ISSN 2075-1117, Russian Journal of Biological Invasions, 2010, Vol. 1, No. 3, pp. 218–226. © Pleiades Publishing, Ltd., 2010.
Original Russian Text © A.N. Chetyrbotskii, A.Yu. Zvyagintsev, A.I. Kafanov, 2010, published in Rossiiskii Zhurnal Biologicheskikh Invasii, 2010, No. 2, pp. 74–88.

Mathematical Modeling and Evaluation of Bioinvasion Status of Barnacles on the Shelf of Japan

A. N. Chetyrbotskii[a], A. Yu. Zvyagintsev[b], and A. I. Kafanov[b]†

[a]*Far Eastern Geological Institute, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, 690022 Russia*
[b]*Zhirmunsky Institute of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, 690041 Russia*
E-mail: chetyrbotsky@yandex.ru, ayzvagin@gmail.com

Received February, 16, 2010

Abstract—The results of a statistical analysis of spatiotemporal distribution of the barnacles *Amphibalanus improvisus*, *A. amphitrite*, and *A. eburneus* on the shelf of the Sea of Japan are presented for the period of 1935–2000. The locations of barnacle finds coincide with the areas of huge sea ports and electric power plants. The empirical patterns of barnacle bioinvasion to the Sea of Japan are described under the statistical analysis of sampling data. The computational model of barnacle invasion is developed and analyzed. This model takes into account empirical data and suggested parametric factors, such as natural population growth, intra- and interspecific competition, sea environmental conditions, and natural settling activity, and anthropogenic factors, such as navigation intensity anthropogenic load. The algorithms of population dynamics and evaluation of model adequacy are suggested. Significant concordance between model and field data is obtained.

DOI: 10.1134/S2075111710030148

Key words: invasion, model, parametric identification, barnacles.

INTRODUCTION

The numerical assessment of species invasion and evaluation of forthcoming events are the key problems of modern ecological research. Uncontrolled species invasion has been taking place in different areas of the World Ocean for the last 50–60 years and is mostly a result of increasing sea traffic. Sometimes not only single species penetrate into a new environment, but the species complexes and even fauna invasion may lead to global changes in the aboriginal communities. Fouling species, such as barnacles (suborder Balanomorpha), are transported with vessels and are the most common invaders. About 9% of species of world barnacle fauna may be found in the vessel fouling communities [Zevina, 1982]. In most cases, they are found in the boreal and tropical climatic areas, and their resettlement takes place permanently. Not only species but also morphotype invasion may change the aboriginal community dramatically [Protasov, 2003]. That is why the assessment of their ecological similarity to the aboriginal species is necessary. For example, in Peter the Great Bay (PGB), Sea of Japan, the invasion of only two new barnacle morphotypes led to significant changes in the fouling and benthic communities. Nearly all the fouling barnacle species inhabiting the Sea of Japan come to PGB by vessel transport, but only the most ecologically flexible species survive here. We have registered successful invasion of only two barnacle species, common to the Japanese coast, *Amphibalanus improvisus* and *A. amphitrite*. The first one was able to succeed as a self-maintaining population; the second one exists as a temporal summer species, which is totally eliminated during cold winter period. Both species are quite tolerant to antifouling coating toxicants and may slow down the vessel speed greatly [Poltarukha et al., 2006; Zvyagintsev, 2007].

Rapid economical development of the Asian Pacific region has affected the growth of sea transport in this area, which has led to species expansion in the Sea of Japan. As a result, 48 new species have invaded by vessel transport (fouling communities and uncontrolled ballast water discharge) in PGB [Radashevskii et al., 2008].

The studies of biological invasions are a live issue to find practical ways of hydrometeorological and ecological monitoring. Indeed, owing to high ecological plasticity of some species to the specific environment, the community structure may be evaluated as the integral characteristics of the local conditions of the marine environment. The body size of *Lepas anatifera* (Crustacea, Lepadidae) may indicate upwelling [Turpaeva and Yampol'skii, 1979]. Regard must be paid to the preplanning of effective protection of water development facilities (WDF), coast-trade vessels (CTV), and foreign-going ships (FGS) from fouling.

A cost effective solution of such a problem includes first multidisciplinary investigations based on tradi-

†Deceased.

tional methods and state-of-the-art ones, such as distributional patterns of the environmental characteristics and anthropogenic load impact. As a result, a computational model of the process is developed. In the present study, the development of the bioinvasion model was based on selective spatiotemporal patterns of three barnacle species, *Amphibalanus improvisus, A. amphitrite*, and *A. eburneus*, along the Japanese coast, which is circumfluous by the Sea of Japan and the Pacific Ocean. These species were tested since they belong to the key fouling species [Zevina and Gorin, 1975; Zvyagintsev, 2005] and since unique original material was accessible. Most of the invasive species in PGB were previously registered as the invaders of the Japanese coast also [Otani, 2002], which became the basis to create the appropriate model and to give forecasting.

MATERIALS AND METHODS

The study was based on numerous publications, mostly by Otani [2002], the archive of temperature and salinity of the coastal waters of the Sea of Japan in 1927–2001 [Rudykh, 2008], and original data (courtesy of N.I. Rudykh).

Here we focus on three barnacle species:

1. *Amphibalanus amphitrite* is widespread in subtropical and tropical waters and in the fouling communities of WDF and CTV along the coast of Japan, China, and Vietnam [Davidoff, 1952]. It is a secondary species for vessels and WDF in PGB, where it was transported by FGS. Currently, it is still not found in the benthic communities of PGB, but occasional settling on the experimental plates was registered [Zvyagintsev, 2005]. This species survives water temperatures below zero Celsius [Calcagno et al., 1997].

2. *A. eburneus* is a common tropical–subtropical sublittoral species, which is quite sensitive to the water temperatures below zero Celsius. It was found for the first time in the fouling communities of shallow and well-heated small inlets of PGB. It may appear in the warm years, but cannot develop a self-maintaining population in PGB [Zevina and Goin, 1975; Zvyagintsev, 2005].

3. *A. improvisus* is also a common tropical–subtropical species, which has penetrated around the world over the last decades [Davidoff, 1952]. It is usually found as a subdominant species in the fouling communities of CTV and FGS along the coasts of Southeast Asia. This species is tolerant to a wide range of water temperature and salinity [Zevina and Strelkov, 1983]. It dominates in the fouling communities of FGS sailing from the Vladivostok seaport to the harbors on eastern coast of Japan. As a rule, it usually can be found in the fouling communities of WDF and CTV in PGB. Currently, it has been naturalized in the PGB benthic communities and is tolerant to water temperatures below zero Celsius.

The first findings in 1935–2000 of these three species are presented in Fig. 1 (Japanese coasts).

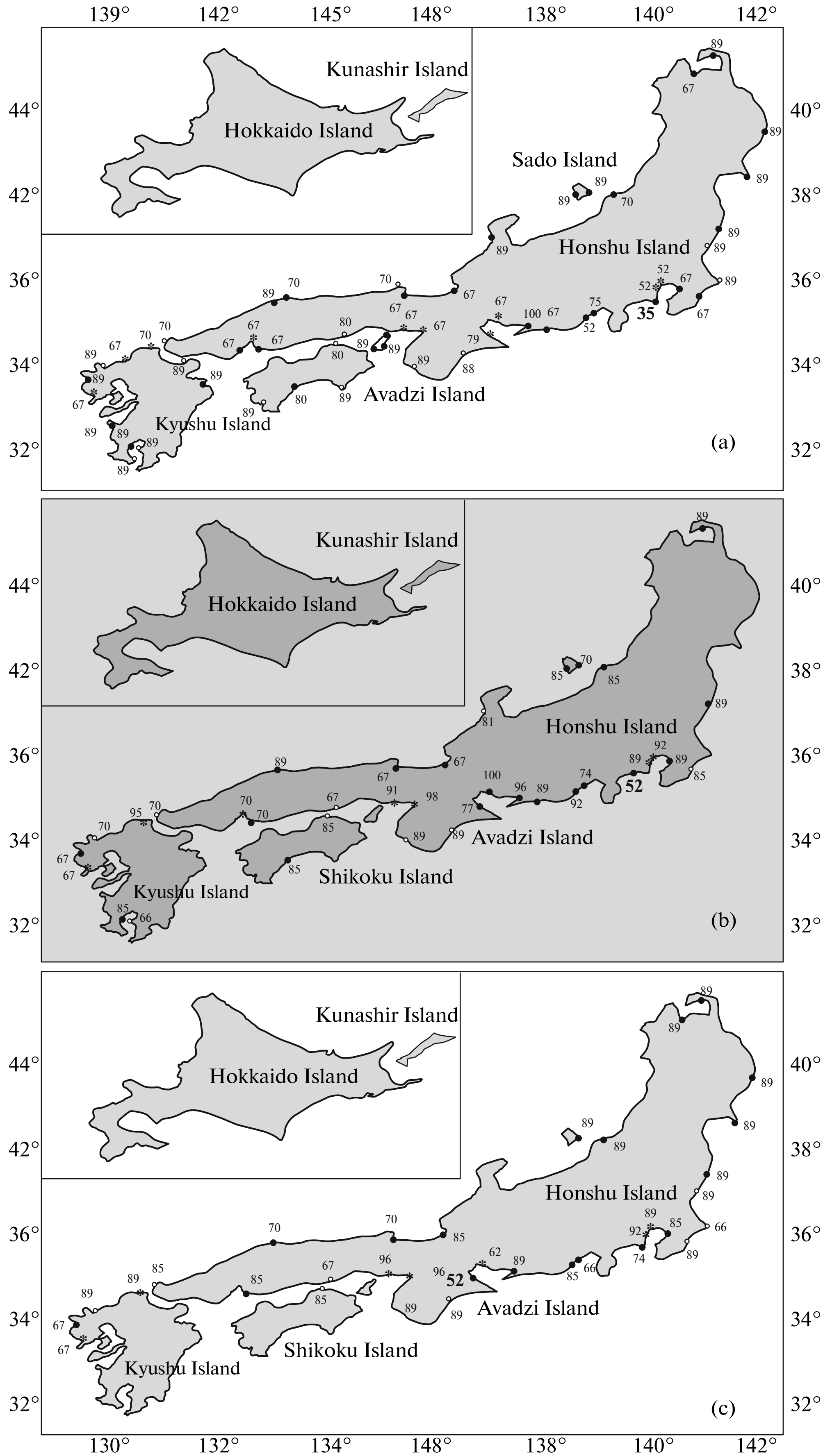
Statistical analysis of spatiotemporal distributional patterns of these species for the period of 1935–2000 exhibits a close location of finding sites to big cities (Fig. 1), especially huge sea harbors, Tokyo (139.75° E, 35.69° N; 12400000 population; 1952), Hiroshima (132.47° E, 34.40° N; 2800000 population; 1967), Kitakyushu (130.85° E, 33.90° N; 1020000 population; 1970). This can be easily explained by the close relationship between the navigation intensity and harbor capacity. The more prominent the harbor, the greater the volume of ballast waters bringing adults and larvae of invasive species. The abundance of invaders may also increase owing to the reproduction of species in vessel fouling communities. If the environment is favorable, they reproduce and resettle actively.

The first finding of barnacles were also registered near several small cities, Tsuruga (135.06° E, 35.65° N; 68000 population; 1967), Maizuru (135.18° E, 35.53° N; 94000 population; 1967), Aomori (140.75° E, 40.82° N; 131000 population; 1967). This may be linked with the waterways of intensive navigation and favorable environment for settlement. A nuclear power plant is located in Tsuruga. Once barnacle larvae penetrated into the waters via ballast waters and vessel fouling communities, they appeared in the plant discharge waters that have passed through the cooling system. Altogether, these factors facilitate favorable conditions for the barnacles. The same is true for the area along the Maizuru shore, where a well-developed shipbuilding industry, textile industry, and construction industry exist. A sea ferry is permanently operating between the big harbor of Khakodate (140.72° E, 41.76° N; 306000 population; 1967) and Aomori, which also promotes species dispersal.

The location of species findings close to small cities is an indicator of favorable conditions for resettlement. These conditions are formed owing to warm discharge waters, waste disposal, construction platforms, anchor buoys, etc. In particular, the studies performed in PGB exhibit settlement of *A. amphitrite* on artificial substrates during the warm season [Zvyagintsev and Korn, 2003].

The specific distribution of the locations of barnacle findings (Fig. 1) indicates that new findings are registered close to big cities and coincide with the locations of other invasive species resettlement. Bigger

Fig. 1. Sampling area map, coast of the Sea of Japan (by [Otani, 2002]), with locations of the first findings of *Amphibalanus improvisus*, *A. amphitrite*, *A. eburneus*; last two numbers of the year are given; 100—the year 2000. The increased font indicates the finding that was the first for a certain area. The cities of 1000000 population are indicated by asterisks. (a) *Amphibalanus amphitrite*; (b) *A. eburneus;* (c) *A. improvisus*.


139°
142°
145°
148°
138°
140°
142°
44°
42°
36°
34°
32°
40°
38°
Kunashir Island
Hokkaido Island
Sado Island
Honshu Island
Avadzi Island
Kyushu Island
(a)
Kunashir Island
Hokkaido Island
Honshu Island
Avadzi Island
Shikoku Island
Kyushu Island
(b)
Kunashir Island
Hokkaido Island
Honshu Island
Avadzi Island
Shikoku Island
Kyushu Island
(c)
130°
132°
134°
148°
138°
140°
142°

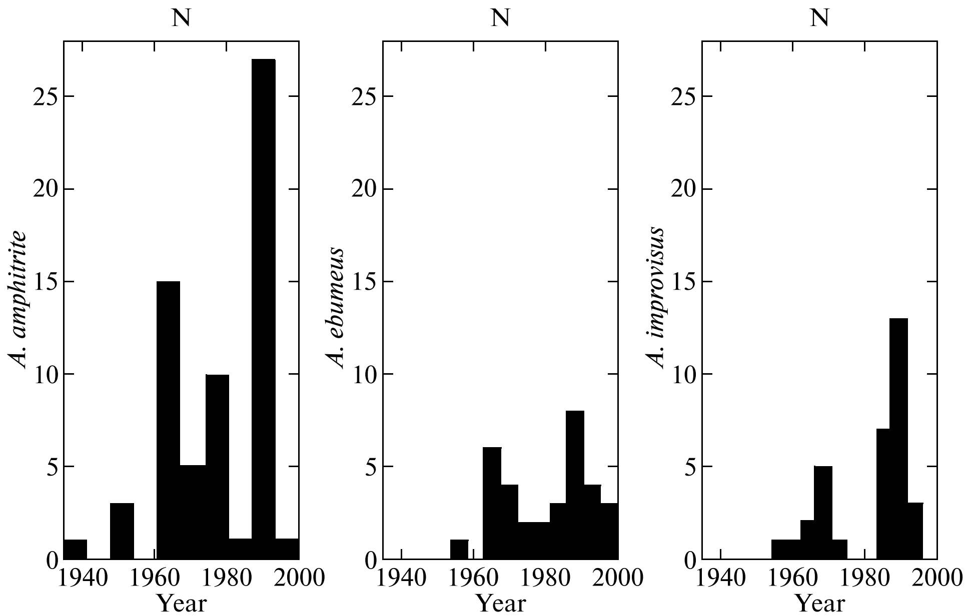


Fig. 2. Histograms of barnacle area distribution along the Japanese coast, with the number of locations of the first findings for the period of 1935–2000 (x axis is years of observations; y axis is number of locations).

cities are characterized by larger resettlement areas. Comparison of the locations in Fig. 1 shows the coincidence of the dates of simultaneous findings of different barnacle species.

The number of findings of all three studied species together is 25% of the total number of observations, which may be treated as evidence of interspecific relationships between them.

Histograms of number of barnacle area findings along the Japanese coast for the period of 1935–2000 are presented on Fig. 2. The second part of 20th century is characterized by a rapid increase of such locations, which may be linked with the increase in navigation activity.

However, in some years, there was a total absence of these species. Probably, this may reflect a certain period of acclimatization of the invasive species to the local environment. After this period ends, the species resettles along new location.

The analysis of these distributional patterns allows searching for key factors of barnacle invasion along the Japanese coast. The first one is governed by abiotic factors; the second, by barnacle fecundity; the third, by barnacle motor performance; and the fourth, by navigation intensity and anthropogenic load.

RESULTS

Computational Model

In marine biology, the problems described earlier are usually solved by step-by-step computation, which compares the species lists for certain areas, evaluation of these results, and further analysis of such comparisons [Andreev, 1980]. The new method applied takes into account the evolutional peculiarities of the species and includes a set of data analysis methods and computational modeling.

The problems of developing a model of the species dynamics are closely related to a restricted number of field observations, fragmentary and irregular data collection, labor intensity and expensiveness of simultaneous measurements of biomass, environmental factors, anthropogenic load, etc. Such models have too many parameters that are hard to evaluate, and that is why they are usually replaced by artificial laboratory systems.

A specific class of bioinvasion models originates from equations that, for the one-dimensional case, take the following form [Lewis and Pacala, 2000; Neubert et al., 2000]:

$$B(x, t+\Delta t) = \int_{-\infty}^{\infty} k(x, y) f(B(y, t)) B(y, t) dy, \quad (1)$$

where $B(x, t)$ is the biomass at location x at time t, Δt is the temporal discreteness, $k(x, y)$ is the kernel of the integral equation (it is taken into account to compute the influence of biomass at location y to the biomass at location x), and $f(B(y, t))$ is species fecundity.

The model specification appears as $k(x, y)$ and $f(B(y, t))$. The applicability of such models is restricted and may be applied for description of the invasion expansion process.

A wide spectrum of models originates from an equation that, in the one-dimensional case, has the following form [Lobanov et al., 1999; Weinberger, 2002]:

$$\partial B/\partial t = f(B)B + \partial(D\partial B/\partial x)/\partial x, \quad (2)$$

where $f(B)$ is species fecundity and D is the diffusion coefficient (in the general case, it appears as a function of external area and B). Equation (2) characterizes the system of "reaction-diffusion" principle, where the dispersal of both juveniles and adults is taken into account. This is the advantage of Eq. (2) compared to Eq. (1). Analyzing the same class and varying $f(B)$ and D, one can obtain numerous and various invasion models. Among them, a common linear dependence of $f(B)$ on B is usually used:

$$f(B) \equiv \alpha - \beta B, \quad (3)$$

where α is the natural growth rate and β is the natural mortality rate.

The model classes cited earlier suffer from the total absence of such factors as navigation intensity, water disposal, etc. When these parameters are included in the model, it becomes more practical and may be used to assess different cases, including cultural noise and accidents.

Development of such a model was performed within the scope of Eqs. (2) and (3), where the analysis results and several assumptions were included:

(1) The dynamics of invader biomass is governed by its natural growth, mortality, dispersal, and anthropogenic load of the settlements (also by navigation intensity).

(2) The environmental factors include water temperature and salinity.

(3) Natural growth and mortality rates are affected by the environment and substrate competition.

(4) A linear dependence of barnacle and human populations is assumed.

(5) One-dimensional diffusion is assumed as a process of barnacle dispersal since the shoreline is a narrow area and the spatial position of the specimens may be located by the arc length s along the island contour.

According to the factors listed above, a natural modification of (2) may appear as

$$\partial B_i/\partial t = [\alpha_i(T, S) - \beta_i(T, S)(B_1 + B_2 + B_3)]B_i + \gamma_i(T, S)N + D_i\partial^2 B_i/\partial s^2, \quad (4)$$

$$dN/dt = \varphi(x, t),$$

where $x \equiv (x_1, x_2)$ a point on the coordinate frame on the area of Fig. 1 (computational unit is longitudinal degree); t is the current time point (computational unit is year); $B_i \equiv B_i(x, t)$ is the barnacle biomass of the ith species ($i = 1$, *A. amphitrite*; $i = 2$, *A. eburneus*; $i = 3$, *A. improvisus*); $T \equiv T(x, t)$ and $S \equiv S(x, t)$ are the water temperature and salinity; $\alpha_i(T, S)$ is the biomass increase of the ith species; $\beta_i(T, S)$ is the species mortality rate as a result of interspecific competition; $\gamma_i(T, S)$ is the biomass dynamics, which is specified by navigation intensity and city anthropogenic load; $N \equiv N(x, t)$ is the human population for the settlement at location x for t year; $D_i \equiv D_i(x, t)$ is the diffusion coefficient; s is the arc length of the island contour; and $\varphi(x, t)$ is the human population dynamics for the settlement at location x for t year.

The first term of the right part of Eq. (4) is the modification of the logistic growth model [Svirezhev and Logofet, 1978]; the second one is the biomass dynamics, which is affected by navigation intensity and city anthropogenic load; the third one represents the natural distribution. Model (4) takes into account that these processes are proportional to the population of the nearest harbor city.

The parameterization of $\{\alpha_i(T, S), i = 1–3\}$ includes several assumptions. Each of the species is acclimated to certain range of environmental temperature T and salinity S. Inclusion of such parameters is performed by incorporation of optimal T_i^* and S_i^* values for each species. Since the deviations of temperature ($T - T_i^*$) and salinity ($S - S_i^*$) from the optimal range negatively impact the species dynamics, $\alpha_i(T, S)$ is a decreasing function of even degrees of such deviations. A simple approximation of $\alpha_i(T, S)$ can be written in the form

$$\alpha_i(T, S) = \alpha_{i,1} - \alpha_{i,T}(T - T_i^*)^2 - \alpha_{i,S}(S - S_i^*)^2, \quad (5)$$

where $\alpha_{i,1}$, $\alpha_{i,T}$, $\alpha_{i,S}$, T_i^*, and S_i^* are nonnegative computational coefficients. Their physical meaning is as follows: $\alpha_{i,1}$ characterizes the optimal natural biomass increase of the ith species, which is observed for the coincidence of optimal temperature and salinity for this species; $\alpha_{i,T}$ and $\alpha_{i,S}$ indicate the growth dynamics, which is affected by deviation of T and S from their optimal values.

Since deviations of temperature and salinity from the optimal values cause the increase in barnacle mortality, $\beta_i(T, S)$ is an increasing function. The same method can be applied to Eq. (4) to approximate $\beta_i(T, S)$:

$$\beta_i(T, S) = \beta_{i,1} + \beta_{i,T}(T - T_i^*)^2 + \beta_{i,S}(S - S_i^*)^2, \quad (6)$$

where $\beta_{i,1}$, $\beta_{i,T}$, and $\beta_{i,S}$ are nonnegative computational coefficients, which show inter- and intraspecific competition. According to (6), deviations of temperature and salinity from the optimal values cause an increase in barnacle mortality. The physical meaning of the process may be described as follows: if the temperature and salinity coincide with optimal values for the ith species, then natural mortality is characterized by $\beta_{i,1}$, and $\beta_{i,T}$ and $\beta_{i,S}$ characterize the dynamics of mortality affected by deviations T and S from the corresponding values.

The parameterization of $\gamma_i(T, S)$ was recalculated earlier by equations that took into account the distance between the harbors [Chetyrbotskii, 2008]. We have employed the same assumptions that were used for (5) and (6):

$$\gamma_i(T, S) = \gamma_{i,1} - \gamma_{i,T}(T - T_i^*)^2 - \gamma_{i,S}(S - S_i^*)^2, \quad (7)$$

where $\gamma_{i,1}$, $\gamma_{i,T}$, and $\gamma_{i,S}$ are computational coefficients. Their physical meaning is that $\gamma_{i,1}$ characterizes survival rate of the ith species specimens transported by a vessel at optimal salinity and temperature of the environment; $\gamma_{i,T}$ and $\gamma_{i,S}$ characterize the decrease in survival rate affected by the temperature and salinity deviations from the optimal range.

Taking into account all the factors and assumptions listed above results in the following barnacle invasion model:

$$\begin{aligned}
\partial B_i/\partial t &= [\alpha_i(T, S) - \beta_i(T, S)(B_1 + B_2 + B_3)]B_i \\
&\quad + \gamma_i(T, S)N + D_i\partial^2 B_i/\partial s^2, \\
dN/dt &= \varphi(x, t), \\
\alpha_i(T, S) &= \alpha_{i,1} - \alpha_{i,T}(T - T_i^*)^2 - \alpha_{i,S}(S - S_i^*)^2, \\
\beta_i(T, S) &= \beta_{i,1} + \beta_{i,T}(T - T_i^*)^2 + \beta_{i,S}(S - S_i^*)^2, \\
\gamma_i(T, S) &= \gamma_{i,1} - \gamma_{i,T}(T - T_i^*)^2 - \gamma_{i,S}(S - S_i^*)^2,
\end{aligned} \quad (8)$$

where $i = 1–3$.

It is natural to set the initial conditions to (8) as

$$B_i(x, t_0) = 0 \quad (9)$$

and the zero flows on the contour borders as

$$\partial B_i/\partial s|_\Gamma = 0.$$

Assessment of the Model Parameters and Forecasting of the Bioinvasion Status

When developing the model, we took into account the common principles listed below. The division of total problem into the separate steps is quite conventional. The order of the steps usually shows up during the computation, which is usually an iterative process. In the process of computing, the primary data are supplemented with unaccounted-for or new details, which altogether lead to improvement of the model. The computational algorithm is adjusted in a same manner, and the search for an optimal solution of the problem and an appropriate method of analysis and presentation of data are performed. The modeling process and selection of results usually go together. The experiments need to be interpreted via the model, and the model has to be checked by the experiments [Oran and Boris, 1987]. The computational estimations of parameter values and checking of the model's adequacy to the natural conditions are usually performed by searching for the extreme of the targeted function (discrepancy). The last is a measure of the inadequacy of observed and recalculated values of studied parameters. Meanwhile, the type of targeted function specifies the method of parameter assessment.

The recommendations given in previous studies were taken into account [Moiseev et al., 1978].

The numerical procedure of the nonlinear assessment of the parameters during the computation is an implementation of algorithms of searching for the extreme(s) of the functional. The choice of its type is mainly governed by the environment during the observations and existing information about the model distribution a priori. The problem of parameter assessment was described by Bard [1979]. Let p be a vector of desired model parameters, and $\Phi(p)$ be the measure of the deviation of observed values from their model images, i.e., so-called discrepancy. Then the problem consists in searching for the vector p which minimizes $\Phi(p)$:

$$\min\Phi(p) \text{ for } p \in P, \quad (10)$$

where P is the region of allowable parameter values. It may be assumed that this region corresponds to an n-dimensional hypercube when the limitation of generality is absent. In case of recalculation of (10) by the least-squares procedure, $\Phi(p)$ has the form

$$\Phi(p) = \sum_{i=1}^{3}\sum_{Y=1935}^{2000}\sum_{m=1}^{7}\sum_{k\subset I(i,Y,m)}(B_{i,Y,m,k}^{(D)} - B_{i,m,k}(Y,p))^2, \quad (11)$$

where $\{B_{i,Y,m,k}^{(D)}\}$ is the sample collection of the species location distribution (Fig. 1); i is the species, $i = 1–3$; Y is the year of observations ($Y = 1935–2000$); $m = 1–7$ corresponds to the enumeration of Japanese islands ((1) Kyushu Island, (2) Shikoku Island, (3) Avadzi Island, (4) Honshu Island, (5) Sado Island, (6) Hokkaido Island, (7) Kunashir Island); and k is the element of $\{I(i, Y, m)$: $i = 1–3$, $Y = 1935–2000$, $m = 1–7\}$ of the m^{th} island location set, where the ith species specimens were found in year Y. The original dataset includes 141 observations; the set of parameters of the model (8)–(10) contains 36 elements:

$$p \equiv \{(\alpha_{i,1}, \alpha_{i,2}, \alpha_{i,3}, T_i^*, S_i^*, \beta_{i,1}, \beta_{i,2}, \beta_{i,2}, \gamma_{i,1}, \gamma_{i,2}, \gamma_{i,3}, D_i), i = 1–3\}.$$

The temporal step of the model (8)–(10) is one year.

The parametric identification of the model is specified by the number of observations and the level of its statistical significance. Here, we employ the data set of spatiotemporal distribution of the barnacles *A. amphitrite, A. eburneus*, and *A. improvisus* in the coastal waters along the shore of Japan [Otani, 2002]. The observations coincide with the data on species distribution [Kafanov and Kudryashov, 2000]. The quantitative assessments of biomass were based on numerous field observations; i.e., the biomass of *A. amphitrite* was 5.2 kg m^{-2}; *A. eburneus*, 1.4 kg m^{-2}; and *A. improvisus*, 1.4 kg m^{-2} [Zevina and Strelkov, 1983; Zvyagintsev and Korn, 2003; Zvyagintsev, 2005].

Numerical estimates of the model parameters, with 95% confidence intervals given

	$i = 1$	$i = 2$	$i = 3$		$i = 1$	$i = 2$	$i = 3$
$\alpha_{i,1} \times 10^2$	9.16 ± 2.01	9.04 ± 1.99	9.06 ± 1.24	$\gamma_{i,1} \times 10^2$	4.95 ± 2.78	4.99 ± 2.74	0.93 ± 0.16
$\alpha_{i,T} \times 10^4$	1.04 ± 0.32	1.13 ± 0.29	1.05 ± 0.31	$\gamma_{i,T} \times 10^5$	5.48 ± 0.71	5.51 ± 0.80	1.04 ± 0.23
$\alpha_{i,S} \times 10^4$	2.57 ± 0.93	2.48 ± 1.10	0.14 ± 0.02	$\gamma_{i,S} \times 10^5$	1.09 ± 0.34	1.32 ± 0.31	1.22 ± 0.11
$\beta_{i,1} \times 10^2$	5.49 ± 1.27	5.01 ± 0.98	5.33 ± 0.82	$D_i \times 10^3$	5.11 ± 2.06	5.02 ± 1.68	3.54 ± 0.62
$\beta_{i,T} \times 10^4$	5.51 ± 0.83	5.04 ± 0.77	1.26 ± 0.38	T_i^*	17.5 ± 4.9	17.4 ± 5.1	25.1 ± 1.6
$\beta_{i,S} \times 10^4$	2.63 ± 1.34	2.55 ± 1.12	1.07 ± 0.13	S_i^*	30 ± 5.3	28 ± 9.3	32.5 ± 6.4

The data on the population of cities were obtained from Internet resources (http://world-gazetteer.com; http://ru.wikipedia.org/wiki/List_of_cities_proper_by_population; http://news.leit.ru/archives/3954; http://search.japantimes.co.jp/cgi-bin/nn20081228a3.html). The numerical recalculations were performed by MATLAB software [Rudakov and Safonov, 2000]. In computing the model (8)–(10), the modules of the GIS system "Ice Coverage of the Sea of Japan" were used [Chetyrbotskii, 2005]. In particular, we used the program modules that implement reduction of a multidimensional problem of searching for extremes to a sequence of one-dimensional problems [Strongin, 1978; Chetyrbotskii, 1991], and modules of assessment of parameters of covariance matrix and model adequacy [Chetyrbotskii, 2005].

The limits of the region P of allowable parameter values are usually defined on the basis of a priori information. Here, their variations were defined in interactive debugging according to the computational process of model (8)–(10). The quality control of parameter coincidence was tracked by the correlation coefficient between the observed and modeled distribution. The largest value was 0.739, which was evidence of significant coincidence.

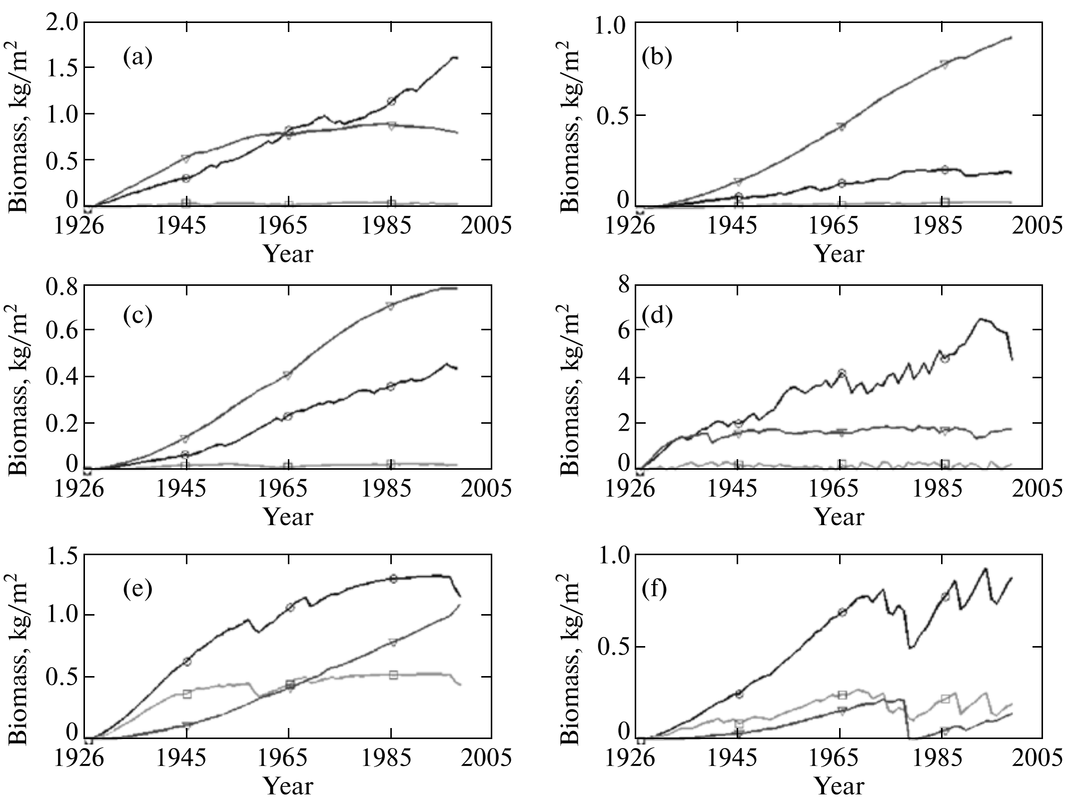


Fig. 3. Modeled dynamics of barnacle biomass in the coastal area of large cities in Japan. (Green squares) *Amphibalanus amphitrite*; (red triangles) *A. eburneus*; (blue circles) *A. improvisus*. (a) Kitakyushu (130.41° E, 33.58° N); (b) Aomori (140.75° E, 40.82° N); (c) Tsuruga (135.06° E, 35.65° N); (d) Tokyo (139.75° E, 35.69° N); (e) Hiroshima (132.47° E, 34.40° N); (f) Maizuru (135.18° E, 35.33° N).

The estimates of parameters are presented in table.

In computing the parameters, the confidence intervals were also recalculated, which were the characteristics of their significance [Bard, 1979]. All of them are positive, i.e., significant [Kendall, 1973].

On the basis of the assessment of parameters, the forecasting of barnacle biomass dynamics was performed for the areas around large Japanese cities for the period of 1926–2001 (Fig. 3).

The analysis of distributional patterns clearly indicates that *A. eburneus* is characterized by less biomass owing to its higher vulnerability to temperature and salinity deviations compared to the other two species (Figs. 3a–3e). The area close to Kitakushu is characterized by the average temperature of 20.62°C and salinity of 33.67‰. This environment appears favorable for both *A. amphitrite* and *A. improvisus*. At location *b* ($\bar{T}_b$ = 17.14°C; $\bar{S}_b$ = 33.51‰), the environment is more friendly to *A. improvisus* than to *A. amphitrite*. The same situation is observed for area *c* ($\bar{T}_c$ = 19.11°C; $\bar{S}_c$ = 33.12‰). Owing to significant water discharge from the large cities, the salinity decreases, and thus the water becomes more favorable for *A. amphitrite*, which dominates there. The same is observed for locations *d–f*, where $\bar{T}_d$ = 18.99°C and $\bar{S}_d$ = 32.54‰, $\bar{T}_e$ = 17.71°C and $\bar{S}_e$ = 33.37‰, and $\bar{T}_f$ = 13.35°C and $\bar{S}_f$ = 32.82‰. The first finding of all three species in the harbor of Vladivostok in 1981 [Kafanov and Zhukov, 1993] can be explained nicely by our model.

CONCLUSIONS

The obtained results are based on a computational model of barnacle invasion. The parameterization of the vessel transport processes has to consider the human population of port cities in the recalculations. The live issue of the present model for the Russian Far East Region is related to the forthcoming construction of a nuclear power plant, university center, and seaquarium on Russkiy Island, in Vladivostok. Altogether, this will increase the navigation intensity in Peter the Great Bay and human population growth. The expected economic development of Primorskiy krai will cause an increase in the anthropogenic load on the coastal ecosystems of PGB. As an example, more than 800 supertankers (150 000–300 000 t deadweight) will transport oil from Russia after opening of the East Siberia–Pacific oil pipeline. This will increase the introduction of many invasive species, primarily barnacles. The free-living larvae of nearly all the benthic species, comprising billions of specimens, will be transported from different areas of the World Ocean to PGB by the ballast waters of supertankers. Meanwhile, the adult specimens in the vessel fouling communities may be ready for reproduction. The acclimatization of fouling species may cause crucial changes in benthic and plankton communities. We note that the thermal load caused by water discharge from industrial plants may result in creating a new warmer environment favorable for acclimatization of warm-water barnacle species.

The original model of barnacle bioinvasion on the Sea of Japan shelf, based on the data set on three species, is an important step in bioinvasion studies in the Far Eastern seas of Russia. The model takes into account the species biomass dynamics, substrate competition, optimal range of water temperature and salinity, distributional type of dispersal along the coast, and transportation of specimens by ballast waters and on the hulls of vessels.

Further studies will include development of a GIS system of coastal distribution of invasive species and development of community models, as well as specification of their parametric identification.

ACKNOWLEDGMENTS

This study was supported by the Federal Program “The World Ocean” (2008–2012, state contract no. 01.420.1.2.2003) Nov. 7, 2008, Russian Foundation for Basic Research (09-04-98580-r, “Marine Bioinvasion and Role of Ballast Waters in Species Dispersal in 2009–2010”), grant of the Presidium of Russian Academy of Sciences (2008, “Response of Marine Biota to the Changes of Environment and Climate”), “Methodology of Monitoring of Marine Biodiversity” (regional project “Far East”); complex program of Far Eastern Branch of the Russian Academy of Sciences “Biological Safety of Far Eastern Seas of Russia” (2008, 2010), and APN Foundation (ARCP2006-FP14-Adrianov).

Professor A.I. Kafanov was the author of the present studies. He proposed and justified the diffusion distribution theory for barnacle species.

The authors are grateful to I.A. Kashin (Institute of Marine Biology, Vladivostok) for invaluable comments that improved the present manuscript and to N.I. Rudykh (Institute of Oceanology, Vladivostok) for providing hydrological data.

REFERENCES

Andreev, V.L., *Klassifikatsionnye postroeniya v ekologii i sistematike* (Classification Build-Ups in Ecology and Systematics), Moscow: Nauka, 1980 [in Russian].

Bard, Y. *Nonlinear Parameter Estimation*, Academic Press, 1973.

Davidoff, C.N., Contribution a L’Etude des Invertebres de la Faune Marine Benthique de’l’Indochine, *Bull. Biol. France-Belgique,* 1952, suppl. 37, pp. 128–129.

Calcagno, J.A., López Gappa J., and Tablado, A., Growth and Production of the Barnacles *Balanus amphitrite* in an Intertidal Area Affected by Sewage Population, *J. Crust. Biol.*, 1997, vol. 17, no. 3, pp. 417–423.

Chetyrbotskii, A.N., *Metody i algoritmy resheniya zadach snizheniya razmernosti prostranstva opisaniya* (Methods and Algorithms in Solving a Problem of Descriptor Area Dimension Decrease), Vladivostok: DVO AN SSSR, 1991 [in Russian].

Chetyrbotskii, A.N., *Tekhnologiya postroeniya geoinformatsionnykh sistem dlya ledyanogo pokrova zamerzayushchikh morei (na primere GIS "Ledyanoi pokrov Yaponskogo morya")* (Technology of Developing of the Geoinformation Systems for the Ice Coverage of the Freezing Seas (In Terms of GIS "Ice Coverage of the Sea of Japan")), *Inform. Tekhnol.*, 2005, no. 11, pp. 17–23 [in Russian].

Chetyrbotskii, A.N., *Parametricheskaya identifikatsiya modeli bioinvazii morskikh organizmov verkhnikh otdelov shel'fa*, (Parametrical Identification of the Marine Biological Invasion Model on the Upper Shelf Areas), in: *Sovremennye informatsionnye tekhnologii dlya nauchnykh issledovanii. Vseros. Konf.* (Modern Information Technologies for Scientific Research: All-Russian Conf.), 2008, Magadan [in Russian].

Kafanov, A.I., and Zhukov, V.E., *Pribrezhnoe soobshchestvo vodoroslei makrofitov zaliva Pos'eta* (Nearshore Community of the Macrophytes (Algae) in the Possiet Gulf), Vladivostok: Dal'nauka, 1993 [in Russian].

Kafanov, A.I., and Kudryashov, V.A., *Morskaya biogeografiya* (Marine Biogeography), Moscow: Nauka, 2000 [in Russian].

Kendall, M. and Stuart, A. *The Advanced Theory of Statistics*, New York: Macmillan, 4th ed., 1977, vol. 1.

Lewis, M.A., and Pacala, S., Modeling and Analysis of Stochastic Invasion Processes, *J. Math. Biol.*, 2000, no. 41, pp. 387–429.

Lobanov, A.I., Starozhilova, T.K., and Chernyaev, A.P., *Rezonansnye yavleniya v sistemakh tipa "reaktsiya-diffuziya"* (Resonance Events in the Systems of "Reaction-Diffusion" Type), *Mat. Model.*, 1999, vol. 11, no. 7, pp. 75–82 [in Russian].

Moiseev, N.N., Ivanilov, Yu.P., and Stolyarova, E.M., *Metody optimizatsii* (Optimization Methods), Moscow: Nauka, 1978 [in Russian].

Neubert, M.G., Kot, M., and Lewis, M.A., Invasion Speeds in Fluctuating Environments, *Proc. R. Soc.*, 2000, no. 267, pp. 1603–1610.

Oran, E., and Boris, J., *Numerical Simulation of Reactive Flows*, Elsevier Science, New York, 1987.

Otani, M., Appearance and Latest Trends of Introduced Marine Sessile Animals in Japanese Waters, *Sessile Organisms*, 2002, vol. 19, no. 2, pp. 69–92.

Poltarukha, O.P., Korn, O.M., and Ponomarenko, E.A., *Svobodnozhivushchie usonogie rakoobraznye i fasetotekty* (Crustacea (Thoracica and Facetotecta)), in *Biota rossiiskikh vod Yaponskogo morya* (Biota of the Russian Waters of the Sea of Japan), Adrianov, A.V., Ed.-in-Chief, Vladivostok: Dal'nauka, 2006, vol. 5 [in Russian].

Protasov, A.A., *Biologicheskoe raznoobrazie vodnykh ekosistem v aspekte problemy introduktsii chuzherodnykh organizmov*, (Biodiversity of Aquatic Ecosystems Regarding to the Problem of the Biological Invasion), Bashtanniy, R., and Rabotnev, V., Eds., Odessa, Ukraine, 2003, issue 8, pp. 70–81 [in Russian].

Radashevskiy, V.I., Ivin, V.V., and Zvyagintsev, A.Yu., *Sozdanie bazy dannykh po vidam-vselentsam Severnoi Patsifiki*, (Development of the Alien Species Database for the North Pacific Region), in *Sovremennye problemy morskoi inzhenernoi ekologii: Tez. Dokl. Mezhdunar. Nauch. Konf.*, (Modern Problems of Marine Engineering Ecology: Proc. of Int. Sci. Conf.), Rostov-on-Don, 2008, pp. 210-211 [in Russian].

Rudakov, P.I., and Safonov, V.I., *Obrabotka signalov i izobrazhenii. MATLAB 5.X* (Image and Signal Processing. MATLAB 5.X), Moscow: DIALOG-MIFI, 2000 [in Russian].

Rudykh, N.I., *Zakonomernosti izmenchivosti solenosti vody v Yaponskom more* (Regularities of the Salinity Dynamics in the Sea of Japan), *Extended Abstract of Cand. Sci. (Geogr.) Dissertation*, Vladivostok, 2008 [in Russian].

Strongin, R.G., *Chislennye metody v mnogoekstremal'nykh zadachakh* (Numerical Methods in Multiextremal Problems), Moscow: Nauka, 1978 [in Russian].

Svirezhev, Yu.M., and Logofet, D.O., *Ustoichivost' biologicheskikh soobshchestv* (Consistence of the Biological Communities), Moscow: Nauka, 1978 [in Russian].

Turpaeva, E.P., and Yampol'skii, A.D., *O vozmozhnosti obnaruzheniya pod'ema vod po okeanicheskomu obrastaniyu* (About the Possibility of Upwelling Finding by the Biological Fouling), *Okeanologiya,* 1979, vol. 19, no. 6, pp. 1116–1124 [in Russian].

Weinberger, H.F., On Spreading Speeds and Traveling Waves for Growth and Migration Models in a Periodic Habitat, *J. Math. Biol.*, 2002, no. 45, pp. 511–548.

Zevina, G.B., *Usonogie raki podotryada Lepadomorpha Mirovogo okeana. Chast' II* (Barnacles (Suborder Lepadomorpha) of the Ocean, Part II), Leningrad: Nauka, 1982 [in Russian].

Zvyagintsev, A.Yu., *Morskoe obrastanie v severo-zapadnoi chasti Tikhogo okeana* (Marine Fouling in North-Western Pacific), Vladivostok: Dal'nauka, 2005 [in Russian].

Zevina, G.B., and Gorin, A.N., *Flyuktuatsiya usonogikh rakov v obrastaniyakh buev zaliva Petra Velikogo* (Fluctuations in the Population Dynamics of Barnacles in the Buoy Fouling Communities in the Peter the Great Bay), in *Obrastaniya v Yaponskom i Okhotskom moryakh* (Fouling in the Sea of Japan and the Sea of Okhotsk), Vladivostok: Far-East Scientific Research Center of the USSR Academy of Sciences, 1975, pp. 71–78 [in Russian].

Zevina, G.B., and Strelkov, V.I., *Morfologicheskie izmeneniya tablichek Balanus improvisus v raznykh raionakh areala* (Morphological Changes of Plates in *Balanus improvisus* Inhabiting Different Areas), in *Biologicheskie resursy Kaspiiskogo morya* (Biological Resources of the Caspian Sea), Moscow: Moscow State U., 1983, pp. 136–146 [in Russian].

Zvyagintsev, A.Yu., *Problema morskikh bioinvazii v zalive Petra Velikogo s ballastnymi vodami i obrastaniem sudov* (Problem of Marine Biological Invasion in the Peter the Great Bay by the Ballast Waters and Ship Fouling), in *Chteniya pamyati akademika A.V. Zhirmunskogo* (Read. in Memory of Academician A.V. Zhirmunskiy), Vladivostok: Dal'nauka, 2007, pp. 22–34 [in Russian].

Zvyagintsev, A.Yu., and Korn, O.M., *Usonogii rak Balanus amphitrite Darwin v zalive Petra Velikogo Yaponskogo moray* (Barnacle *Balanus amphitrite* Darwin, in the Peter the Great Bay, the Sea of Japan), *Biol. Morya*, 2003, vol. 29, no. 1, pp. 50–58 [in Russian].