

# Long-term dynamics of three benthic *Ampelisca* (Crustacea-Amphipoda) populations from the Bay of Morlaix (western English Channel) related to their disappearance after the 'Amoco Cadiz' oil spill

Jean-Christophe Poggiale<sup>1,\*</sup>, Jean-Claude Dauvin<sup>2</sup>

<sup>1</sup>Centre d'Océanologie de Marseille, Campus de Luminy, CNRS UMR 6535, Case 901, 13288 Marseille Cedex 09, France

<sup>2</sup>Station Marine de Wimereux, UPRES A 8013 ELICO, CNRS, Université de Lille des Sciences et Technologies de Lille, 28 Avenue Foch, BP 80, 62930 Wimereux, France

**ABSTRACT:** Many studies have dealt with the effects of the 'Amoco Cadiz' wreck. In particular, they describe the influence of the oil spill on the benthic populations dynamics off northern Brittany coasts (western English Channel). Several mechanisms have been proposed to explain how communities have recolonised the area during these last 20 yr. In this paper, we focus on the dynamics of the Pierre Noire *Ampelisca* populations which constitute the dominant part of the total fine sand *Abra alba* community. We propose a discrete population dynamics model that takes into account the sea temperature, the amount of pollutant and competition. The model permits the simulation of long term changes in abundance for each of the more abundant *Ampelisca* species. It provides a tool for testing assumptions and for understanding the different processes occurring during recolonisation.

**KEY WORDS:** Population dynamics · Recurrent model · Recolonisation · *Ampelisca* · English Channel

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## INTRODUCTION

Ampeliscids are the dominant species in many soft-bottom communities inhabiting the cold temperate waters and arctic waters in the Pacific, Atlantic and Arctic Oceans. Despite this, they rarely form dense populations (>10 000 ind. m<sup>-2</sup>) in littoral or shallow (<30 m) subtidal zones (Bellan-Santini & Dauvin 1988). In such habitats, ampeliscid assemblages are generally composed of several species of the 3 dominant genus of the family: *Ampelisca*, *Byblis*, and *Haploops* (Stoner 1980, Schaffner & Boesch 1982, Dauvin et al. 1993, Oliver et al. 1983). In the Bay of Morlaix (western English Channel), the Pierre Noire fine sand community supports the most abundant benthic amphipod community yet

recorded in European seas (Dauvin et al. 1993). Very dense populations of *Ampelisca* were observed in 1977 (3 species dominated, density >40 000 ind. m<sup>-2</sup>) when a benthic survey of temporal changes of that community was initiated. One year after the beginning of sampling in spring 1978, the station was impacted by hydrocarbons from the 'Amoco Cadiz' which caused the disappearance of the dominant *Ampelisca* populations, leaving behind a single species (*Ampelisca sarsi*) after the stress in very low density (Dauvin 1987). Of the 220 000 tonnes of oil spilled into the sea from the 'Amoco Cadiz' wreck, between 10 000 and 92 000 tonnes were trapped in subtidal sediments (Dauvin 1984). The presence of hydrocarbons in the subtidal bottom sediments of the Morlaix Bay was evident at the beginning of April, just 2 wk after the wreck (Cabioch et al. 1978). At Pierre Noire, the levels of hydrocarbons in the sediments (mg kg<sup>-1</sup> dry sediment) measured by infrared spectrophoto-

\*E-mail: poggiale@com.univ-mrs.fr

tometry reached 200 ppm in summers 1978 and 1979, but did not exceed 50 ppm after winter 1981 (Dauvin 1984). In the English Channel, a megatidal sea, fine sediments are confined to the shallow waters of bays and estuaries. Such fine sand and muddy fine sand communities as that of Pierre Noire are, therefore, isolated from each other, separated by rocky bottoms, pebbles, coarse sand and maerl. Lacking pelagic larvae, the amphipods characteristic of these communities form insular populations (Dauvin 1987). Recolonisation by *Ampelisca* was retarded due to the combination of demographic strategy of amphipods (absence of pelagic larvae, large capacity of dispersion, low fecundity), and the distance from non-perturbed populations which could supply recruits (Dauvin 1987). Nevertheless, the populations were able to recover their densities rapidly. Indeed, within 15 yr, the densities on the impacted site attain high values similar to those found before the pollution accident ( $>40\,000$  ind.  $m^{-2}$  at the end of summer 1993) (Dauvin et al. 1993, Dauvin 1998)

A 20 yr survey (1977 to 1996) at Pierre Noire station, with regular sampling of temporal changes of the community and dominant species, especially *Ampelisca*, and environmental variables (temperature, salinity, sediment characteristics) is now available. Data on the biology of each species are also available. The objectives of this paper are to produce a discrete model of the population dynamics of 3 *Ampelisca* species which constitute 90% of the total community. It simulates temporal changes of the populations during recolonisation after a chemical stress, and takes into account competition and environmental variables such as temperature and hydrocarbon concentration.

Many population dynamics models have been proposed. Murray (1989) proposed a review of the different forms of population dynamics models. De Angelis (1994) gave the main principles of community models. Although there are many modelling studies for some particular processes such as recruitment, population growth, predation and so on (Day & Taylor 1997, Higgins et al. 1997), only a small number of models are devoted to the study of recolonisation after chemical stress (e.g. Hallam et al. 1996). In some cases, community structure can be used as an indicator of pollution (White 1984). In such circumstances, there is a clear need for deeper understanding of the relationships between pollutants and community composition.

## MATERIALS AND METHODS

**Study area.** The Pierre Noire station (PN), in the *Abra alba-Hyalinoecia bilineata* fine sand macrobenthic community is located in the eastern part of the Bay of Morlaix, Brittany (Western English Channel)

( $48^{\circ}42'30''$  N;  $3^{\circ}51'58''$  W), at a depth at low tide of 17 m. The sediment is fine sand (median particle size: 148 to 184  $\mu$ m). Bottom water temperature varies between  $8^{\circ}$ C in March and  $15.5^{\circ}$ C in September, and salinity between 34.5 psu in winter and 35.3 psu at the beginning of October (Dauvin 1984).

**Sampling.** Ten replicate samples (Smith McIntyre grab,  $0.10$   $m^2$ ) were taken at the Stn PN 5 times a year at the beginning of March, June, August, October and December from 1977 to 1996 (20 yr), in order to estimate the density of the macrofauna. After collection, the sediment was sieved (1 mm circular mesh) and the retained material fixed with 10% neutral formalin, sorted twice, and identified. The use of a 0.5 mm sieve in 1985–1986 and on 2 occasions in 1987 (August, October) significantly increased the number of *Ampelisca* juveniles collected during the period of recruitment (June to October). Therefore, to obtain a better estimation of the density of each species at each date, the 1.0 mm mesh density of each species at each date has been corrected by the number of individuals retained on a 0.5 mm sieve mesh (Dauvin 1988c,d, 1989a,b). The correction factors are different for each species and vary from March to December.

**Model description.** We propose a model taking into account sea temperature, environmental pollution and competition. Sea temperature affects reproduction processes. Pollution and competition increase individual mortality. We assumed competition for space or resources, and introduced a carrying capacity for each species in the model. The resulting effect was that if the total biomass of the community was greater than a given value then it affected the potential of surviving and abundances shall decrease.

Since we disposed of 5 samplings  $yr^{-1}$  and since we dealt with non-overlapping generation populations, we proposed a time discrete model. We call *period* the duration between 2 successive times where data were available. The model was based on the following assumptions: (1) For each population, the sex ratio was equal to 1 (refer to Dauvin 1988a,d and 1989b, for *Ampelisca tenuicornis*, *armoricana* and *sarsi* respectively). Therefore we considered only the females. Furthermore, the females were distributed over 2 age classes: juvenile and adult individuals. (2) For each population, the abundance of juveniles at time  $t + 1$  was obtained by adding the survivors of the juveniles existing at time  $t$  that were still juveniles at time  $t + 1$ , the number of produced juveniles during the period and a migration term. (3) For each population, the abundance of adults at time  $t + 1$  was obtained by adding the surviving adults existing from time  $t$ , the surviving individuals that were juveniles at time  $t$  and are adults at  $t + 1$  (i.e. juveniles that change age classes during the period) and a migration term.

(4) The survival rate of an individual was defined as the probability that an individual would survive from time  $t$  to time  $t + 1$ . It depended on the carrying capacity of the environment with respect to the population considered and on a 'pollution factor' which depended on the environmental pollution and is a number between 0 and 1 (0 = no pollution, 1 = strong pollution).  
 (5) Migration terms were obviously needed in order to define recolonisation of the station. However, no quantitative information is available on this particular process. The different *Ampelisca* species are known to be insular, which is the reason why the migration terms are as low as possible. The values of these migrations terms are 1 ind. m<sup>-2</sup> period<sup>-1</sup>. This is sufficient to permit recolonisation and is just a small perturbation of the demographic processes.

The general equations for the model read :

$$\begin{cases} N_j^i(t+1) = \mu^i[p, N^i(t)](1 - \lambda^i)N_j^i(t) + r_i(\theta)N_A^i(t) + m_j^i & (1) \\ N_A^i(t+1) = \mu^i[p, N^i(t)]\lambda^i N_j^i(t) + \sigma_i[p, N^i(t)]N_A^i(t) + m_A^i & (2) \end{cases}$$

where  $i$  is the index of population (*armoricana* = 1, *sarsi* = 2, *tenuicornis* = 3),  $N_j^i(t)$  is the abundance of juveniles in population  $i$  at time  $t$ ,  $N_A^i(t)$  is the abundance of adults in population  $i$  at time  $t$ ,  $N^i(t)$  is the total abundance of species  $i$  at time  $t$ ,  $\mu^i[(p, N^i(t))]$  is the survival rate of juveniles in population  $i$ ,  $\sigma^i[(p, N^i(t))]$  is the survival rate of adults in population  $i$ ,  $\lambda^i$  is the probability that, in population  $i$ , a juvenile at time  $t$  passes into the adult stage at time  $t + 1$ ,  $r_i(\theta)$  is the reproduction rate adult<sup>-1</sup> of population  $i$ , where  $\theta$  is the water temperature,  $m_j^i$  is the migration term for juveniles in population  $i$ ,  $m_A^i$  is the migration term for adults in population  $i$ .

Fig. 3 presents the comparisons between simulations and observed data for each species. Since the previous variables  $N_j^i(t)$  and  $N_A^i(t)$  corresponds only to female abundances in the 2 stages (juveniles and adults), the total abundance (male and female) for each species is given by

$$N^i(t) = 2[N_j^i(t) + N_A^i(t)] \quad (3)$$

Fig. 3 presents these quantities for each species.

In order to remain as clear as possible, the precise mathematical expressions are given in Appendix 1. Here we explain the main steps used for the construction of the reproduction and survival rates. These rates are obtained as products of different factors: reproduction rate = maximum reproduction rate  $\times$  temperature factor, for instance, and survival rate = pollution factor  $\times$  competition factor.

We chose this formulation according to the 'Shelford Tolerance Law' (Ramade 1984). This law claims that for each environmental factor there exists a range of values for which all ecological processes, under the

dependence of this factor, will normally be possible. In other words, we assumed that for each environmental factor there is a range within which life is possible and there is a value of the factor concerned for which the life conditions are optimal. In our case, we considered temperature and pollution as the main environmental factors.

The 'temperature factor' (TempFact) is a function between 0 and 1 which has the form described by Fig. 1a. It takes the value 1 for a 'good' temperature  $\theta_0$  and is non-zero only in a given range of temperature values around the value  $\theta_0$ . It means that the maximum reproduction rate is reached at  $\theta_0$  and if the temperature was too far from this value, the reproduction rate vanishes. Temperature data were used as inputs in the model. The temperature factor was calculated as explained in Appendix 1. The range of temperatures for which reproduction is possible dependet on the species, but they seem to be very similar from one species to the

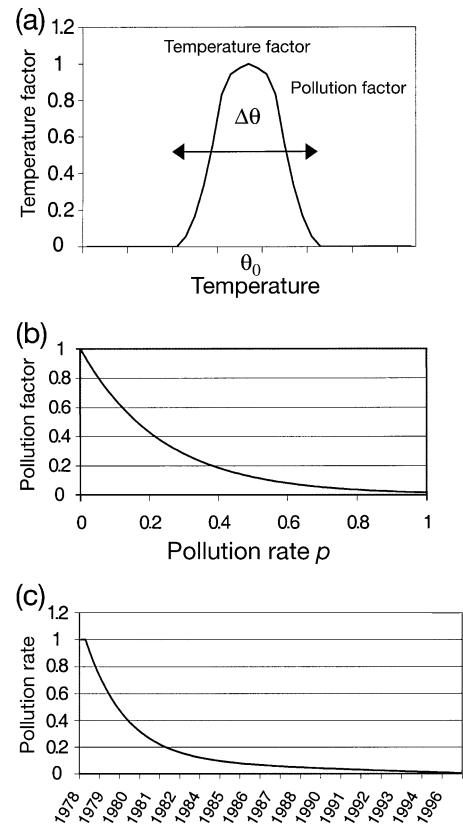


Fig. 1. (a) Change of temperature factor with respect to temperature. It is maximal (equal to 1) when temperature is close to 'good' temperature  $\theta_0$ , and is 0 when temperature is outside an interval of length  $\Delta\theta$  around  $\theta_0$ . (b) Change of pollution factor. It is maximal for small values of pollution rate and vanishes when pollution rate increases and crosses threshold value  $p_s$ . (c) Pollution rate  $p$  versus time. Pollution rate decreases exponentially. The value reached in 1981 is approximately a quarter of the initial value

other, according to the simulations (see 'Parameters' section below).

The 'pollution factor' (PolFact) is a coefficient between 0 and 1 which has the form described by Fig. 1b. It depends on a 'pollution rate' ( $p$ ) and on the species. The pollution rate characterises the presence and the concentration of hydrocarbon in the sediments. When the hydrocarbon quantity is large, this rate is close to 1; when there is no hydrocarbon, this rate vanishes. It may be, for example, the hydrocarbon concentration  $\text{mass}^{-1}$  of dry sediment. The pollution factor is calculated using the mean of this pollution rate as explained in the Appendix. This factor characterises the capability of the individuals to tolerate pollution. When pollution is important, the pollution factor is close to 0: the conditions are bad and mortality is high. When pollution decreases the pollution rate also decreases and the pollution factor increases: the conditions get better and mortality decreases.

Finally, the 'competition factor' (CompFact) is a number between 0 and 1 depending on the abundance of each species and on their carrying capacities. The mathematical expression is provided in the Appendix. For high abundances, the competition factor is close to 0 (low survival) and if there are only few individuals, the competition effect decreases and this factor is close to 1 (more survival).

Recolonisation takes place in 2 steps: the first step consists of yearly dispersal and colonisation from other sites where pollution did not affect the populations and act as the role of a reservoir. When the pollution factor is high (close to 1), the immigrant individuals can not survive. As the pollution factor decreases (human actions, biological, environmental or hydrodynamical effects), there is a year where the dispersal leads to recolonisation. Recolonisation is fast for *Ampelisca sarsi* and is late for *A. tenuicornis*. The second step is governed by competition.

**Initial conditions.** For the simulations, the initial conditions for the model were chosen to be equal to the actual data. Since we started in March 1978, we assumed that in winter, for each population, all individuals are in the adult classes. Thus we started with 0 juveniles for each population, and the number of adult females was half of the total abundance, assuming that the sex-ratio is 1. Nevertheless, these initial conditions are not really important for long term simulation because in April 78 the pollution rate was equal to 1 and thereafter all the individuals disappeared.

**Parameters.** There are 6 parameters by species: the maximum population growth rate  $r_{\max}^i$ , the carrying capacity  $K^i$ , the optimal growth temperature  $\theta_0^i$  the temperature

amplitude where reproduction is possible  $\Delta\theta^i$ , the probability for a juvenile to pass into the adult stage  $\lambda^i$  and a parameter  $\alpha^i$  which measures the strength of the effects of hydrocarbons on individuals of species  $i$ . Appendix 1 and Fig. 1b,c illustrate the way that this parameter is used in the model. The pollutant is assumed to decrease exponentially with time (Fig. 1c). We define a pollution rate  $p$  (e.g. the mass of pollutant  $\text{mass}^{-1}$  of dry sediment) which is exponentially decreasing with time. We know that at Pierre Noire, the quantity of hydrocarbons decreased by a factor of 4 between 1978 and 1981 (Dauvin 1984). So we used a decreasing exponential function of time, which starts from 1 in 1978 and equals about 0.25 in 1981, to approximate the pollution rate  $p$ . In fact, the actual value of this rate is not important to the model, but the product  $\alpha^i p$  is meaningful. This is the reason why, for simplicity, we chose a pollution rate between 0 and 1. Because we do not precisely define the units for  $p$  and  $\alpha^i$ , the product  $\alpha^i p$  has no unit. Finally, Table 1 summarises the units and values of all the parameters used in the model.

The model parameters were estimated by using Downhill Simplex optimisation techniques, with a routine in FORTRAN and the Numerical Recipes Library (Press 1992). We minimised the distance between simulated and observed values, i.e. we used observed data to calibrate the model. In fact, for each species, we used the data contained in the recolonisation period: for *Ampelisca armoricana* and *A. sarsi*, we used observations made from 1978 to 1991, while for *A. tenuicornis* data from 1978 to 1994 were used.

The optimisation method allowed us to determine 5 parameters for each species: the carrying capacity, the maximal reproduction temperature, the temperature amplitude where reproduction is possible, the parameters  $\alpha^i$  and the probability that a juvenile becomes adult  $\lambda^i$ . For reproduction rates, we used the mean fecundity determined by Dauvin (Dauvin 1988a,d, 1989b). The estimated values of those parameters are summarised in Table 1. Note that the model is simple enough to allow the numerical simulations to be performed on a personal computer, by using the software Excel (Microsoft Corp., Redmond) for example.

Table 1. Parameter values for each *Ampelisca* species used in the model

Parameters	Unit	<i>armoricana</i>	<i>sarsi</i>	<i>tenuicornis</i>
$r_{\max}$	No. of ind. $\text{m}^{-2} \times \text{time}^{-1}$	42	16	32
$K$	No. of ind. $\text{m}^{-2}$	5900	19 700	14 200
$\theta$	$^{\circ}\text{C}$	18	18.1	18.2
$\Delta\theta$	$^{\circ}\text{C}$	10	10.2	9.59
$\alpha$	–	3.86	2.21	14
$\gamma$	–	0.1	0.1	0.39

## RESULTS

### Main characteristics of *Ampelisca* populations

*Ampelisca* characteristically inhabit soft bottoms, except for 2 species (*Ampelisca rubella* Costa, 1844 and *A. lusitanica* Bellan-Santini & Marques, 1986) which have been sampled exclusively on hard substrata. They are tubicolous amphipods, and are either suspension or surface deposit feeders, although some species are both suspension and deposit feeders (mixed species). At Pierre Noire station, 9 species of *Ampelisca* were identified during the 20 yr survey, but the occurrence and the abundance of 4 of them—*A. spinipes* (Boeck, 1860), *A. spooneri* (Dauvin & Bellan-Santini, 1982) *A. spinimana* (Chevreux, 1887) and *A. diadema* (Costa, 1853)—were negligible, and those of 2 other species—*A. brevicornis* (Costa, 1853), and *A. typica* (Bate, 1856)—were low. The main characteristics of the biology of the 5 dominant species are given in Dauvin (1988d) for *A. armoricana* (Bellan-Santini & Dauvin 1981), in Dauvin (1988b) for *A. brevicornis* (Costa, 1853), in Dauvin (1989b) for *A. sarsi* (Chevreux, 1887), in Dauvin (1988a) for *A. tenuicornis* (Liljeborg 1855) and in Dauvin (1988c) for *A. typica* (Bate, 1856). However, as the abundances of *A. brevicornis* and *A. typica* are very low with respect to those of *A. armoricana*, *A. sarsi* and *A. tenuicornis*, we focused on the latter 3 species.

### Macrobenthic community

Fig. 2 shows the temporal changes of the Pierre Noire community from 1977 to 1996. *Ampelisca* formed in 1977, and from 1990 to 1996, about 90% of the total abundance (Fig. 2). The community changed seasonally with maximum abundance at the end of the summer (October) and minimum at the end of winter (March) or during spring (June). The abundance decreased rapidly in 1978 just after the 'Amoco Cadiz' oil spill due to the disappearance of the *Ampelisca* population; the community as a whole then maintained very low density until 1985. An exception was during summer 1982, when a peak in abundance of the opportunistic polychaete *Polydora pulchra* occurred. Soon after the pollution, however, the recolonisation of *Ampelisca* was effectively underway and total abundance of the community reflected that of other *Ampelisca* populations. In 1993, summer abundance reached 40 000 ind. m<sup>-2</sup>, similar to that of 1977. Except

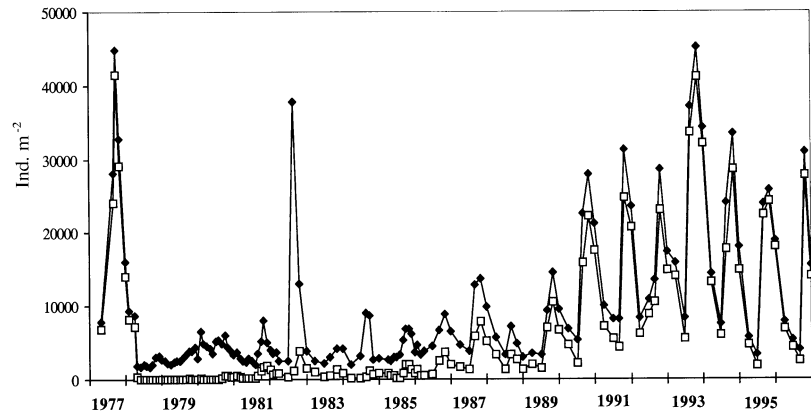


Fig. 2. Annual changes (1977–1996) in (♦) total number of individuals of all species m<sup>-2</sup> and (□) abundance of *Ampelisca* populations m<sup>-2</sup>

in August 1982 when abundance of *Polydora pulchra* was high (>30 000 ind. m<sup>-2</sup>) the density of the other taxa varied between 1600 ind. m<sup>-2</sup> (summer 1978) and 8000 ind. m<sup>-2</sup> (summer 1984).

Although the species number was very high (more than 430 species were reported in the community during the 20 yr survey) only 25 species were among the first 10 dominant species at each annual cycle (14 polychaetes, 8 amphipods and 3 bivalves). Only 6 species occupied the first 3 rankings before the pollution event of 1977, then again at the end of the survey from 1991 to 1996. In 1978, the polychaete *Paradoneis armata* replaced *Ampelisca*, then both Spionidae *Spio decaratus* and *Polydora pulchra* successively occupied the first rank of the community (Dauvin 1998).

### Total *Ampelisca* community

Fig. 3a presents a comparison between the total abundance data of the community and the simulation. This figure shows that, except for summer 1994 where there is a difference between both values, the computed abundances are rather close to the data. The overall trend of the simulation is qualitatively, and quantitatively the same as the observed overall trend. The simulated data fits the beginning of recolonisation, growth and stabilisation for the total population abundance. Furthermore, seasonal variations are well described by the simulation.

### *Ampelisca armoricana*

*Ampelisca armoricana* disappeared in 1978 and recolonised with a small number of individuals in 1981, but population abundance remained very low from

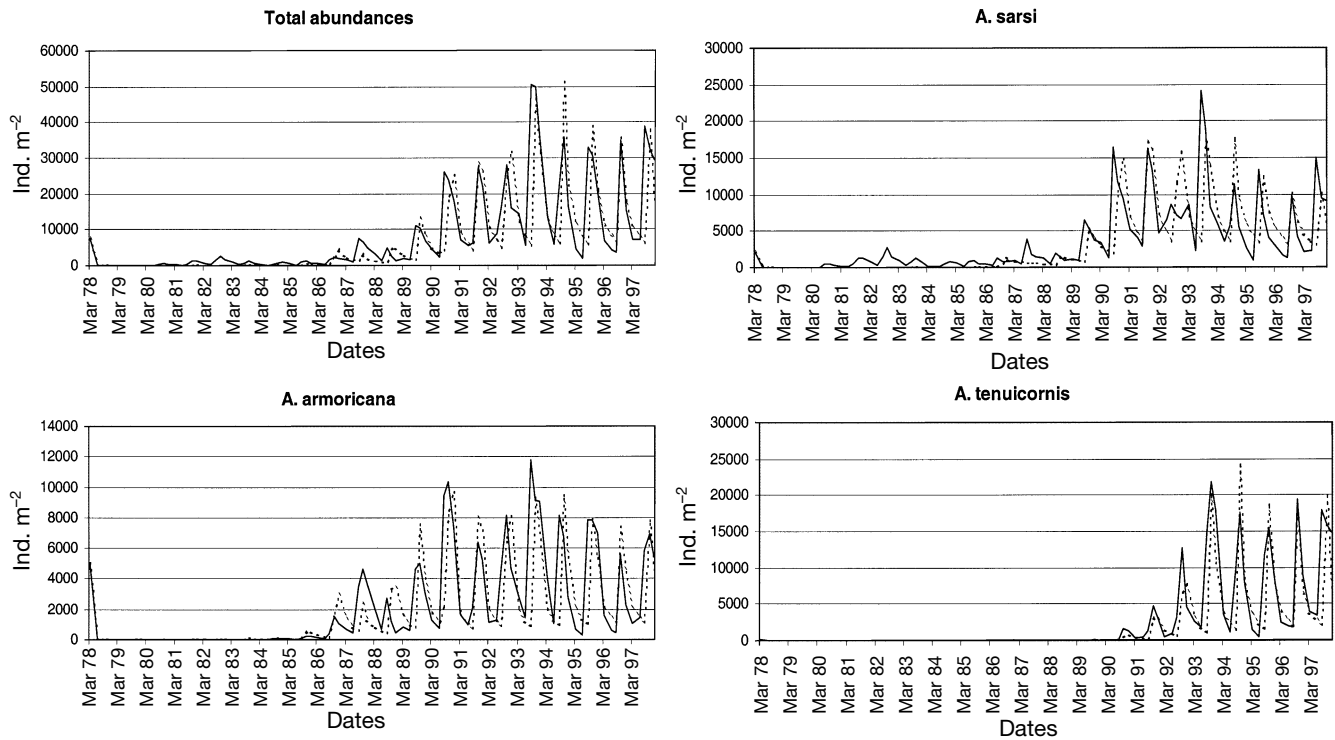


Fig. 3. Temporal variations in (a) the abundance of total *Ampelisca* populations, and (b) *A. armoricana*, (c) *A. sarsi* and (d) *A. tenuicornis* from March 1978 to March 1997 (5 data yr<sup>-1</sup>). Comparison between observed data (solid lines) and computed data (dashed lines). Simulations performed on HP9000 with a FORTRAN 77 routine

1982 to 1986. Abundance rose from 1987 to 1991 and then stabilised from 1991 to 1996 (Fig. 3b). Seasonal variations were minimal in winter or in spring (between December and June) and maximal in summer or in autumn (August, October). Each winter, the abundance fell to a value below 1000 ind. m<sup>-2</sup>. Each summer, it increased to a value of between 8000 and 11 000 ind. m<sup>-2</sup>. The overall trend of the computed values is close to the observed overall trend. The seasonal variations are well simulated.

#### *Ampelisca sarsi*

Only a few specimens of *Ampelisca sarsi* remained in 1978. This species only actively recolonised the community in 1987, even though it was present in low abundance after 1982. From 1987 to 1991, its abundance increased from about 2000 ind. m<sup>-2</sup> to 15 000 ind. m<sup>-2</sup>. From 1992 to 1996, the maximum abundance for each year was closed to 10 000 ind. m<sup>-2</sup>, except in 1994 when it reached 24 000 ind. m<sup>-2</sup>. Every year in spring, *A. sarsi*'s minimal abundance was less than 5000 ind. m<sup>-2</sup> (sometimes as low as 1000 ind. m<sup>-2</sup>). As shown in Fig. 3d, the model simulated this overall trend (low abundance before 1987, increasing to about

15 000 ind. m<sup>-2</sup> and stabilisation around 10 000 ind. m<sup>-2</sup> after 1992) and the seasonal changes.

#### *Ampelisca tenuicornis*

*Ampelisca tenuicornis* is the species which seemed to be most affected by the pollution. Indeed, it disappeared in 1978 and recolonised only in 1988. However, from 1991 to 1994, its abundance increased from 2000 to 20 000 ind. m<sup>-2</sup>. This high abundance was maintained until 1996. Once again, Fig. 3e shows that the model reflects the overall trend and the seasonal variations.

#### Model adequacy

We can see in Fig. 3, that the model gives a 'correct' trend and also correctly simulates seasonal variations. However, if one looks at the figures more closely, we observe that in some years maximum abundance was not reached at exactly the same period for the model as for the observations. For example, for *Ampelisca armoricana* in 1995, the abundance observed maximum was reached in June (7863 ind. m<sup>-2</sup>) and abundance in

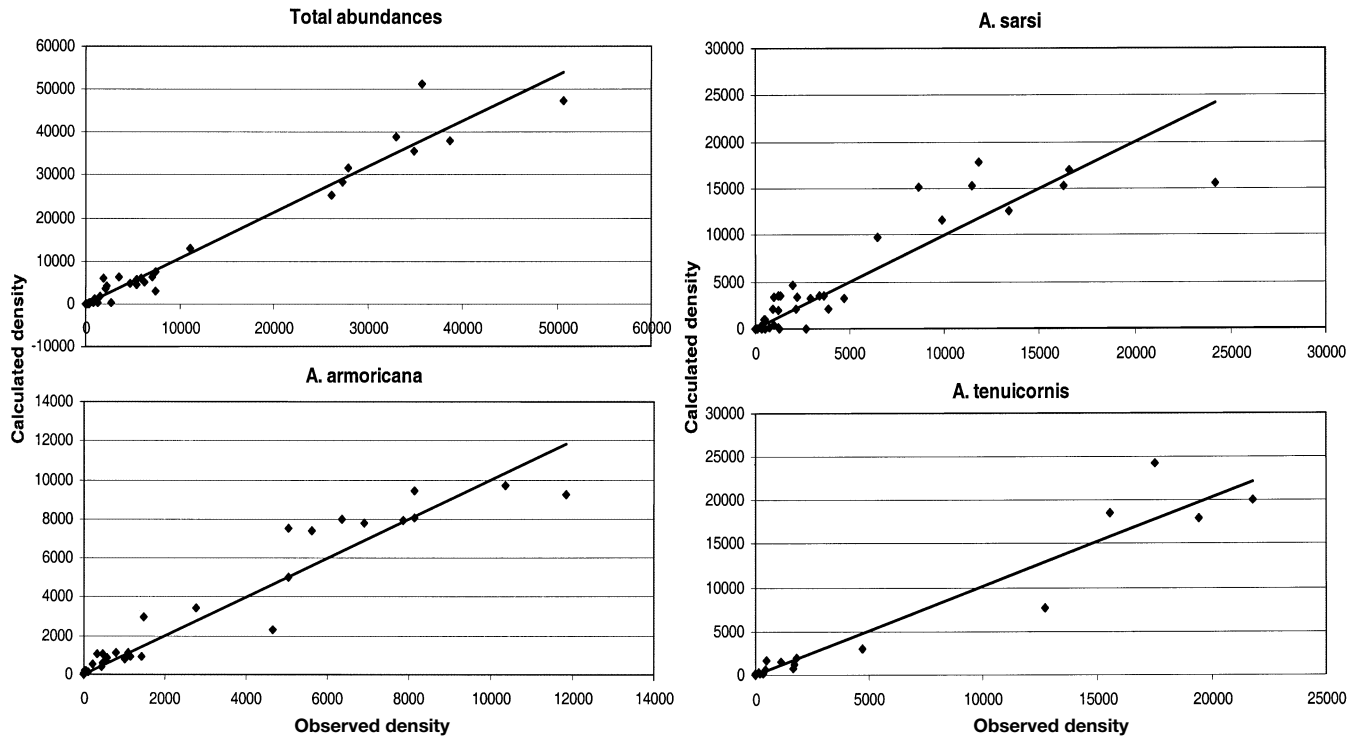


Fig. 4. Comparison between calculated and observed values for (a) total abundance (b) *Ampelisca armoricana*, (c) *A. sarsi* and (d) *A. tenuicornis*

August a little bit lower (7801 ind.  $m^{-2}$ ) while simulated abundances reached the maximum in August (7651 ind.  $m^{-2}$ ). This difference could have been induced by the sampling dates: if the sampling in June had been carried out 1 or 2 wk earlier, it is possible that sampling took place just before the production of offspring and, in this case, the observed maximum would not have been observed in June but in August. Thus, there are some differences in the periods where the maximum is reached which represent a delay in the model, but not for all the years. Moreover, there are 100 observations by species, that is 300 observations compared with 300 simulations, each one containing an error. For this reason, if we try to compare the model and the observations by mean of a rigorous statistical tool, the model is always rejected. However, the model allows us to reproduce the global trend, the seasonal variations and the seasonal amplitudes: for each of the 20 yr, the model can approximate both the maximum and minimum abundance for each species, as illustrated by Fig. 4, which shows for each year the maximum and the minimum simulated densities versus the maximum and the minimum observed densities, respectively. If the points are all on the straight line defined by  $y = x$ , then it means that the simulated density equals the observed one and we can conclude that the model is valid. The number of points on each figure is 40 (1 maximum and

1 minimum each year for 20 yr). Fig. 4a presents the cumulative densities for the 3 species: the points are almost on the straight line  $y = x$ . Actually, a linear regression for this set of points gives the straight line  $y = 1.06x$  ( $r^2 = 0.96$ ,  $n = 40$ ). Fig. 4b corresponds to *A. armoricana* and the linear regression gives the straight line  $y = 1.01x$  ( $r^2 = 0.96$ ,  $n = 40$ ). For *A. sarsi* (Fig. 4c) we get the straight line  $y = 0.99x$  ( $r^2 = 0.83$ ,  $n = 40$ ) and for *A. tenuicornis*, (Fig. 4d), we get the straight line  $y = 1.02x$  ( $r^2 = 0.94$ ,  $n = 40$ ).

## CONCLUSIONS

A population dynamics model has been proposed here in order to describe the recolonisation of *Ampelisca* populations of Pierre Noire between 1978 and 1997, following the severe effects of the 'Amoco Cadiz' wreck which affected *Ampelisca* abundances. This community was composed of 3 *Ampelisca* species which formed 90% of the total community in normal conditions. The major factors taken into account in the model are pollution, sea temperature and competition. The pollution term manages the beginning of the recolonisation. After recolonisation, all species densities grew and then fluctuated around a mean value. The competition term explains why the growth of pop-

ulation densities was limited. The temperature term generated seasonal fluctuations.

The results of the model are encouraging, and the simulated dynamics are quite close to the actual data. Moreover, we tried to use a minimal number of processes. Indeed, a more precise model should be attained by adding more processes (see below), but for each process we must introduce supplementary parameters. However, if we do not dispose of particular data for the estimation of these parameters, then we just add degrees of freedom for the optimisation techniques (see 'Parameters' sub-section): the more parameters there are, the closer the model is to the observed data, but it is not necessarily a better model. Thus, the more parameters there are, the more data one needs to validate the model.

Of course, this model is open to some criticisms among which we have identified the following. Firstly, we take into account dispersal and colonisation by using a simple constant deterministic term, that is we assume that at each period there was a fixed number of immigrants of each species which came from others sites and colonised the Pierre Noire station. This is an important assumption. Actual dispersal movements probably varied with time (i.e. with season and year) but this is very difficult to estimate. In fact, a stochastic approach could be used in order to avoid all such assumptions. Indeed, in such models the amount of migrant individuals is calculated on the basis of probabilities. They are powerful tools, but they need much data for calibration. In our case, we would need the distribution of the amount of migrant individuals during the year, estimated by the mean of many years of migration data, in order to determine the number of migrants at each period. This is the main argument for having used a deterministic approach for ascertaining migration. Furthermore, some studies focus on deterministic migration models, but they generally deal with pelagic organisms. For example, Thiébaud (1996) studied the effects of hydrodynamics on the migration and retention of larvae. Auger & Poggiale (1996) and Bernstein et al. (1999) investigated the relationships between migratory behaviour and demographic processes. Renshaw (1991) gave some details and references about population modelling in space, where movements are important.

However, as we explained in the paper, we focused on benthic species which do not possess any larval stage. Migrations are limited and are not the main process which induced colonisation of the species after their disappearance in 1978 (Dauvin 1987). This is the reason why we tried to understand recolonisation by using a limited migration term.

The second point is that there are many abiotic and biotic factors which can act on the temporal changes of *Ampelisca* populations, such as hydrodynamics, re-

lated changes in sediment composition, the input of organic matter into the water column, predation, competition with other populations, etc. However, we focused on pollution and competition. Indeed, the 'Amoco Cadiz' oil spill was the main factor affecting the community. Some recent works have proven the correlation between the surviving number of individuals and the concentration of hydrocarbon (Ho et al. 1999) and ecotoxicological studies have identified the chemical compounds of hydrocarbons which are really toxic for individuals (Werner et al. 1998). Note that these 2 studies deal with *Ampelisca abdita* species. Some other authors focus on the modelling of pollutant dynamics (e.g. Wania & Mackay 1999). Finally, Coyle & Highsmith (1994) proposed a model to describe how biotic interaction such as competition and predation can explain the size structure of an amphipod community. Our perspective is located somewhere in the large spectrum defined by these different works. Our model allows us to describe the structure of the *Ampelisca* community during a 20 yr span by means of a combination of competition and resistance to pollutants.

Note that during the 20 yr, there were no remarkable climatic phenomena such as a very rigorous winter or exceptional winter storms, and the community studied was located in a protected site (low hydrodynamic). Consequently, it is not possible to test the robustness of the model stress for exceptional temperature values.

#### Appendix 1.

Notation as in text. Reproduction rate:

$$r^i(\theta) = r_{\max}^i \times \text{TempFact} \quad (\text{A1})$$

where  $r_{\max}^i$  is maximum number of juveniles produced by 1 adult during 1 period, for species  $i$ , and

$$\text{TempFact} = \begin{cases} \exp\left(\frac{(\theta - \theta_0)^2}{(\theta - \theta_0 - \Delta\theta/2)(\theta - \theta_0 + \Delta\theta/2)}\right)^a & (\text{A2}) \\ 0 & b \end{cases}$$

where  $\theta$  is observed temperature,  $\theta_0$  is most favourable temperature and  $\Delta\theta$  is length of interval around  $\theta_0$  where TempFact is non-zero.

Survival rate calculated as:

$$\mu^i[p, N^i(t)] = \text{PolFact} \times \text{CompFact} \quad (\text{A3})$$

with PolFact =  $\exp(-\alpha^i p)$ , where  $p$  is pollution rate, and

$$\text{CompFact} = \exp\left(-\frac{N^i}{K^i}\right)$$

where  $N^i$  is the abundance of population  $i$ ,  $N^i = 2(N_{\text{J}}^i + N_{\text{A}}^i)$  (sex ratio equals 1, factor 2 due to presence of males, which arise in competition), and  $K^i$  is carrying capacity for  $i$ th species

<sup>a</sup>if  $\theta \in [\theta_0 - \Delta\theta/2; \theta_0 + \Delta\theta/2]$

<sup>b</sup>if  $\theta \notin [\theta_0 - \Delta\theta/2; \theta_0 + \Delta\theta/2]$



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## LITERATURE CITED

- Auger P, Poggiale JC (1996) Emergence of population growth models: fast migration and slow growth. *Theor Biol* 182: 99–108
- Bellan-Santini D, Dauvin JC (1988) Eléments de synthèse sur les *Ampelisca* du nord-est Atlantique. *Crustaceana Suppl* 13:20–60
- Bernstein C, Auger P, Poggiale JC (1999) Predator migration decisions, the ideal free distribution and predator-prey dynamics. *Am Nat*, 153 (3):267–281
- Cabioch L, Dauvin JC, Gentil F (1978) Preliminary observations on pollution of the sea bed and disturbance of sub-littoral communities in northern Brittany by oil from the 'Amoco Cadiz'. *Mar Pollut Bull* 9:303–307
- Coyle KO, Highsmith RC (1994) Benthic amphipod community in the northern Bering Sea—analysis of potential structuring mechanisms. *Mar Ecol Prog Ser* 107:233–244
- Dauvin JC (1984) Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de la baie de Morlaix et leur perturbation par les hydrocarbures de l'Amoco Cadiz'. Thèse de doctorat d'Etat, Université de Paris
- Dauvin JC (1987) Evolution à long terme (1978–1986) des populations d'Amphipodes des sables fins de la Pierre Noire (Baie de Morlaix, Manche Occidentale) après la catastrophe de l'Amoco Cadiz. *Mar Environ Res* 21: 247–273
- Dauvin JC (1988a) Biologie, dynamique et production de populations de crustacés amphipodes de la Manche occidentale. 1. *Ampelisca tenuicornis* Liljeborg. *J Exp Mar Biol Ecol* 118:55–84
- Dauvin JC (1988b) Biologie, dynamique et production de populations de Crustacés Amphipodes de la Manche occidentale. 2. *Ampelisca brevicornis* (Costa). *J Exp Mar Biol Ecol* 119:213–233
- Dauvin JC (1988c) Biologie, dynamique et production de populations de Crustacés Amphipodes de la Manche occidentale. 3. *Ampelisca typica* (Bate). *J Exp Mar Biol Ecol* 121: 1–22
- Dauvin JC (1988d) Life cycle, dynamics, and productivity of Crustacea-Amphipoda from the western English Channel. 4. *Ampelisca armoricana* Bellan-Santini et Dauvin. *J Exp Mar Biol Ecol* 123:235–252
- Dauvin JC (1989a) La méiofaune temporaire d'un peuplement subtidal de sédiment fin de la Manche occidentale. Echantillonnage, composition qualitative et quantitative. *Ann Inst Océanogr* 65:37–55
- Dauvin JC (1989b) Life cycle, dynamics and productivity of Crustacea-Amphipoda from the western part of the English Channel. 5. *Ampelisca sarsi*. *J Exp Mar Biol Ecol* 128: 31–56
- Dauvin JC (1998) The fine sand *Abra alba* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. *Mar Pollut Bull* 36:669–676
- Dauvin JC, Bellan-Santini D, Bellan G (1993) Les genres *Ophelia* et *Ampelisca* de la région de Roscoff : exemples d'allotopie et de syntopie dans les communautés marines de substrat meuble. *Cah Biol Mar* 34:1–15
- Day T, Taylor PD (1997) Von Bertalanffy's growth equation should not be used to model age and size at maturity. *Am Nat* 149:381–393
- De Angelis DL (1994) Dynamics of nutrient cycling and food webs, populations and communities. *Biology series* 9. Chapman & Hall, London
- Hallam TG, Canziani GA, Lika K (1996) On the relationships between bioassays and dynamics in chemically stressed, aquatic population model. *Ecol Austral* 6:45–54.
- Higgins K, Hastings A, Botsford LW (1997) Density dependence and age structure: non-linear dynamics and population behaviour. *Am Nat* 149:247–269
- Ho K, Patton L, Latimer JS, Pruell RJ, Pelletier M, McKinney R, Jayaraman S (1999) The chemistry and toxicity of sediment affected by oil from the North Cape spilled into Rhode-Island Sound. *Mar Pollut Bull* 38:314–323
- Murray JD (1989) *Mathematical biology*. *Biomathematic texts* 19, Springer-Verlag, Berlin
- Oliver JS, Slattery PN, Silberstein MA, O'Connor EF (1983) Gray whale feeding on dense Amphipod communities near Bamfield, British Columbia. *Can J Zool* 62:41–49
- Press WH, Teukolsky SA, Vetterling WT, Flannery BP (1992) *Numerical recipes in FORTRAN, the art of scientific computing*. Cambridge University Press, Cambridge
- Ramade F (1984) *Eléments d'écologie, écologie fondamentale*. McGraw-Hill, New York
- Renshaw E (1991) *Modelling biological populations in space and time*. *Cam Stud Math Biol*, Cambridge University Press, Cambridge
- Schaffner LC, Boesch DF (1982) Spatial and temporal resource use by dominant benthic Amphipoda (*Ampeliscidae* and *Corophiidae*) on the Middle Atlantic Bight outer continental shelf. *Mar Ecol Prog Ser* 9:231–243
- Stoner AW (1980) Abundance, reproductive seasonality and habitat preferences of amphipod crustaceans in seagrass meadows of Apalachee Bay, Florida. *Contrib Mar Sci* 23: 63–77
- Thiébaud E (1996) Distribution of *Pectinaria koreni* larvae (Annelida : polychaeta) in relation to the Seien river plume front. *Estuar Coast Shelf Sci*, 43:383–397
- Wania F, Mackay D (1999) The evolution of mass-balance models of persistent organic pollutant fate in the environment. *Environ Pollut* 100 (1–3):223–240
- Werner I, Kline KF, Hollibaugh JT (1998) Stress protein expression in *ampelisca-Abdita* (Amphipoda) exposed to sediments from San Francisco Bay. *Mar Environ Res* 45 (4–5):417–430
- White HH (1984) *Concepts in marine pollution measurements, a Maryland Sea Grant Publication*. University of Maryland, College Park

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