2004; Switzer et al. 2011). These reductions in fitness could be explained by the soft tissue of the shellfish being damaged by direct exposure to chemical applications if they have gaping or imperfectly sealed valves prior to exposure (eg acetic acid; see Le Blanc et al. 2007 for discussion). Such issues may be reduced if stock is disturbed by shaking prior to treatment, encouraging shellfish to close their valves.

The addition of culture media to suspended culture was also detrimental to fitness, particularly for clams. Although culture media can successfully scour biofouling from shells, and may lower encounter rates between cultured shellfish and settling larvae, they can limit access to fresh seawater and food when present in high densities, suppressing growth and condition (Marshall and Dunham 2013). However, at lower media densities, this AF strategy may elicit fewer fitness impacts, highlighting the need to quantify the efficacy of lower densities of culture media on stock fitness in future (Marshall and Dunham 2013).

Biological control, ie the use of various animals to control the settlement and growth of biofouling species, is a comparatively more effective AF strategy in terms of its impact on stock fitness, perhaps because it does not cause the direct impacts discussed above. Crabs, periwinkles and urchins all reduce biofouling without impacting stock fitness within both scallop and oyster culture operations, and the use of biological control agents remains a viable AF strategy in these industries (particularly given the relatively low ongoing maintenance costs; eg Lodeiros and Garcia 2004; Zhanhui et al. 2014). Indeed, periwinkles enhanced stock growth, and crabs enhanced stock size, relative to bivalves without biological control agents. However, the feasibility of this technique is questionable for large-scale operations or in any situation where the organisms being used for biocontrol cannot be contained, such as mussel culture (eg Comeau et al. 2012).

Manual removal of biofouling also appears to be a relatively useful method. However, the wide fitness confidence intervals coupled with the substantial amount of data contributing to these response ratio estimates suggests that under certain circumstances this method can reduce stock fitness. Therefore, the implementation of any manual AF strategy should be combined with thorough monitoring of stock performance. In addition, any removal technique must be performed diligently so as not to prompt any indirect effects on fitness. For example, dead foulers left attached (eg after air drying mussel lines) may cause localised conditions to become unsuitable (eg low water flow, low oxygen or release toxic byproducts), or they may smother shellfish, affecting oxygen uptake and feeding rates. For example, dead colonies of the densely tufted hydroid *E. crocea* smothered experimental mussels and were capable of reducing feeding rates (Sievers et al. 2013). Given that manual removal is typically time- and labour-intensive, and the likelihood of removing all biofouling remnants is low, the cost of manual removal strategies must also be taken into consideration to determine the viability of implementation.

There was little evidence for relationships between the effectiveness of treatments reducing biofouling and the effect of the treatments on stock fitness. The one significant relationship observed involved the use of culture media; shellfish growth increased (ie was less impacted) as biofouling loads increased, indicating that the more effective the treatment (eg more culture media or more abrasive media), the greater the reduction in stock fitness. Given that the addition of culture media was one of the more ineffective methods overall, this result further highlights the need to monitor stock fitness when implementing more severe AF strategies during times of heavy fouling loads. The overall lack of significant relationships from other treatment strategies may stem from a paucity of paired fouling load and stock fitness data, or simply from the fact that treatments may affect stock independently of how successful they are at removing biofouling (or *vice versa*).

Importantly, variations in the level of fouling and the composition of the fouling community will likely affect the extent to which shellfish fitness is reduced, as well as influencing the necessity of removal. Impacts also differ across temporal and spatial scales due to the effects of food availability and temperature on feeding and other physiological processes. Sophisticated analyses investigating these patterns, however, were not possible due to a lack of sufficient data. Regardless, tailoring treatments to the fouling community present, and optimising the timing and frequency of removal strategies will likely result in more beneficial outcomes, such as greater fouling reductions, increases in stock fitness and enhanced farm productivity. For example, a comprehensive study into the impact of pressure washing on stock fitness highlights the fact that modifying the timing and frequency of treatment can considerably influence the outcome (Arens et al. 2011).

Similarly, modifying the concentration or length of exposure of immersion/spraying treatments will allow a more targeted approach to kill biofouling organisms whilst reducing impacts to stock (Carman et al. 2016). Clearly, further research is essential to optimise many of the biofouling mitigation strategies discussed here, in addition to manipulative experiments that aim to tease apart the potential impact of biofouling from the potential impact of removal practices.

An additional implication of biofouling not considered in this meta-analysis is the impact of biofouling on farm productivity beyond reductions to stock fitness. Firstly, biofouling, particularly by calcareous species, reduces aesthetics and consequently product value and saleability (Campbell and Kelly 2002). A survey conducted in the USA noted that almost half of the respondents indicated that biofouling affected their ability to market their stock (Adams et al. 2011). In addition to marketability, biofouling communities add considerable weight to stock and culture equipment, causing stock detachment (Witman and Suchanek 1984) and increasing the costs associated with buoyancy and anchoring systems (Claereboudt et al. 1994; Woods et al. 2012). For industries that rely on wild spat, fouling communities can reduce total spat collection, and fouling species are also known to predate shellfish larvae (Zajac et al. 1989; Fitridge and Keough 2013). Biofouling organisms also add to total farm deposition rates, with potential ecological impacts to the wider ecosystem in which farms preside (Lacoste, Gueguen, et al. 2014; Lacoste and Gaertner-Mazouni 2015). Finally, a significant proportion of many fouling communities is made up of exotic species (McKindsey et al. 2007) which, if allowed to grow and reach maturity, may further impact natural systems surrounding farms.

Therefore, while it is important to investigate the direct fitness implications of both biofouling and biofouling control, a more practical estimator of whether (or how) to treat stock would focus on net profit at harvest, determined via a cost–benefit analysis. Ideally, economic models would weigh up the monetary inputs and gains of treating against not treating in each particular scenario. Data required to conduct these analyses are currently unavailable and thus must be a focus of future research. Therefore, although this meta-analysis highlights the potential inadequacies of current biofouling treatment practices in terms of decreasing stock fitness, the additional benefits outlined above may make the associated costs more defensible.

Novel AF methods

Based on the findings of the present study, many current treatment methods, while typically reducing biofouling, do so at the expense of stock fitness. Consequently, a shift towards passive prevention approaches and novel AF strategies would be strategic for the industry. The practicality of each new method needs to be scientifically evaluated through experiments of treatment efficacy on fouling removal, and effect on stock fitness. Importantly, some biofouling control methods likely never undergo rigorous scientific experimentation, but are rather the outcome of trial and error conducted by farmers. Some examples of methods being developed and tested are detailed below.

Recent research has investigated natural compounds that inhibit larval metamorphosis, such as polygodial, that may be used as future antifoulants in bivalve aquaculture (Cahill et al. 2012, Cahill, Burritt, et al. 2013; Moodie et al. 2017). These compounds are suggested to have little environmental impact and could be applied not only to farm infrastructure but also the shells of bivalves (Cahill, Heasman, Jeffs, et al. 2013). These products have several advantageous properties such as having a primarily contact active mode of action, whereby effects are limited to coated surfaces (Cahill and Kuhajek 2014). Further research is still required to ensure these compounds do not effect stock fitness (although current evidence suggests polygodial does not negatively affect the physiological health of green-lipped mussels (Cahill, Heasman, Hickey, et al. 2013) prior to the development of application strategies within aquaculture settings.

Research in Korea has revealed that extracts from mussel periostracum exhibit AF properties that may be harnessed and used in AF materials (Kang et al. 2016). Periostracum dichloromethane extracts containing 19% oleamide (an AF compound) significantly reduced algal spore settlement (Kang et al. 2016). Similarly, crude periostracum extracts made using solvents inhibited the attachment of barnacles, diatoms and marine bacteria (Bers et al. 2006). Shellfish periostraca and biogenically derived microtopographies, thus, present a non-toxic, environmentally friendly substratum to prevent the settlement and attachment of a range of fouling organisms. Developing suitable methods to apply compounds to stock is, however, a major challenge that may not be easy to overcome. Coating shellfish with a natural product laced AF formulation may be unviable from a logistical, fiscal, or consumer perspective. However, with additional research these products may become a useful future tool for use in the shellfish aquaculture industry, if only to protect infrastructure.

A developing strategy currently being tested to combat non-indigenous species via biosecurity incursion responses is encapsulation, whereby fouled structures are wrapped in material, essentially denying the organisms of nutrients and light (Roche et al. 2015; Atalah, Brook, et al. 2016). In addition to limiting food and light, toxic compounds inevitably build up and contribute to high mortality rates of the attached biofouling (Coutts and Forrest 2007; Vaquer-Sunyer and Duarte 2010). Empirical evidence suggests that combining encapsulation with chemical dosing using acetic acid may greatly reduce effective treatment times (Forrest et al. 2007; Denny 2008). Encapsulation was largely developed for use on boat hulls, pontoons and piles (see Atalah, Brook, et al. 2016 and references within), and is unlikely to be appropriate for use directly on shellfish (eg wrapping mussel lines). Although it may be an option for removing biofouling from the infrastructure associated with shellfish aquaculture such as mooring lines, buoys and trays, the logistics and time required to deploy and decommission wrap may be prohibitive.

Finally, although in its infancy, selective breeding of fouling resistant stock remains a potential future option. For example, in New Zealand, scientists have been investigating the fouling resistant properties, among other factors, of genetic variants of the Greenshell^{TM} mussels (*Perna calaniculus*), with current efforts extending beyond pilot-scale trials to large-scale intensive efforts (Camara and Symonds 2014). In addition to mussels, efforts to selectively breed shellfish has extended to Pacific oysters (*Crassostrea gig*as) and abalone (*Haliotis iris*).

Avoiding biofouling and synchronising husbandry practices

The strategies to control and remove biofouling in bivalve aquaculture analysed here focus on reactive treatment rather than proactive prevention, under the assumption that fouling cannot be avoided in areas where it is unpredictable or settling persistently throughout the year (Fitridge et al. 2012). However, in locations where fouling is seasonal, avoiding biofouling by synchronising husbandry practices with fouling patterns may be feasible (Sievers et al. 2014). Knowledge of fouling patterns will provide insight into what the next dominant fouling species will be, when it will settle, and where it will be most challenging, allowing the movement of stock away from areas during peak settlement times by problematic fouling species. Common fouling species may also vary in the depth at which they settle (eg Woods et al. 2012), and methods such as ‘subbing’ (whereby lines are submerged deeper in the water column to avoid fouling) may be practical and cheap solutions to decouple stock and settling biofoulers. Furthermore, recent computer modelling of mussel spat-fall in New Zealand has allowed farmers to actively avoid mussel fouling by informing when and where to deploy lines (Atalah et al. 2017), with the resultant data used to create an interactive application readily accessible to farmers (Atalah, Rabel, et al. 2016).

In addition to avoidance techniques, management and removal practices can be tailored ahead of periods of intense biofouling, to suit the needs of each farm. The ability to focus these practices more precisely will increase their efficacy and reduce overall production costs, especially since future antifouling methods will likely focus on specific action against target organisms in localised regions (Berntsson and Jonsson 2003; Guenther et al. 2011; Paetzold and Davidson 2011; Cahill, et al. 2012). Therefore, the monitoring of biofouling at appropriate spatial and temporal scales is likely to deliver benefits that outweigh the costs for many aquaculture industries where biofouling affects efficient production, including reducing the necessity or frequency of many of the harsh, fitness-reducing treatment options discussed here.

Conclusion

Despite efforts by scientists and managers, biofouling and its removal will remain problematic for industry, with farmers relying primarily on anecdotal evidence to develop husbandry practices. In light of this, the findings from robust manipulative experiments that concurrently quantify both the efficacy of treatments at reducing fouling and the impacts to stock fitness are critical. Information from such experiments will have limited use if not trialled, and if successful, adopted by commercial farms. In the short term, biofouling removal strategies will continue to rely on the methods analysed here, despite a discernible lack of empirical evidence of their overall efficacy in increasing farm productivity. Promisingly, novel methods harnessing natural compounds and developed through interdisciplinary research may provide a means to mitigate the impacts of biofouling without reducing stock fitness or impacting the environment. The success of these novel strategies is heavily reliant on future research addressing how such methods impact stock fitness, aesthetics, marketability, and edibility, as well as the potential environmental implications of wide-scale applications.

Disclosure statement

No potential conflict of interest was reported by the authors.

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