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Risk-Based Probabilistic Approach to Assess the Impact of False Mussel Invasions on Farmed Hard Clams

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The purpose of this article is to provide a risk-based predictive model to assess the impact of false mussel *Mytilopsis sallei* invasions on hard clam *Meretrix lusoria* farms in the southwestern region of Taiwan. The actual spread of invasive false mussel was predicted by using analytical models based on advection-diffusion and gravity models. The proportion of hard clam colonized and infestation by false mussel were used to characterize risk estimates. A mortality model was parameterized to assess hard clam mortality risk characterized by false mussel density and infestation intensity. The published data were reanalyzed to parameterize a predictive threshold model described by a cumulative Weibull distribution function that can be used to estimate the exceeding thresholds of proportion of hard clam colonized and infestation. Results indicated that the infestation thresholds were 2–17 ind clam^{-1} for adult hard clams, whereas 4 ind clam^{-1} for nursery hard clams. The average colonization thresholds were estimated to be 81–89% for cultivated and nursery hard clam farms, respectively. Our results indicated that false mussel density and infestation, which caused 50% hard clam mortality, were estimated to be 2,812 ind m^{-2} and 31 ind clam^{-1}, respectively. This study further indicated that hard clam farms that are close to the coastal area have at least 50% probability for 43% mortality caused by infestation. This study highlighted that a probabilistic risk-based framework characterized by probability distributions and risk curves is an effective representation of scientific assessments for farmed hard clam in response to the nonnative false mussel invasion.

KEY WORDS: False mussel; hard clam; invasion risk; modeling; risk assessment

1. INTRODUCTION

Recently, the relationship between invasive nonnative false mussel *Mytilopsis sallei* (bivalvia: *Dreissenacea*) and invasion risk in farmed hard clam *Meretrix lusoria* populations was an important aquaculture issue in Taiwan.(1) Hard clam is an economically important species in Taiwan aquaculture industry. The production of hard clams is currently 24,000 ton per year (http://www.fagov.tw/chn/index.php). The invasive false mussel could dramatically alter trophic and nutrient dynamics in hard clam farms due to its extreme prolificacy and fecundity.(1–6) The fouling mussel forms dense monocultures that exclude most other hard clam populations, leading to a potential damage for ecological and commercial hard clam stocks.

M. sallei was first discovered on the southwestern coast of Taiwan(2) and were distributed widely on Taiwan coastal areas recently.(1) Chang(2) reported that *M. sallei* ranging from 17.5 mm to 30 mm were infested on oyster shells and colonized 20–30 specimens on each spit of oyster bed. In the western United States, the fouling mussels such as zebra

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mussel (*Dreissena polymorpha*) and quagga mussel (*D. bugensis*) have also posed the potential ecological and economic damage.[6–8]

Chou and Yeh[1] reported that *M. sallei* invaded nursery hard clam farms during the May–June periods. The pelagic larvae of *M. sallei* were introduced to hard clam nursery farms via seawaters. The settlement period for larvae of *M. sallei* is less than one week. Juvenile mussels grow rapidly, attaining a size of 8–10 mm within a month of settlement. Juvenile mussels infested on embryo or larva of hard clam by fouling hard clam's whole body, which interferes with physiological behavior of feeding and moving, leading to a decrease in the growth rate of hard clam and even causing mortality. Therefore, invasive *M. sallei* causes not only the abundance declines in native hard clam but also the undesirable changes in aquaculture system function and economic losses. After establishment in hard clam farms, most invasive *M. sallei* are not easily eradicated. Recently, no attempt has been made to estimate most nonmarket losses, including reduction in native biodiversity and declines in aquaculture goods and services.

The actual spread of invasive species has been predicted using analytical models based on advection-diffusion and gravity models.[9,10] The simple advection-diffusion model has been shown to provide satisfactory estimations of the spread of many invasive species.[9,11–16] A general gravity model from transportation theory, allowing flexible dependence of spread potential on distance and the density sizes of invasive species and native species, has been used successfully to predict the dispersal of many invasive species.[10,17–20] Generally, gravity model is used to characterize the human-mediated transport of invasive species.

A number of studies have developed various statistical models to predict quantitatively the impact of invasion risk of nonnative species on marine, freshwater, and terrestrial environments.[21–27] Ricciardi *et al.*[21] developed mechanistic models based on Poisson statistics to predict the impact of invasive *Dreissena* mussels on native freshwater unionid bivalves in terms of the proportion of unionids colonized by mussels ($r^2 = 0.90$, $p < 0.0001$) and infestation intensity (i.e., mean number of invasive mussels attached to unionids) ($r^2 = 0.81$, $p < 0.0001$). Based on their predictive models, an explicit threshold of 1,000 m^{-2} of *Dreissena* field density was estimated, indicating that above the threshold, there is an increased probability of mortality for native unionids. Ricciardi *et al.*[28,29] further indicated that increased infestation levels would reduce condition and survivorship of unionids, whereas infestation levels would continue to grow as invasive mussels increase in abundance. The predictive models from Ricciardi *et al.*[21] have also applied to predict successfully the effects of zebra mussels invasion on long-term dynamics of native unionid bivalve populations in Hudson River.[30]

Linkages between false mussel invasions and economic losses of farmed hard clam in the Taiwan aquaculture industry have received great attention in recent years. Yet there remains little direct mechanistic understanding for predicting the impact of false mussel invasions on hard clam survivorship. The purpose of this article was to provide a risk-based predictive model to assess the impact of false mussel invasions on hard clam farms in the southwestern region of Taiwan. In this research, the proportion of hard clam colonized and infestation by false mussel were used to characterize risk estimates. A mortality model was parameterized to assess the hard clam mortality risk characterized by false mussel density and infestation intensity.

2. MATERIALS AND METHODS

2.1. Study Site

Fig. 1A shows the map location of hard clam farms situated at Taisi township in the southwestern coast of Taiwan. A schematic representation of the spatially explicit, individual hard clam farm-based settings is illustrated in Fig. 1B. We divided the hard clam farms into four main regions. Region I is a nursery farm and regions II, III, and IV are the cultivated farms. Each region is divided into certain subregional grids based on the map (Fig. 1B). Table I lists the characteristics of selected hard clam farm regions, including measured distances from coastal area, Euclidean distance metrics, and estimated hard clam densities. The ranges of hard clam density were estimated based on the available published and unpublished data together with personal communication from questionnaires conducted in the study sites. Metrics based on Euclidean distance have been effectively applied to a wide array of ecological data and are mathematically simple:[31]

2.2. Spread of Invasive False Mussel

The gravity model allows us to predict the dispersal of invasive species involving human-

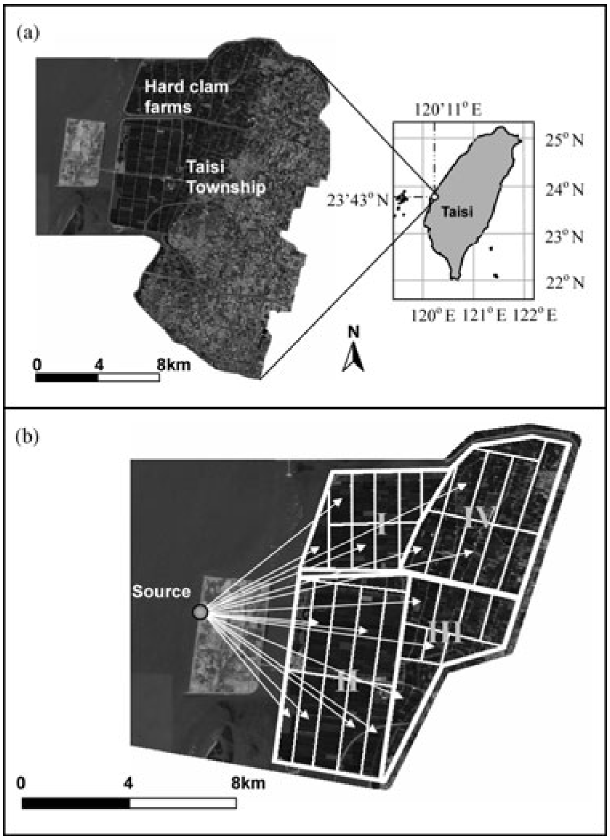

Fig. 1. Study area. (A) Hard clam farms in Taisi township. (B) Subregional grids of hard clam farms in Taisi township. Region I is a nursery farm and regions II, III, and IV are cultured farms (photos are adopted from the Google Map).

mediated transport. The gravity model-derived spread potential depends upon the distance and the density sizes of invasive and native species:(10,19,20)

$$P_{g,ij} = \theta_{ij} \frac{M_i C_j}{x_{ij}}, \quad (1)$$

where $P_{g,ij}$ is the invasive false mussel density due to human-mediated transport (ind m^{-2}), θ_{ij} is the proportionality (m^3 ind^{-1}), M_i is the false mussel density in the source i (ind m^{-2}), C_j is the hard clam density in subregion j (ind m^{-2}), and x_{ij} is the Euclidian distance between i and j (m).

A general advection-diffusion model has been used extensively to describe the spread of invasive species in terrestrial and marine systems:(9,11,12,16)

$$\frac{\partial P_{ad}(x,t)}{\partial t} = f(P_{ad}) + D\left(\frac{\partial^2 P_{ad}}{\partial x^2}\right) - v\left(\frac{\partial P_{ad}}{\partial x}\right), \quad (2)$$

where $P_{ad}(x,\ t)$ is the advection-diffusion-derived false mussel density through distance x and time t (ind m^{-2}), $f(P_{ad})$ is a function describing net population change due to birth and death, D is the size-independent diffusion coefficient (m^2 d^{-1}), and v is the size-independent advection coefficient (m d^{-1}).

Here a homogeneous, unstructured population growing exponentially and spreading in a uniform environment without advection are assumed to simplify Equation (2). A parsimonious version of Equation (2) is then obtained as:(11)

$$\frac{\partial P_{ad}}{\partial t} = D\left(\frac{\partial^2 P_{ad}}{\partial x^2}\right) + r_m P_{ad}, \quad (3)$$

where r_m is the intrinsic rate of population growth for false mussel (d^{-1}). Thus, Equation (3) can be used to predict the spread potential of invasive false mussel density introduced to hard clam farm communities. The rate of spread V (m d^{-1}) of invasive false mussel can also be calculated based on a diffusion-growth scheme:(11,12)

$$V = 2\sqrt{r_m D}. \quad (4)$$

Here we consider a steady-state diffusion-growth scheme in order to link the spread potential of false mussel based on the gravity model. The solution to Equation (3) with a steady-state condition and boundary conditions of $P_{ad}(0) = P_0$ and $P_{ad}(L) = 0$ is:

$$P_{ad}(x) = P_0(\cos mx - \cot mL \sin mx), \quad (5)$$

where $m = \sqrt{r_m/D}$ is defined to simplify Equation (3) (m^{-1}), P_0 is the initial false mussel density in the source, and L is the maximum length of geometry boundary of hard clam farm regions. Thus, we can estimate the total false mussel density (P_t) invaded to hard clam farms based on Equations (1) and (5) of $P_t = P_{g,ij}(x_{ij}) + P_{ad}(x)$ for all x.

2.3. Predictive Risk Model

A framework to predict false mussel-induced invasion risk in hard clams requires three elements: (1) the dominant determinants of risk factor that reflects a basis for risk assessment of invasive false mussel, (2) dose-response models for describing the relationships between the dominant risk factors caused by false mussel invasion and invasion risk of hard clams, and (3) probabilistic risk model by which the maximum tolerable invasion risk can be predicted. Thanks to the excellent published data of dreissenid mussels-native unionid bivalves system from previous researches,(21,28) the relationships between infes-

Table I. Characteristics of Hard Clam Farms and Parameters Used in Advection-Diffusion Model and Gravity Model

	Selected Hard Clam Farm Regions[a]			
	I (Nursery)	II (Cultivated)	III (Cultivated)	IV (Cultivated)
Advection-diffusion model				
Source to centroid distance (x, m)	6,369	5,779	9,337	10,155
Initial false mussel density (P_0, ind m^{-2})[b]	10,000			
Population growth rate (r_m, d^{-1})[c]	0.02			
Spread velocity (V, m d^{-1})[c]	650			
Diffusion coefficient (D, km^2 d^{-1})[d]	5.3			
Source to boundary distance (L, m)	14,000			
Gravity model				
Centroid Euclidian distance (x_{ij}, m)[e]	7,821	6,079	9,345	11,315
Hard clam density in subregion j (C_j, ind m^{-2})	$N(1304.1, 300.3)$[f]	$N(125.2, 10.8)$	$N(145.0, 10.7)$	$N(175.0, 10.8)$
Source false mussel density (M_i, ind m^{-2})[g]	$N(20095.1, 6112.6)$			
Proportionality for subregions i and j (θ_{ij}, m^3 ind^{-1})[h]	$\theta_{ij} = -3.10 \times 10^{-2} + 8.74 \times 10^{-5} x_{ij} - 6.08 \times 10^{-9} x_{ij}^2$			

[a]See Fig. 1B.
[b]Estimated from website information: http://www.envi.psu.ac.th/mwsd2008/presentations%20on%20Jan%2011/12Suebpong&Kringpaka.pdf.
[c]Adopted from Grosholz.(12)
[d]$D = V^2/(4r_m)$, adopted from Grosholz.(12)
[e]$x_{ij} = \sqrt{x_i^2 + x_j^2}$.
[f]Normal distribution with mean and standard deviation.
[g]Adopted from Tan and Morton.(5)
[h]Fitted equation based on gravity model-induced false mussel densities ranged from 10% to 90% of advection-diffusion-induced false mussel densities.

tation intensity and proportion of bivalve colonized by mussel and native bivalve survivorship can be established. Moreover, a well-established framework was also provided for characterizing the correlations among unionid mortality, mussel density, and infestation intensity.

Ricciardi *et al.*(21) developed a predictive model for assessing the intensity and impact of nonnative dreissenid mussels (including *D. polymorpha* and *D. bugensis*) on native unionid bivalves based on mussel field density. They used proportion of colonized bivalves and infestation intensity (i.e., the number of mussels attached to bivalves) as predictors. The proportion of unionid colonized-based assessment approach uses a fitted Poisson model to describe the relationship between proportion of unionids colonized and mussel density. On the other hand, a linear regression model shows that the mussel field density strongly predicts the infestation intensity. Recently, no published data regarding proportion of clam colonized and infestation for *M. sallei* are available. However, *M. sallei* is a member of the same species group of *Dreissenidae* and has a similar growth form of *D. bugensis* and *D. polymorpha*.(7)

In this study, we used a biologically based empirical three-parameter Hill equation to reconstruct the dose-response profile describing the relationship between proportion of clam colonized and false mussel density:

$$C_n(P_t) = \frac{C_{n,\max}}{1 + \left(\dfrac{C_n 50}{P_t}\right)^n}, \tag{6}$$

where $C_n(P_t)$ is mussel density (P_t)-dependent response of proportion of clam colonized, $C_{n,\max}$ is the maximum response, $C_n 50$ is the mussel density that causes half the maximal response of $C_{n,\max}$, and the exponent n is a fitted Hill coefficient. The parameters in Equation (6) can be obtained by fitting Equation (6) to published data from Ricciardi *et al.*(21)

The dose-response model describing the relationship between infestation and false mussel density can be obtained by fitting a nonlinear regression model to pooled published data obtained from Ricciardi *et al.*(21,29) The cumulative distribution function (cdf) of the predicted dose-response functions for a given false mussel density can be expressed as the conditional cdf of $P(C_n \mid P_t)$ for proportion of clam colonized and $P(I_f \mid P_t)$ for infestation (I_f).

Risk characterization is the phase of risk assessment where the results of the invasion and quantitative effect assessments are integrated to provide the risk estimates resulted from proportion of clam colonized and infestation for the specific false mussel density under study. The risk at a specific false mussel density can be calculated as the probability density function (pdf) of region-specific false mussel density multiplied by the conditional probability of proportion of clam colonized and infestation, respectively. Therefore, a joint probability function (JPF) can be used to calculate the response-specific risk probability and can be expressed mathematically, respectively, for proportion of clam colonized and infestation risks as:

$$P\left(R_{C_n}\right) = P(P_t) \times P\left(C_n \mid P_t\right), \tag{7}$$

and

$$P\left(R_{I_f}\right) = P(P_t) \times P(I_f \mid P_t), \tag{8}$$

where $P(R_{C_n})$ and $P(R_{I_f})$ represent the probability risks for proportion of clam colonized and infestation, respectively, and $P(P_t)$ is the pdf of false mussel density.

A risk profile was generated from the cumulative distribution of simulation outcomes. Each point on the risk curve represents both the probability that the chosen proportion of clam colonized will be affected and also the frequency with which that level of effect would be exceeded. The x-axis of the risk curve can be interpreted as a magnitude of effect (proportional of clam colonized or infestation intensity), and the y-axis can be interpreted as the probability that an effect of at least that magnitude will occur.

Here we used relations of surface area between hard clam and unionid in St. Lawrence River to adjust the infestation intensity by false mussel in hard clam farms. After some mathematical manipulations, we can obtain an adjust factor used to adjust infestation on hard clam as (see the Appendix):

$$I_f(SA_1) = I_f(SA_2)\left(\frac{f(SA_1)(1 - f(SA_2))}{f(SA_2)(1 - f(SA_1))}\right)^{-1/n}, \tag{9}$$

with

$$f(SA) = \exp(-\mu P_t SA), \tag{10}$$

where $I_f(SA_1)$ is the hard clam surface area-based infestation on hard clam; $SA_1 = L_1^{1.916}$ ($r^2 = 0.9$) with mean $L_1 = 2$ and 4 cm for nursery and adult hard clams, respectively; $I_f(SA_2)$ is the unionid surface area (SA_2)-based infestation; $SA_2 = L_2^{1.981}$ with mean $L_2 = 9.5$ cm;[21] $\mu = 2.2$ (95% CI 1.2–3.2);[21] and $n = 0.968$ is a fitted Hill coefficient.

2.4. Mortality Model

To investigate the relationships among hard clam mortality, false mussel density, and infestation intensity, available published data were reanalyzed. Ricciardi *et al.*[21] have collected field data from sites in the Great Lakes, St. Lawrence River systems on unionid bivalve mortality associated with zebra mussel density. Ricciardi *et al.*[21,28] have also reported the data on the relationships between zebra mussel-unionid bivalve infestation and mortality for various unionid bivalve populations. We pooled and reanalyzed the above-mentioned published data and reconstructed the dose-response profiles by using nonlinear regression technique to obtain the optimal fitted models.

Similarly, the mortality models can also be expressed by JPF for false mussel density-induced and infestation-induced hard clam mortalities, respectively, as:

$$P\left(R_{M,P_t}\right) = P(P_t) \times P(M_{P_t} \mid P_t), \tag{11}$$

and

$$P\left(R_{M,I_f}\right) = P(I_f) \times P\left(M_{I_f} \mid I_f\right), \tag{12}$$

where $P(R_{M,P_t})$ and $P(R_{M,I_f})$ represent the mortality probabilities based on false mussel density and infestation intensity, respectively, $P(I_f)$ is the pdf of measured infestation intensity, and $P(M_{P_t} \mid P_t)$ and $P(M_{I_f} \mid I_f)$ represent the conditional cdfs.

2.5. Uncertainty and Data Analysis

Optimal statistical models were selected on the basis of least squared criterion from a set of generalized linear and nonlinear autoregression models provided by TableCurve 2D packages (AISN Software Inc., Mapleton, OR, USA) fitted to the study data. A value of $p < 0.05$ was judged significant. To quantify the uncertainty and its impact on the estimation of expected risk, a Monte Carlo (MC) technique was implemented. An MC simulation was also performed with 10,000 iterations to generate 2.5th and 97.5th percentiles as the 95% CI for all fitted models. The Crystal Ball® software (Version 2000.2, Decisionerring, Inc., Denver, CO, USA) was employed to implement MC simulation.

3. RESULTS

3.1. Predicted False Mussel and Hard Clam Densities

We estimated the spread density of false mussel based on the advection-diffusion model and the gravity model. The essential parameters used in model implementation are listed in Table I. We averaged out the sum of estimates of false mussel density in each individual subregional grid to represent lumped spread density (Fig. 2). Fig. 2(a) indicates that region II had a higher false mussel density (6083 ± 899 ind m^{-2}) than those of other regions I (5043 ± 1077 ind m^{-2}), III (3656 ± 895 ind m^{-2}), and IV (1903 ± 1219 ind m^{-2}) driven by the advection-diffusion mechanism. On the other hand, the highest false mussel density estimated by the gravity model appeared in region I to be 939 ± 370 ind m^{-2}, whereas regions II, III, and IV had relatively small amounts of density of 113 ± 37, 79 ± 25, and 55 ± 17 ind m^{-2}, respectively, based on the region-specific hard clam density (Fig. 2(c)), fitted proportionality (θ_{ij}), and Euclidian distance (x_{ij}) relations (Table I).

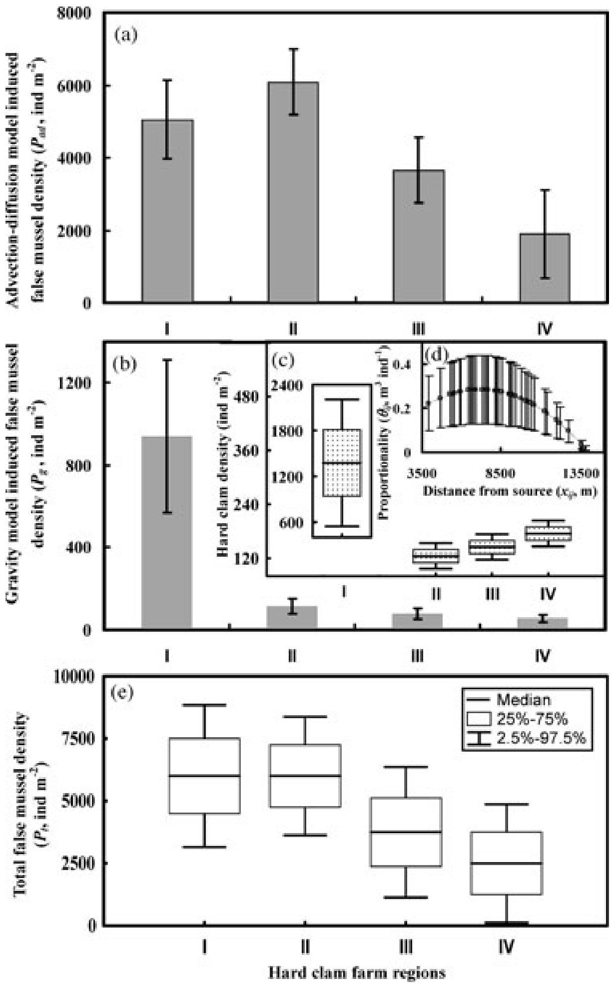

Fig. 2. Estimated and predicted false mussel and hard clam densities. (a) Estimated false mussel density induced from advection-diffusion model. (b) Estimated false mussel density induced from gravity model. (c) represents the corresponding hard clam density and distance-related proportionality for each subregions used in the gravity model. (e) The total estimated false mussel density. Box and whisker represent the ranges of 25th–75th and 2.5th–97.5th percentiles, respectively.

A comparison of estimated hard clam with total invasive false mussel densities reveals that of the selected regions, nursery region I has the highest hard clam and false mussel densities of 1,375 (95% CI 600–2,300) and 6,000 (95% CI 3,100–8,700) ind m^{-2}, respectively, than the other cultivated regions (Fig. 2(c)). The average hard clam densities in cultivated regions II, III, and IV ranged from 125 to 175 ind m^{-2}, whereas the predicted average false mussel densities were estimated to be 2,500–6,000 ind m^{-2} (Fig. 2(c)).

3.2. Risk Estimates for Colonization and Infestation

The reconstructed mussel density and proportion of hard clam colonized profile (Fig. 3(a)) reveal that the Hill model with a 10,000 MC simulation provided an adequate fit for the data ($r^2 = 0.86$, $p < 0.05$). The three fitted parameters in the Hill equation (Equation (6)) were estimated to be: the maximum response $C_{n,\max} = 0.97$, the mussel density that causes 50% colonization effect $C_n50 = 37.54 \pm 15.65$ ind m^{-2} (mean ± se), and the Hill coefficient $n = 0.59$. On the other hand, the fitted model of $y = 0.46x^{1.30} - 0.72$ ($r^2 = 0.84, p < 0.05$) best describes the relationship between dreissenid mussel density and infestation intensity on native unionid bivalves (Fig. 3(b)). Calculated surface area-specific adjust factors of 0.085 for nursery and 0.336 for adult hard clams were incorporated into Fig. 3(b) to adjust appropriately the infestation relations between unionid bivalves and hard clams.

Risk curves shown in Fig. 4 indicate the estimated impacts of infestation and colonization on hard clam farm regions based on false mussel density distributions. The probabilistic model performed from the outcome of the MC simulation followed JPFs (Equations (7) and (8)) can also be used to estimate the region-specific thresholds of infestation and proportion of hard clam colonized that are shown explicitly in Fig. 4. To assess the exceeding thresholds

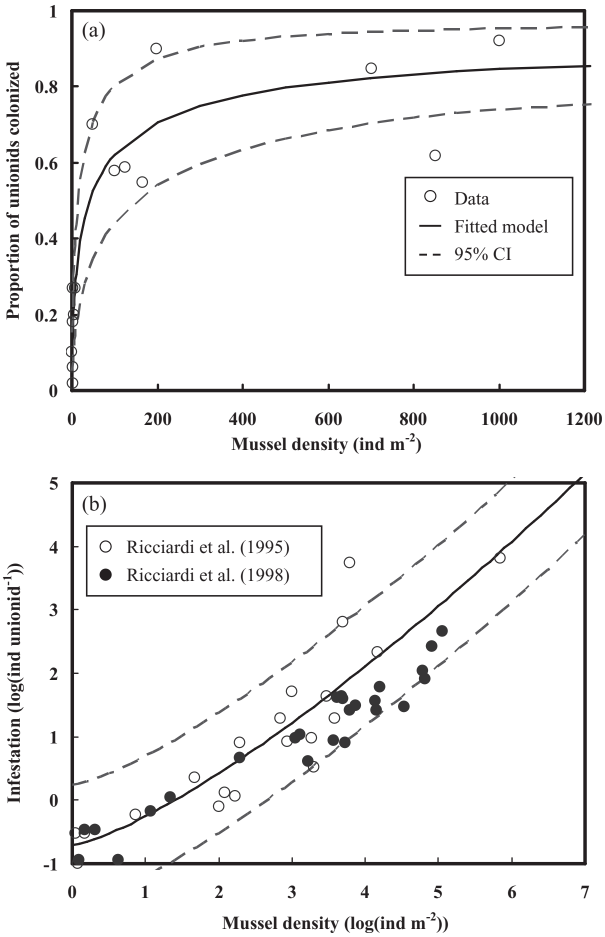

Fig. 3. Does-response models for mussel-induced colonization and infestation. (a) Reconstructed Hill model for mussel proportion of unionid colonized relations. (b) fitted nonlinear model describing the relationships between zebra mussel-induced infestation on unionid bivalves based on Ricciardi *et al.*[21,29]

for infestation and colonization, a cumulative Weibull distribution function with an explicit threshold effect was used to perform the estimation as:

$$F(x) = \begin{cases} 0, & x \le \gamma \\ 1 - \exp\left(-\left(\dfrac{x-\gamma}{\beta}\right)^{\alpha}\right), & x > \gamma \end{cases}, \quad (13)$$

where γ represents a threshold value, and α and β are the scale and shape parameters, respectively. The proposed cumulative Weibull model represents the simplest case in which there is the predictive threshold for both infestation and colonization (Table II). Table II indicates that the infestation thresholds range from nearly 8–17 ind clam^{-1}, whereas 88–91% for colonization thresholds for adult hard clam farms II and III close to the coastal area. For nursery hard clam farm I, the thresholds of infestation and colonization were estimated to be 4 ind clam^{-1} and 90%, respectively (Table II). However, hard clam farm IV that is away from the coastal area had relative low thresholds of infestation (2 ind clam^{-1}) and colonization (64%). The results suggest that there is an explicit threshold, below which the chance of infestation- or colonization-induced risk is zero. Above the threshold, the likelihood that risk would be found increases as the predictor increases (Fig. 4).

3.3. Risk Estimates for Mortality

A three-parameter Hill model was selected to best describe the mortality risk of hard clam in relation to total false mussel density ($r^2 = 0.89$, $p < 0.05$) (Fig. 5(a)). The reconstructed false mussel density-mortality relationship indicates that the false mussel density that caused 50% hard clam mortality was estimated to be 2,812 (95% CI 2,338–3,479) ind m^{-2}. The surface area-adjusted fitted model best describing the relationship between infestation intensity of false mussel and hard clam mortality is a 4-parameter logistic model ($r^2 = 0.84$, $p < 0.05$) that is derived from the original unionid mortality infestation profile (Fig. 5(b)). In the model parameterized for the mortality infestation profile (Fig. 5(b)), the infestation that caused 50% hard clam mortality was estimated to be 31 (95% CI 1–677) ind clam^{-1}.

Fig. 6 shows the exceedence risks for false mussel-induced and infestation-induced hard clam mortality based on false mussel and infestation mortality response profiles (Fig. 5) taking into account the uncertainty in estimating risk derived from variability and uncertainty in model parameters. Table III gives the probabilities that 50% or more of the hard clam mortalities are induced by false mussel density and infestation at four clam farm regions. Table III indicates that hard clam farms I and II, which are close to the coastal area have the higher false mussel- and infestation-induced mortalities of nearly 97% and 43%, respectively, for risk = 0.5. Yet, relatively lower false mussel-induced mortality of 19% and infestation-induced mortality of 39% were found for hard clam farm IV, which is much away from the coastal region. The results suggest that false mussel density and infestation pose significant mortality risk to hard clam farm regions I, II, and III, whereas a relative high false mussel-induced mortality risk for regions I and II is alarming in Taisi Township (Table III).

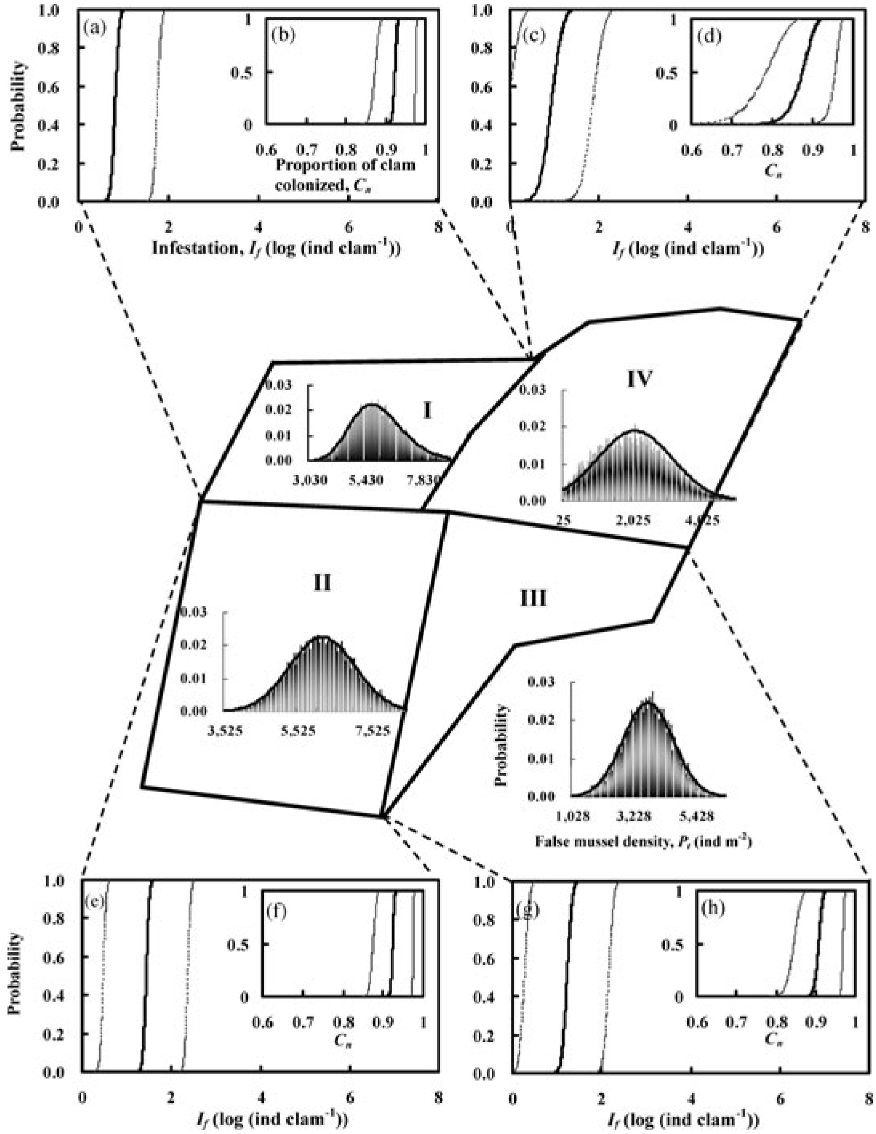

Fig. 4. Estimated risk probabilities of infestation (a, c, e, and g) and proportion of hard clam colonized (b, d, f, and h) depended on the invasive mussel density distributions of four hard clam farms.

Table II. Estimated Thresholds of Infestation and Proportion of Hard Clam Colonized for Selected Hard Clam Regions in Taisi Township

Selected Hard Clam Farm Regions			
I	II	III	IV
Infestation (I_f, ind clam^{-1})			
3.7 (3.979, 0.280)[a]	16.6 (4.295, 0.235)	8.0 (4.00, 0.358)	1.6 (4.00, 0.801)
Proportion of clams colonized			
0.897 (6.00, 0.027)	0.911 (4.00, 0.014)	0.880 (4.00, 0.031)	0.640 (10.00, 0.244)

[a] γ (α, β) represents a cumulative Weibull function $F(x) = 1 - \exp(-((x-\gamma)/\beta)^{\alpha})$ with a threshold γ, a scale parameter α, and a shape parameter β.

4. DISCUSSION

4.1. Predictive Threshold and Risk Models

In this study, we reanalyzed the published data to parameterize a predictive threshold model described by a cumulative Weibull distribution function that can be used to estimate the exceeding thresholds of proportion of hard clam colonized and infestation. Our results found out that the infestation thresholds were 2–17 ind clam^{-1} for adult hard clams, whereas 4 ind clam^{-1} for nursery hard clams. On the other hand, the average colonization thresholds were estimated to be 81% and 90% for cultivated and nursery hard clam farms, respectively. Although relations with either measures of infestation and proportion of clam colonized might be used for predictive purposes, data on infestation are simple and cheap to collect and hence more cost effective than colonization estimations. We parameterized predictive threshold models that should reduce the costs of invasion risk monitoring in hard clam aquaculture of Taiwan. Our results indicate that false mussel density and infestation that caused 50% hard clam mortality were estimated to be 2812 ind m^{-2}and 31 ind clam^{-1}, respectively. This study further indicates that hard clam farms that are close to the coastal area have at least 50% probability for 43% mortality caused by infestation.

To estimate the effects of major false mussel invasion on the mortality rates through existing limited data is a challenging task. The extensive data on false mussel populations and parameters used in the mechanistic models might provide an excellent opportunity to test the present predictions. Successfully eradicating false mussel invasions requires detecting the introduction early.[32] Concentrating detecting efforts in areas of greatest risk will allow farm managers to enhance the capacities of their early detection programs. Similarly, detecting an invasive species population shortly after it is introduced will decrease treatment costs associated with an eradication program. Therefore, it better has the ability to predict the mortality risk impact of such fouling invasive species before their introduction to aquaculture farms.

Suedel *et al.*[33] have applied traditional ecological risk assessment developed by USEPA[34] to systematically reconstruct a risk assessment framework for aquatic nuisance species. A fecundity-based risk assessment developed by Keller *et al.*[35] was used to predict environmental nuisance probability caused by nonnative freshwater molluscs. Whittier *et al.*[8] recently used a calcium-based invasion risk assessment for zebra and quagga mussels by defining risk based on calcium concentrations in rivers and streams. It is known that at all stages the invasive false mussel tended to have wide temperature or salinity tolerance and rapid life histories. Moreover, the aquaculture system impacts of further introductions to other cultured farms are not easy to assess. Therefore, given the clear potential for these impacts to happen by a predictive risk model, control measures can be put in place immediately to prevent them.[36,37]

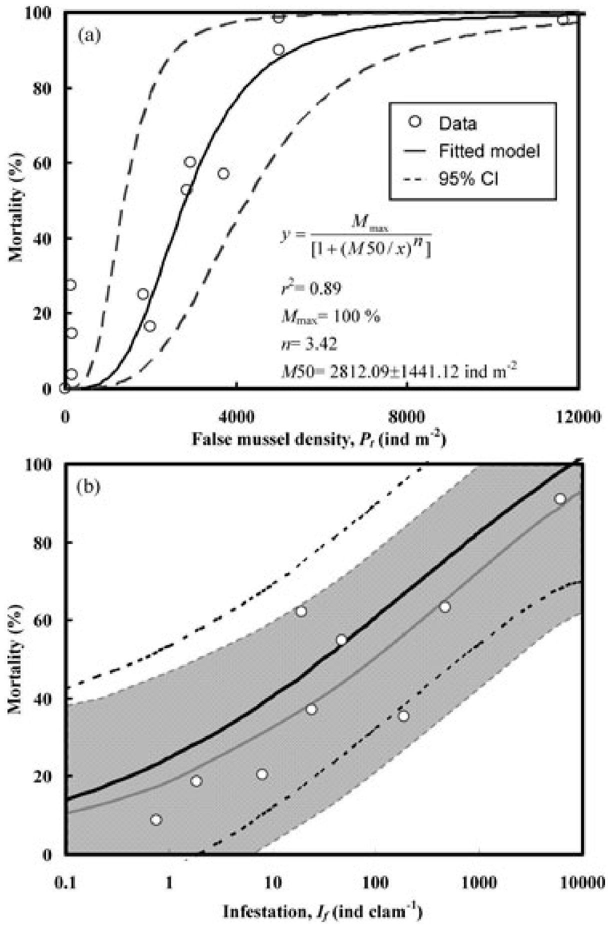

Fig. 5. Dose-response models for false mussel- and infestation-induced hard clam mortality risk. (a) Reconstructed Hill model for false mussel-mortality profile. (b) Fitted logistic model ($y = a + (b/(1 + (x/c)^d))$) describing the relationships between infestation and mortality. Shaded region represents the infestation-induced mortality profile in zebra mussel-unionid bivalve system ($a = -1.21$, $b = 140.69$, $c = 812.20$, $d = -0.27$), whereas the adjusted infestation-induced mortality profile in false mussel-hard clam system ($a = -1.21$, $b = 140.75$, $c = 244.32$, $d = -0.27$) is illustrated by solid and dash lines.

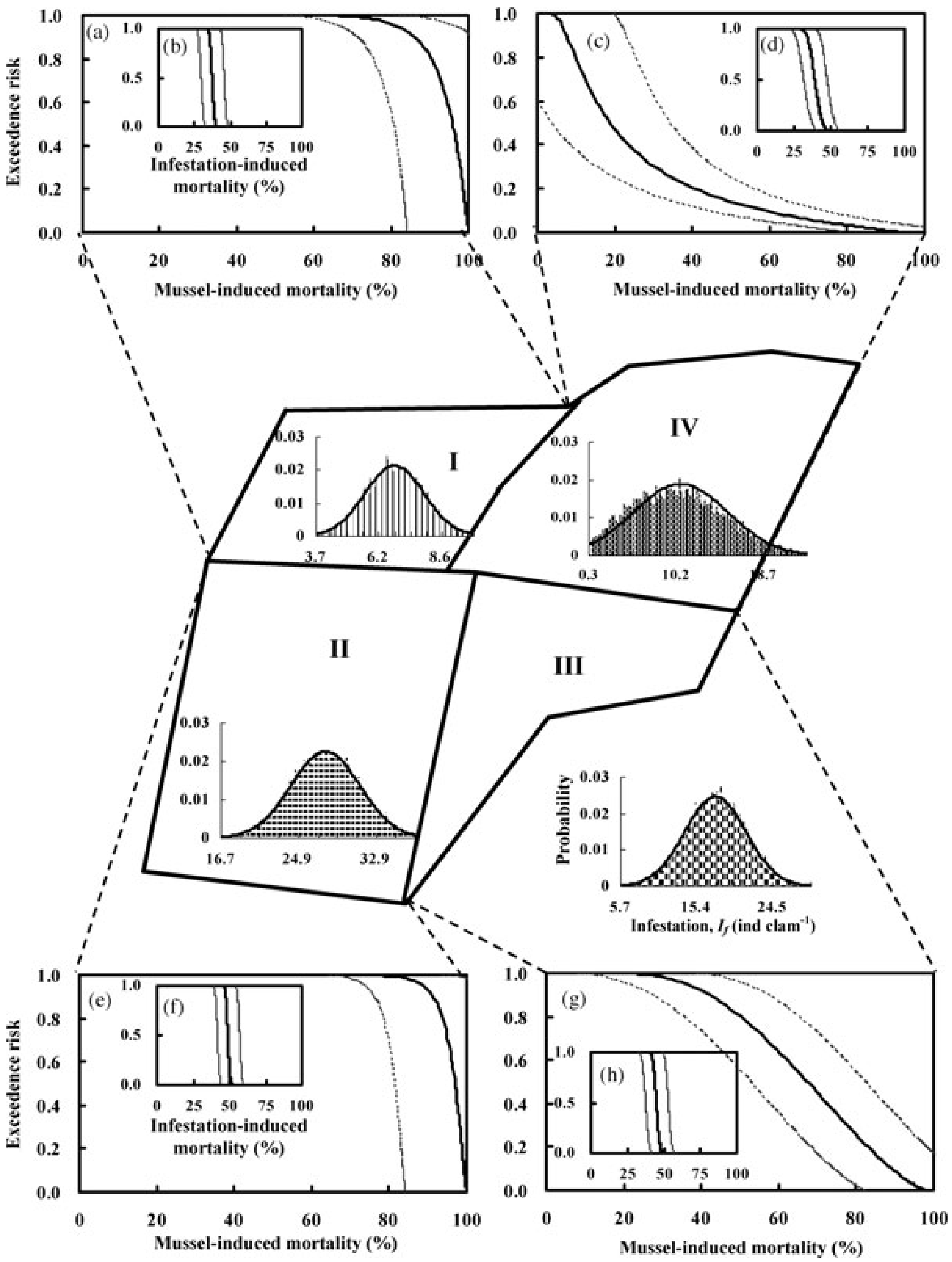

Fig. 6. Estimated exceedence risk profiles of invasive mussel density-induced (a, c, e, and g) and infestation-induced (b, d, f, and h) hard clam mortalities. Estimated infestation distributions induced by invasive mussel density in four hard clam regions are also shown.

Table III. Proportion (Median with 95% CI) of Hard Clam Mortalities Induced by False Mussel Density and Infestation Intensity for Exceedence Risk = 0.5 at Selected Hard Clam Farm Regions in Taisi Township

Selected Hard Clam Farm Regions			
I	II	III	IV
False mussel-induced mortality (%)			
96.0 (80.4–100)	97.1 (81.4–100)	67.4 (52.6–82.2)	18.8 (3.5–34.1)
Infestation-induced mortality (%)			
37.3 (29.1–45.3)	48.9 (41.1–56.5)	44.8 (37.0–52.6)	39.1 (31.0–47.0)

Direct estimates of mortality during realistic events have to come from the long-term monitoring studies that record species densities at the age-structured scales.[32,38] This study offers a preliminary solution to this longstanding problem of false mussel invasion in hard clams. By estimating the false mussel infestation and colonization thresholds, the changes in hard clam density caused by recent and future false mussel invasions can be predicted. Such a framework is essential for understanding the dynamics of false mussel invasions on hard clam farms. This understanding can, in turn, facilitate informed policy and management decisions that aim to protect the hard clam aquaculture.

4.2. Management and Control Implications

The importance of efficaciously assessing the potential risks for invasion and establishment of nonnative invasive species is an increasingly important management issue.[26,33,39,40] The false mussel had caused significant economic losses in hard clam aquaculture industry. Control measures for eradiating false mussel include biocides, chlorine, thermal treatment, and mechanical/manual removal.[41−45] Biological control of fouling organisms is also recognized as an important method for aquaculture husbandry and management. Magoulick and Lewis[46] indicated that native fish predators have the potential to suppress initial invasive zebra mussel colonization and recolonization of adult zebra mussel. Ross *et al.*[47] reported that sea urchins and hermit crabs have a strong potential for biological control of fouling that is an efficient and environmentally sound method in suspended scallop cultivation. Greene and Grizzle[48] suggested that the introduction of predatory fishes or seastars into or onto the cages could provide the potential control on the growth of fouling organisms.

In Taiwan, farmers usually used grass shrimp larvae as a predator to attack pelagic larvae of *M. sallei* in nursery farms.[1] A biological control program by using native fish snubnose pompano (*Trachinotus blochii*) as top predator was commonly used in adult hard clam farms not only to eradicate invasive false mussel but also to slow down the speed and spread pattern of biological invasion.[1] Little is explored, however, about the possible control strategies for hard clam subjecting to a predation-competition interaction between false mussel and native fish predators. Predator-prey interaction in aquaculture systems is one of the simplest drivers affecting the farm species population dynamics and can help us to understand the mechanisms and processes underlying biological invasiveness.[49] Model structure in relation to the predation and competition between native fish predators and false mussel in both time and space on the impacts of hard clam density is thus worthwhile to explore.

4.3. Data Limitation and Model Validation

To our knowledge, no published data are available related to the issue of false mussel invading the hard clam farms in Taiwan. Due to the limited data on *in situ* measured parameters and some essential data required for the modeling, the predicted risks associated uncertainties and variabilities would be increased. There are a number of areas in which further researches could reduce the uncertainties and limit the variabilities in this study. Among these are three areas that offer an opportunity for the most useful researches. First, there is a need to conduct a more extensive characterization of false mussel invasions in given hard clam populations. This would require the collection of more detailed information on the characterization of colonization and infestation probabilities. Second, there is a need for global sensitivity analysis using the MC simulation model with more detailed data sets as inputs. The ranges and distributions of parameters can then be combined by use of the MC simulation model to generate a response surface. Relationships between the input ranges and model output should then be assessed to identify the relationship between output variability and input uncertainties and variabilities. Finally, on the basis of results of the sensitivity analysis, research should be directed to those parameters that, if better characterized, could most effectively reduce variability and increase reliability in the results.

We recognized that if the hard clam farm was invaded severely by false mussels, most aquaculture strategies of the hard clam farm owners were to rebuild the hard clam farms. Under the real situations we could not obtain the available data, to validate our predictions. Due to limited published data on the hard clam-false mussel system, we therefore used the available data in the unionid-zebra mussel system to validate the present integrated model. First, we used two fully developed spread models to estimate the densities of invasive false mussels. We assumed that the initial false mussel density is 10,000 ind m^{-2}. We found the effect of human-mediated transport (gravity model)[10,19,20] is less significant than that of false mussel invasive spread (advection-diffusion model).[9,11,12,16] According to the adopted geographical data of the hard clam farms in Taisi Township, we might estimate the total density of native false mussels based on a stochastic approach combining gravity and advection-diffusion models. While we knew the invasive false mussels might invade into the selected four hard clam farm regions through the aforementioned pathways, the impacts of colonization and infestation effects were needed to be estimated. The possible mortalities of the different hard clam farms were also concerned. Second, we could employ a surrogate system (i.e., unionid-zebra mussel system)[21,28,29] with a surface area-adjusted technique (see the Appendix) to validate the threshold parameters and mortality risk profiles.

In conclusion, this study provided a risk-based predictive model to assess the impact of false mussel invasions on hard clam farms at Taisi Township in the southwestern region in Taiwan. Proportion of hard clam colonized and infestation by false mussel were used as the predictors. The dose-response models describing the relationships between false mussel density and predictors were reconstructed. A predictive threshold model was developed to estimate the exceeding thresholds for colonization and infestation by false mussel. A mortality model was parameterized to assess the potential hard clam mortality risks induced by false mussel and infestation intensity. This study highlights that a probabilistic risk-based framework characterized by probability distributions and risk curves as illustrated in Figs. 4 and 6 is an effective representation of scientific assessments for farmed hard clam in response to nonnative false mussel invasion. Our results suggest that false mussel density and infestation pose significant mortality risk to hard clam farms close to the coastal regions in Taisi Township.

APPENDIX: ADJUST FACTOR FOR HARD CLAM INFESTATION

Based on a fitted Poisson infestation model for St. Lawrence River unionids describing the relationship between C_n and bivalve surface area (SA) given by Ricciardi *et al.*[21] linked to our present reconstructed Hill-based model describing $I_f - C_n$ relationship, a bivalve surface area-based empirical model to correlate C_n and I_f can be expressed as:

$$C_n = 1 - \exp(-\mu P_t SA) = 1 - f(SA) = \frac{1}{1 + \left(\dfrac{K50}{I_f(SA)}\right)^n}, \tag{A1}$$

where P_t is the total mussel density (ind m^{-2}), $\mu = 2.2$ (95% CI 1.2–3.2) is a preference parameter, $K50 = 0.896$ is fitted infestation yielding 50% colonization effect, and $n = 0.968$ is a fitted Hill coefficient.

Thus, a general relationship between $I_f(SA)$ and $f(SA)$ can be rewritten based on Equation (A1) as:

$$I_f(SA) = K50\left(\frac{f(SA)}{1 - f(SA)}\right)^{-1/n}. \tag{A2}$$

When the values of surface area for hard clam (SA_1) and unionid (SA_2) are available, then:

$$I_f(SA_1) = K50\left(\frac{f(SA_1)}{1 - f(SA_1)}\right)^{-1/n}, \tag{A3}$$

$$I_f(SA_2) = K50\left(\frac{f(SA_2)}{1 - f(SA_2)}\right)^{-1/n}, \tag{A4}$$

where $I_f(SA_1)$ is the hard clam surface area-adjusted infestation for hard clam and $I_f(SA_2)$ is the unionid surface area (SA_2)-based infestation.

The surface area-adjusted infestation intensity for hard clam can thus be obtained as:

$$I_f(SA_1) = I_f(SA_2)\left(\frac{f(SA_1)(1 - f(SA_2))}{f(SA_2)(1 - f(SA_1))}\right)^{-1/n}. \tag{A5}$$

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