Numerical modelling of dispersal of *Ampelisca* (Amphipoda Gammaridae) during their diel migration

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ABSTRACT

The aim of this study is to analyse and model the dispersal of *Ampelisca*, a benthic genus of amphipod crustaceans, in the fine sand community of the Bay of Morlaix (western English Channel), during their nocturnal migration in the water column. Based on sampling of the suprabenthos (in the water column adjacent to the bottom) and surface plankton on 17 June 1994, Dauvin and Zouhiri (1996) studied the vertical distribution of *Ampelisca* during a spring swarming reproductive period. Statistical modelling techniques and specific numerical models were combined to simulate the effects of tidal currents, wind direction and speed on *Ampelisca* dispersal. As an illustration to constant pluriannual seasonal pattern, the dispersion of *Ampelisca* individuals considered as passive particles was studied at two reproductive periods, on a short night (17th-18th June 1994) during a neap tide, and on long night (7th-8th September 1994) during a spring tide. These models are used to investigate whether *Ampelisca* can be dispersed beyond the fine sand community in the immediate area of their small-scale benthic habitat (only 6 km^2) during their diel vertical migration. According to the results, the speed and direction of currents will determine the trajectory of *Ampelisca* and the degree of dispersal outside their benthic habitat during a nighttime pelagic sortie. These simulations, particularly during spring tides, are incompatible with population stability, as they appear to be excessively dispersive. Short-term dispersal simulations for twenty minutes in the plankton allow the optimal return of individuals to the fine sand benthic habitats. We hypothesize there is an adaptative advantage for *Ampelisca* over time to short diel migrations. However, we currently do not know whether each individual makes a single migration, or several migrations in the water column during a night.

1. Introduction

Marine sublittoral benthic communities of fine sand and muddy fine sand are located in areas of weak hydrodynamic forcing. They form distinct entities in Brittany along the coasts of the Bay of Biscay and the English Channel in the north-eastern Atlantic Ocean (Dauvin, 1987). They are surrounded by sediments of other types mainly coarse sands, gravels and pebbles (Dauvin, 1998). These communities are found in shallow waters (<20 m depth) ranging from the Bay of Le Croisic in the north of the Loire estuary to the Rance Maritime in the Normand-Breton Gulf. These isolated types of benthic communities cover small areas and are characterized by a sandy macrofauna including amphipods of the genus *Ampelisca* which can form abundant populations only in sand habitats: i.e., *Ampelisca armoricana* Bellan-Santini and Dauvin, 1981, *A. sarsi* Chevreux, 1888 and *A. tenuicornis* Lijeborg, 1856 (Dauvin et al.,

2021). Other species of *Ampelisca* are more widely distributed in the English Channel and the northern Bay of Biscay on coarse sand to gravelly bottoms and therefore do not display the edaphic character of species of finer sediments (Dauvin, 1987, 1998).

Before the hydrocarbon pollution from the wreck of the oil tanker Amoco Cadiz in March 1978, the populations of *Ampelisca* very largely dominated the Pierre Noire (hereafter named PN) fine sand community in the Bay of Morlaix covering a small area of 6 km^2 (up to 40,000 individuals per m^2 in 1977) (Dauvin, 1987). Areas with very high abundances of *Ampelisca* populations are very rare at the scale of the world-wide ocean (Dauvin et al., 2021). Moreover, in these areas with high abundances, we noticed the presence of sympatric *Ampelisca* populations: nine *Ampelisca* species found at PN (Dauvin et al., 2021). This benthic community was very sensitive to the toxicity of oils and had almost completely disappeared by the beginning of April 1978 (Dauvin,

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1987; Poggiale and Dauvin, 2001). The recolonization was slow, effectively bearing witness to the arrival of individuals probably from the south of Brittany, since all the fine sand habitats were polluted along 350 km of coast from the Bay of Douarnenez to the Bay of Lannion. Ten years after the pollution, *Ampelisca* populations again dominated the macrofauna communities in the Morlaix Bay site (more than 30,000 individuals per m² in the early 1990s) (Poggiale and Dauvin, 2001). This recolonization was probably due to the arrival of individuals present in areas that had not been polluted by the spill from the Amoco Cadiz, being transported by the residual drift current from southern Brittany to the Normand-Breton Gulf.

It is well known that amphipods which have a biological cycle without a planktonic larval dispersal phase perform diel migrations in the water column at night (Dauvin and Zouhiri, 1996). The amphipod *Ampelisca* is benthic during the daytime, living in tubes extending above the sediment surface by a few centimetres, and then disperse in the water column during the night (Dauvin and Zouhiri, 1996).

Moreover, the *Ampelisca* as well as other amphipods show more intense diel migration in the water column, during the reproductive phase, which might lead them to drift away from their optimum benthic habitat due to current activity during their presence in the water column (Dauvin and Zouhiri, 1996). Since this migration is in principle dispersive, the sustainability of populations in such small areas remains an enigma.

After their last moult, mature males acquire several modifications, such as long antennae with numerous setae and large uropods 3 also with long setae. All these morphological differences were favourable to a pelagic life of males; therefore, pelagic males are scare in the day benthic collections and absent in collections at night (Sheader, 1977). Females do not transform their body and appendices, and they return to the sediment after coupling in the water column while the males die after mating. The mating and fertilization occur in the water column, mainly at the beginning of the reproductive periods (Ruppert et al., 2004), i.e., May-June and September-October in the western part of the English Channel (Dauvin et al., 2021).

These vertical movements in the water column have been described as diel migrations (Dauvin et al., 2000). Apart from during the swarming period, the females of *Ampelisca* can show diel migrations at other periods of the year, but their abundance in the water column remains low. This endogenous pattern is common in the Ampeliscidae family as well as in other amphipods, the peracarids and the decapods. It corresponds to a response to changes in light conditions in the sea water and at the sea bed and the nocturnal sinking of phytoplankton during the night. Grazing in response to food sinking drives migration down to 200 m for populations living on the continental shelf (Dauvin et al., 2000). Some crustaceans, mainly amphipods, cumaceans and mysids, can even reach the sea surface and can be collected by light trap (Fage, 1924). Deep amphipods also show nocturnal emergence, but their abundance near the sea bottom and in the sea water column remains low (Dauvin et al., 1995).

Several questions arise in relation to this diel migration: 1) Is the hydrodynamic forcing due to the wind and tide in the Bay of Morlaix sufficiently strong to disperse *Ampelisca* during its night-time pelagic migration? 2) Can *Ampelisca* minimize its dispersal by adapting the time spent in the water column to ensure a return on the PN fine sand community? To address to these questions, this study uses a Lagrangian numerical model to estimate the spatial dispersal of *Ampelisca* and compares the effects of tide on transport during 1) spring sampling in 1994 throughout a swarming phase with real tidal currents and winds occurring at the same date and 2) the 1994 equinox spring tide in September, during a period of seasonal ordinary climate evolution.

2. Materials and methods

2.1. Study site

The PN station is located in the *Abra alba-Hyalinoecia bilineata* fine sand macrobenthic community in the eastern part of the Bay of Morlaix, Brittany (Western English Channel) (48° 42′ 30′′ N; 3° 51′ 58′ W), at a depth of 17 m at low tide (Dauvin, 1998) (Fig. 1). The sediment is fine sand (median particle size: 148 to 184 μm). The fine sand community at PN occurs within a small area of about 6 km² surrounded by other sediment habitats mainly coarse sand and sand dune (Fig. 1).

The bottom water temperature varies between 8 °C in March and 15.5 °C in September, and salinity between 34.5 psu in winter and 35.3 psu at the beginning of October (Dauvin, 1998). At this PN benthic station, the Ampelisca populations show very high abundances:

- 31,500 ind.m⁻² for *A. armoricana* in October 1977 (Dauvin et al., 2021);
- 17,500 ind.m⁻² for *A. tenuicornis* in October 1997 (Dauvin, unpublished data) and 6640 ind.m⁻² in October 1987 (Dauvin et al., 2021);
- 17,500 ind.m⁻² in October 1994 (unpublished data) for *A. sarsi*;
- 2000 ind.m⁻² in October 1987 for *A. typica* (Dauvin et al., 2021).

Additionally, nine Ampelisca species were recorded at PN station:

- *A. armoricana* Bellan-Santini and Dauvin, 1981;
- *A. brevicornis* (Costa, 1853);
- *A. diadema* (Costa, 1853);
- *A. pectenata* Reid, 1951;
- *A. sarsi* Chevreux, 1888;
- *A. spinimana* Chevreux, 1887;
- *A. spinipes* Boeck, 1861;
- *A. tenuicornis* Lijeborg, 1856.
- *A. typica* (Spence Bate, 1856).

In 1977, three species were dominant with *A. armoricana, A. sarsi* and *A. tenuicornis* representing 90 % of the abundance, 38 % of the biomass and 50 % of the secondary production of the community (Dauvin, 1998). *Ampelisca* spp. are very sensitive to hydrocarbon pollution and the species disappeared from the fine sand community as a consequence of the Amoco Cadiz oil spill, which occurred in March 1978 in North Brittany (western English Channel), (Dauvin, 1998; Dauvin et al., 2021). In 1990, 12 years after the Amoco Cadiz oil spill, the abundances of *Ampelisca* spp. were of the same order of magnitude as those observed before the disaster (Dauvin, 1998).

2.2. Diel migration of Ampelisca

To collect swimming species near the sea bottom, suprabenthic sledges were used to filter the sea water just above the sea-bed but without sampling the sediment which can be resuspended due to the effects of the sledge on the sea-bed sediment especially on soft bottoms with medium and fine sand (Dauvin et al., 2000; Dauvin and Zouhiri, 1996). The modified MACER-GIROQ sledge has proved efficient for sampling the suprabenthos and was used during several campaigns in shallow to deep waters of the English Channel and the Bay of Biscay (Dauvin et al., 1995, 2000). Zooplankton nets serve to collect animals present in the water column or at the sea water surface.

This study does not take into account that *Ampelisca* would be interfered by other species during their diel migration in the water column.
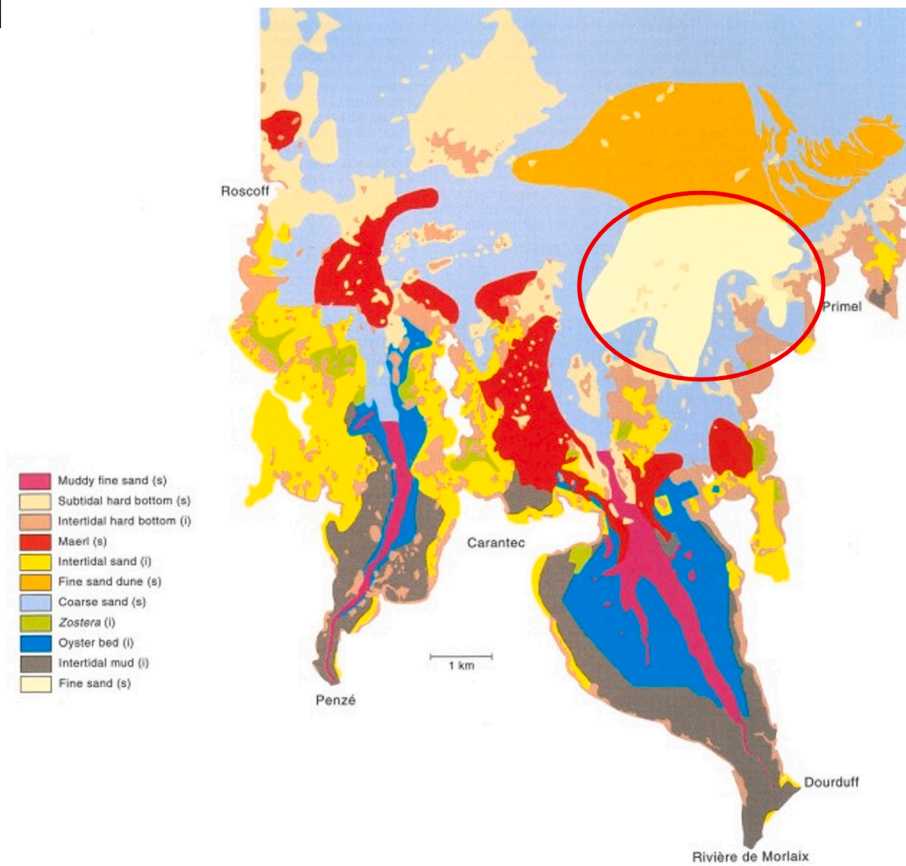
2.3. Suprabenthos sampling

In the English Channel, studies of the suprabenthos, corresponding to organisms that migrate at night in the lower water layers and remain in
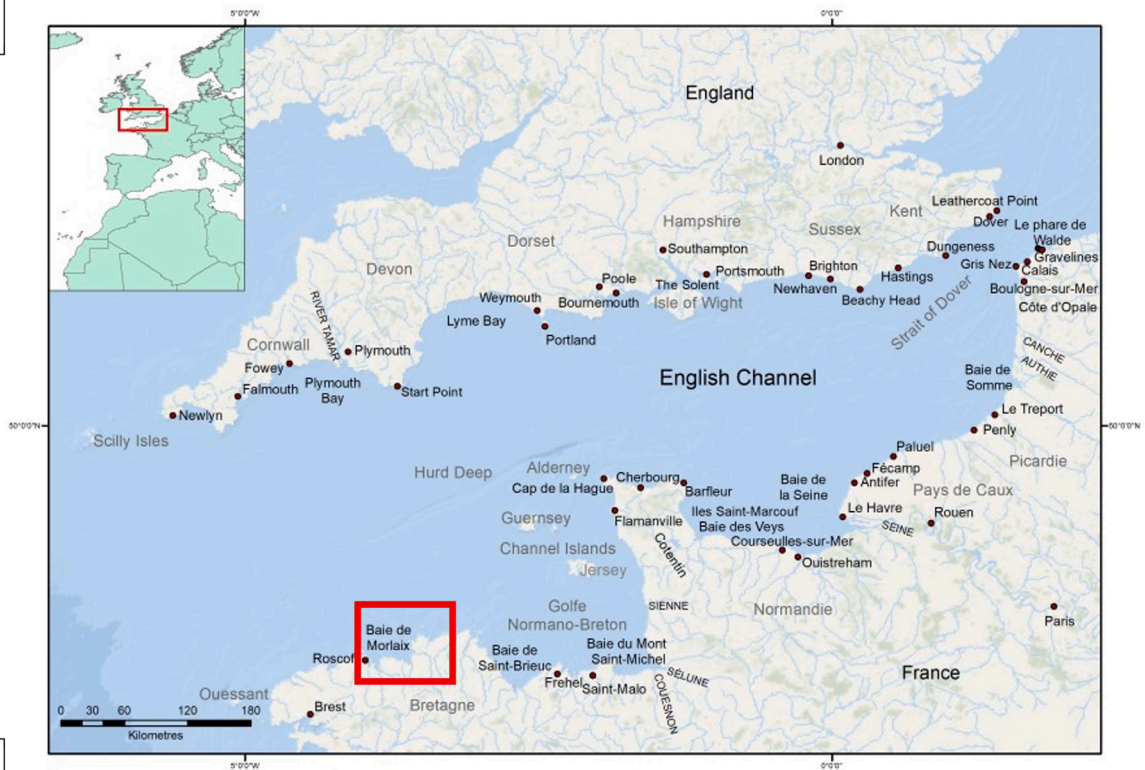
Fig. 1. Map of (a) the English Channel with location of the Bay of Morlaix (from Dauvin, 1999) and (b) the benthic communities from the Bay of Morlaix (from Améziane et al., 1996). i: intertidal zone, and s: subtidal zone. The position of the fine sand Pierre Noire community is indicated by a red circle.

the sediment during the day, has been undertaken since the beginning of the 1990s, not only on the estuarine and shallow coastal zones but also offshore in the circalittoral zones (Dauvin et al., 2000). This overview draws up the general patterns of the suprabenthic communities at the scale of this macrotidal sea, which is subject to high hydrodynamic forcing due to tidal currents but also wind effects mainly in shallow waters (Salomon and Breton, 1991, 1993).

A suprabenthic sledge similar in design to the GIROQ version of the MACER sledge (Dauvin et al., 1995) was deployed on the fine sand PN community on 17 June 1994 with a tidal range of 6 m and a low tide at 17h07 GMT (Dauvin and Zouhiri, 1996). In this sledge, four Working Party 2 (WP2) zooplankton nets (0.5 mm mesh size) were suspended at four levels above the sea bed (Table 1). TSK (Tsurimi-Seiki-Kosakusho) flow meters were placed in the centre of each net to estimate the volume water filtered which in the five hauls (two during the day, two at night, and one at sunset) from 111.4 m^3 to 143.8 m^3 (Table 1). The light level decreased rapidly between 18h00 and 20h00 GMT (Dauvin and Zouhiri, 1996). The abundances of *Ampelisca* are given per 100 m^3 (Table 1).

Four *Ampelisca* species were collected in the sledge, but no individuals were sampled before the sunset (hauls 1 and 2), and some individuals were collected in haul 3 (Table 1) (Dauvin and Zouhiri, 1996). Then, three species (*A. armoricana*, *A. sarsi* and *A. tenuicornis*) showed very high abundances in hauls 4 and 5, while *A. typica* showed low abundance in haul 4 and moderate abundance in haul 5 (Table 1). The abundances of *A. armoricana* and *A. sarsi* increased from net 1 to net 4, while the maximum abundance for the two other species was observed in the lower nets (Table 1). Disparity of abundances in the four nets reflected the difference of swimming activities of the four *Ampelisca* species with higher swimming activity of both *A. armoricana* and *A. sarsi* species than the two others *A. tenuicornis* and *A. typica* (Dauvin and Zouhiri, 1996; Dauvin et al., 2000).

Among all *Ampelisca* collected by the sledge near the sea bottom (0.1 to 1.45 m), the males represented 96.7 % for *A. armoricana*, 92.1 % for *A. sarsi*, 97.4 % for *A. tenuicornis* and 96.4 % for *A. typica* (Dauvin and Zouhiri, 1996). The high percentage of males in the collection shows that the June sampling corresponds to a swarming reproductive emergence of *Ampelisca*. It is noteworthy that all the four *Ampelisca* species show the presence of swimming males at the same date.

A surface planktonic haul with a WP2 zooplankton net (0.5 mm mesh size) was operated on 17 June 1994 at 22h40 (GMT). The mean speed during the 5-min haul was 1.5 knots. Three *Ampelisca* species were collected: *A. sarsi* (16 individuals per 100 m^3), *A. tenuicornis* (6 individuals per 100 m^3) and *A. typica* (1 individuals per 100 m^3). No *A. armoricana* was collected in this zooplankton net. Thus, most of the species were able to reach the sea surface during their diel migration.

2.4. Numerical modelling

To assess the influence of met-oceanic conditions (semi-diurnal tides and wind) on *Ampelisca* behavior in the water column, the ICHTHYOP larval dispersal model is coupled with the hydrodynamic model CROCO. This work concerns coastal/regional scales from o(100 m) to o(10 km) in space and from o(hours) to o(days). Both models are described here as well as the physical and numerical parameters.

Our simulations were based on 30 years old observations (June 1994), during a phase of high abundances of benthic *Ampelisca* populations, 16 years after the disappearance of the *Ampelisca* populations due to the toxicity of the oil from the Amoco Cadiz wreck in 1978 (Dauvin, 1998). However, the hypothesis we tested is timeless: is the nocturnal migrations of the amphipods *Ampelisca* and therefore their dispersal in the water column compatible with the sustainability of these populations in a very small benthic community of fine sands (6 km^2)? *Ampelisca* migrate mainly in the water column each year during their breeding seasons (spring and late summer, the two periods chosen for our simulations). Thought, our simulations are representative of actual repetitive seasonal behavior of amphipod populations confined to a very

Table 1
Number of specimens 100 m^3 of the four Ampelisca species collected in the five hauls on 17 June 1994. Time in GMT of the beginning of the haul. N1: net 1, 0.10–0.40 m; N2: net 2, 0.45–0.75 m; N2: net 3, 0.80–1.10 m and N4: net 4, 1.15–1.45 m above the sea-bed (From Dauvin and Zouhiri, 1996).

	Haul 1: 17h51				Haul 2: 19h57				Haul 3: 20h59				Haul 4: 21h58				Haul 5: 22h59			
Mean depth	17.4				20.8				20.8				20.8				20.0			
	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4
Volume of filtered water in m^3	134	143	130	144	119	125	126	124	112	120	117	115	131	129	130	134	111	120	126	120
A. armoricana	0	0	0	0	0	0	0	0	0.9	0	0	0	23	50	252	282	679	1450	3078	4410
A. sarsi	0	0	0	0	0	0	0	0	4.3	6.9	9.5	0	613	2663	6333	7643	3171	4814	6734	7646
A. tenuicornis	0	0	0	0	0	0	0	0	0	0	1.7	0	132	366	733	449	4050	2847	2588	2400
A. typica	0	0	0	0	0	0	0	0	0	0	0	0	3.8	1.5	0	0	7	56	90	32

constrained space in a very dispersive environments of the North Brittany, in the western part of the English Channel.

2.4.1. Larval dispersal model

The ICHTHYOP larval dispersal model was developed to study the coupling of physical and biological factors on fish larval dispersal (ichthyoplankton) (Lett et al. 2008). Basically, ICHTHYOP integrates the most important processes involved in the life cycle of fish: spawning, eggs, larval stage, proper vertical and horizontal movement of larvae, growth, mortality and recruitment of juveniles. It was first tested on the larvae of small pelagic fish (anchovies, sardines and sardinella) of the major upwelling systems of Peru and Benguela, and then expanded to other coastal and offshore marine ecosystems in various seas of the world, as well as fish larvae in Europe (Tanner et al., 2017; Cabral et al., 2021) and invertebrate larvae (Pires et al., 2013; Woodin et al., 2014; McGeady et al., 2019; 2022). For invertebrate larval dispersion other models had been performed, although Le Goff et al. (2017) had implemented a 3D bio-hydrodynamical model (ECO-MARS3D) providing environmental conditions coupling a population dynamics model and an individual eco-physiological model to simulate the king scallop larvae of *Pecten maximus* distribution in the English Channel. Their results showed that larval dispersion by hydrodynamics explained most of the scallop distribution to understand the geographical distribution of *P. maximus* at the scale of the whole English Channel during its whole life cycle.

To our knowledge, ICHTHYOP has never been used in species without pelagic larvae and direct reproduction (young protected in the marsupium of the females, released on the sea bed near the tube of the adults, and constructing a new tube just after their release) such as amphipod crustaceans (no dispersive larval phase) performing diel migrations like langoustine larvae but spending a limited period of time in the water column. This is the first time that this model has been applied to this type of benthic organism. In our innovative approach, we simulate *Ampelisca* dispersal using the Lagrangian numerical model ICHTHYOP (Lett et al., 2008) used in Ajmi et al. (2022a,b, 2023). ICHTHYOP is a modelling tool to assess how the physical and biological parameters influence the dynamics of pelagic organisms, using passive or active particles, by simulating their horizontal and vertical dispersal (Lett et al., 2008). It computes particle movements (Davidson et al., 1995) using:

$$\frac{DP_p}{Dt} = u_p,$$

where u_p and P_p are the particle velocity and position vectors, respectively. The $\frac{D}{Dt}(\bullet)$ mathematical operator corresponds to the material derivative of a quantity that is moved in space and time by the flow velocity such that:

$$\frac{D(\bullet)}{Dt} = \frac{\partial(\bullet)}{\partial t} + u_p \cdot \nabla(\bullet).$$

ICHTHYOP uses an advection numerical scheme based on the Runge Kutta method (4th order) for each time step after interpolation of the velocity field. This advection scheme is efficient for computing the horizontal and vertical dispersal of organisms as explained by Peliz et al. (2007).

Amphipod swimming patterns are influenced by light and dark, tides, lunar phase, wind speed and direction (and thus indirectly by barometric pressure) as well as temperature (Kaartvedt, 1989). Nevertheless, there are few data on the swimming speed of marine amphipods. Ide et al. (2007) observed the direct swimming behaviour in the shallow-water scavenging amphipod *Aroui onagawae* (Takekawa & Ishimaru, 2000) in relation to chemoreceptive foraging and estimated a high speed of 16.8 cm.s^{-1}. Sainte-Marie (1986) gave other swimming speeds for necrophagous Lysianassid amphipods, i.e., 13.6 cm.s^{-1} for *Anonyx sarsi* Steele & Brunel, 1968: 12.1 cm.s^{-1} for *Onisimus litoralis* (Kroÿer, 1845), which are two to three times faster than for *Orchomella*

pinguis (Boeck, 1861) (7.4 cm.s^{-1}) and *Psammonyx nobilis* (Stimpson, 1853) (4.4 cm.s^{-1}).

In this study, the swimming capability of *Ampelisca* is not directly simulated to ensure a reasonable computational cost. However, to still taking account the position variation due to their swimming, different positions within the water column were simulated, one near the surface and one near the sea bottom (Fig. 2). For both cases, the total population is moved over time and distributed over three positions within the water column due to a repartition by thirds. These positions correspond to vertical computational node positions where the flow velocity and water level are previously computed by the hydrodynamic model and interpolate on the Lagrangian model vertical mesh. To determine the time between each position, a mean speed of 10 cm.s^{-1} for the *Ampelisca* spp. is considered. As the mean depth of the water column at PN is about 20 m, the theorical time for an *Ampelisca* to reach the water surface at a speed of 10 cm s^{-1} would be 200 s, i.e., 3 min 20 s. To be large, a time delay of 5 min is chosen between the surface and bottom position and we have chosen to simulate successive periods of presence near the bottom and near the surface corresponding to diel migrations and moreover compatible with the simulation times (Fig. 2).

The presence of *Ampelisca* in the water column is simulated over a period of 20 min and also during all the night. For each simulation, the number of *Ampelisca* on the PN zone (6 km^2) at the beginning of the simulation is fixed at 1000 and their distribution in the polygon is random.

Sensitivity tests with 10,000 individual particles did not show large statistical differences, compared to 1000 particles. Although, 1000 individuals *Ampelisca* are sufficient to represent their dynamics.

This choice was done to limit the computing time and is suitable regarding our objectives that are to study the ensemble motion of the cloud under met-oceanic forcings. If additional particles have been added, the ensemble motion will not be affected.

2.4.2. Hydrodynamic model

The CROCO (Coastal and Regional Ocean Community) model is applied to compute hydrodynamic conditions. The results (i. e. three-dimensional velocity field and water level) are used to force ICHTHYOP and establish the movement of *Ampelisca* under given hydrodynamic conditions.

In this case, CROCO solves the ocean primitive equations using the Boussinesq approximation and hydrostatic assumptions. It computes the coastal dynamics at different spatio-temporal scales (coastal to regional scales). The simulation of air-sea, sea-bottom and sea-ice interactions is made possible by the coupling with atmospheric, sediment/morphodynamic or ice numerical models (e.g., Pianezze et al., 2018). This coupling is managed in two ways by the automatic coupler OASIS (Valcke et al., 2015). However, the dynamic coupling is not used to simulate larval dispersal because the larvae dynamic does not influence hydrodynamics. An offline forcing of ICHTHYOP by CROCO was chosen to simplify modelling in the first instance, but also because the dynamic coupling for this larval dispersal model is not available and not helpful here. The CROCO velocity field and water level are applied over the entire computational domain of ICHTHYOP after a linear interpolation step to calculate CROCO field on the regular vertical mesh of ICHTHYOP, as illustrated in Fig. 3.

In Cartesian coordinates (x,y,z), the governing equations in CROCO and for horizontal momentum components (u, v) of the flow velocity vector $\vec{v}$ are as follows:

$$\frac{\partial u}{\partial t} + \vec{\nabla} \cdot (\vec{v} u) - fv = -\frac{\partial \phi}{\partial x} + \mathscr{F}_u + \mathscr{D}_u$$

$$\frac{\partial v}{\partial t} + \vec{\nabla} \cdot (\vec{v} v) - fu = -\frac{\partial \phi}{\partial y} + \mathscr{F}_v + \mathscr{D}_v$$
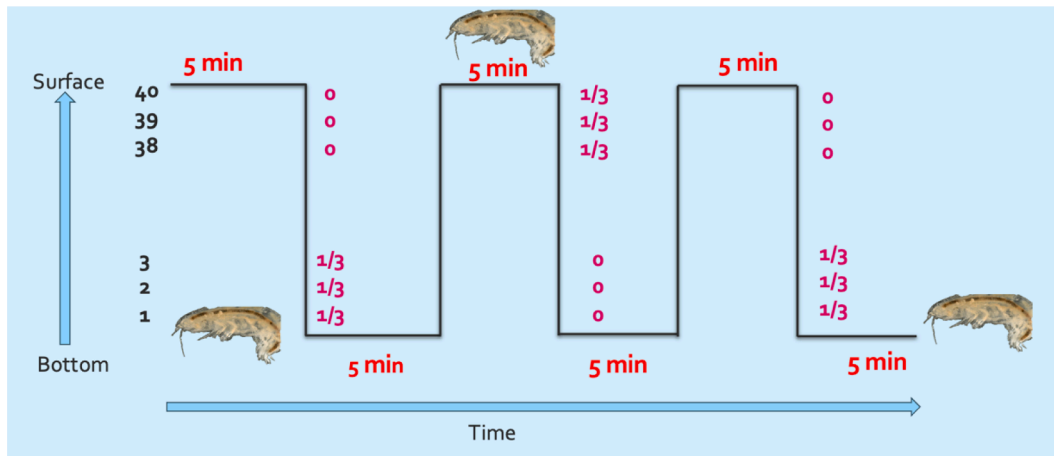
and the continuity equation is:

Fig. 2. Conceptual scheme of *Ampelisca* positions (in grey) over time (horizontal axis) and within the water column (vertical axis). Vertical computational nodes, where *Ampelisca* are located, are named 38,39,40 for the surface case and 1,2,3 for the bottom case. For each case, the total population is injected by thirds (marked by 1/3) on the three nearest vertical nodes. Adapted from Zarrouki (2023).
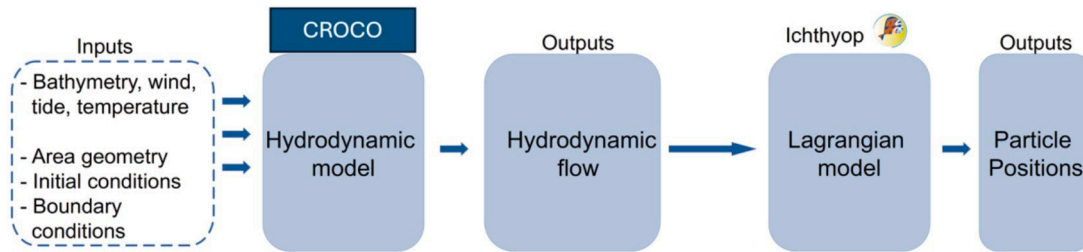

Fig. 3. Conceptual scheme of the coupled model combining CROCO to ICHTHYOP: from input forcing (on the left) to the outputs (on the right). Adapted from Ajmi et al., 2024.

$$\overrightarrow{\nabla} \cdot \mathbf{\overline{v}} = \frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0$$

where $\overrightarrow{v} = (u,v,w)$ is the 3D flow velocity vector. The vertical velocity componenet (w) is computed with the continuity equation. f is the Coriolis parameter, D_u and D_v are the diffusive terms, F_u and F_v are the forcing terms, g is the acceleration due to gravity, ϕ is the dynamic pressure (more details about CROCO in Jullien et al., 2022).

Diffusive terms are computed using turbulence models assuming that the turbulent activity can be represented as a viscous effect depending on both time and space. Thus, for the vertical mixing, the vertical turbulent viscosity is calculated from the RANS (Reynolds Averaged Navier-Stokes) approach using a GLS (General Length Scale) turbulent closure (Warner et al., 2005), the k-ε as proposed by Jones and Launder, 1972. For horizontal mixing, the Smagorinsky model (Smagorinky, 1963) is activated providing a horizontal turbulent viscosity based on the flow velocity gradient and the grid spacing.

The time-evolution of passive tracers (e. g. temperature, salinity) is computed with:

$$\frac{\partial C}{\partial t} + \overrightarrow{\nabla} \cdot (\overrightarrow{v} C) = \mathscr{F}_C + \mathscr{D}_C$$

where C is the tracer concentration. F_C and D_C are the source and diffusive terms, respectively.

Fig. 4 shows the computational domain used to simulate the hydrodynamics in the Bay of Morlaix, which extends from $-4.149°$W to $-3.725°$W and from $48.58°$N to $48.89°$N. The horizontal resolution is set at 50 m and the vertical discretization uses 40 terrain-following levels. The bathymetry is built from a combination of HOMONIM (Shom, 2015) and Litto3d (Shom, 2014) databases.

CROCO was constrained at its wet boundaries (north, east, west) by a tidal forcing derived from the Previmer atlas (Pineau-Guillou et al., 2014). At the surface, wind forcing from CERRA reanalysis (Schimanke et al., 2021) was applied every 3 h. At the initial time, all the hydrodynamic fields are set to zero. They are generated solely by wind forcing and tidal dynamics driven by boundary forcing.

CROCO was run with a time step of 1.5 s over the following time periods: 1994–06–17 to 1994–06–18 and 1994–09–07 to 1994–09–08, using the high-performance computing technique to ensure reasonable computing time: CROCO was run in parallel with simultaneous 140 processors using the MPI (Message Passing Interface) method while ICHTYOP simulations were run in sequential with one processor.

To summarize, the main numerical parameters and physical forcings are listed in the Table 2 for each model and simulated period.

2.5. Main characteristics of the hydrodynamics of the Bay of Morlaix

The hydrodynamic conditions in the Bay of Morlaix are dominated by tidal currents. However, the bay is exposed to north-westerly swells generated by storms in the Atlantic Ocean, which drive the sediment transport of sand (Auffret and Douville, 1974). The tidal regime is semi-diurnal with a slight asymmetry where flood currents are stronger than ebb. The two simulated time periods show different intensities of tidal forcing. The tidal range was about 5 m during the simulated period in June 1994 and about 9 m in September. The current is south-easterly during the flood tide and north-westerly during ebb. During the simulated period in June 1994, the maximum barotropic current (ie. depth-averaged current; it is calculated from the 3D current) varied between 25 cm.s^{-1} during ebb and 30 cm.s^{-1} during flood. In September 1994, the maximum barotropic current varied between 45 cm.s^{-1} and 60 cm.s^{-1}. Furthermore, wind forcing in September 1994, with a north-easterly wind speed at ten meters above sea level of about 7 m.s^{-1},
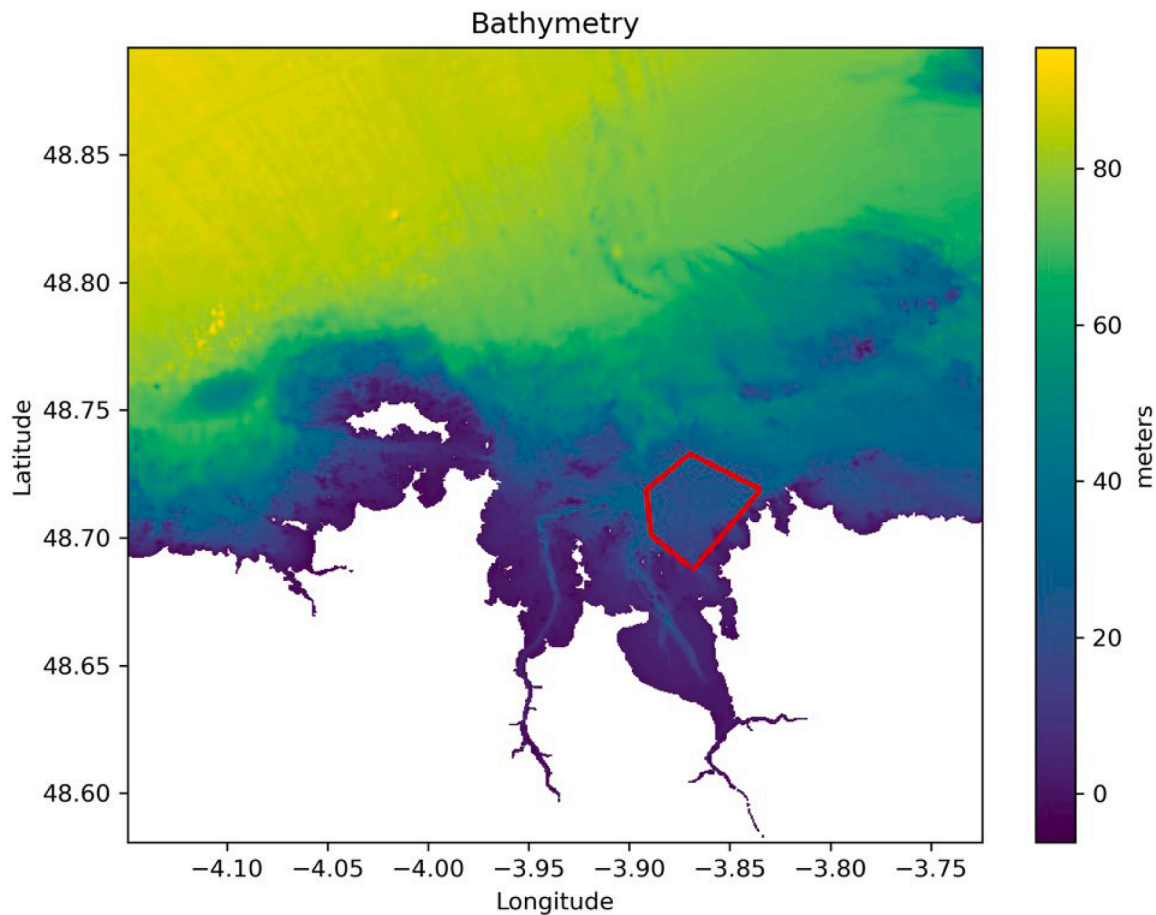
Bathymetry

Fig. 4. Bathymetric map of the computational domain on the north Brittany coast including the Bay of Morlaix and the Pierre Noire site (red box).

Table 2
Summary of the numerical parameters used in CROCO and ICHTYOP for both periods (neap and spring tide).

	Neap tide period	Spring tide period
Horizontal grid spacing for CROCO	Δx= 50 m; Δy= 50 m	Δx= 50 m; Δy= 50 m
Total number grid points for CROCO	623 × 690 × 40	623 × 690 × 40
Number of vertical levels for CROCO	N= 40	N= 40
CROCO time step	Δtc = 1 s	Δtc = 1 s
ICHTYOP time step	Δti = 0.04 s	Δti = 0.04 s
Dates	1994–06–17 1994–06–18	1994–09–07 1994–09–08
Physical forcing for CROCO	- Tide - Wind	- Tide - Wind
Physical forcing for ICHTYOP	- Flow velocity - Water level	- Flow velocity - Water level

induced acceleration during the flood tide and a more pronounced asymmetry between flood and ebb phases.

With regard the sea states, as the wind magnitude reaches a maximum value of 7 m.s^{-1}, the corresponding maximum significant wave height varies between 0.79 m (using the formulation from the WAM model and derived by Pierson et al., 1991 and Chen et al., 2002) and 1.2 m (using the formulation of Pierson-Moskowitz, 1964). Thus, for the simulated time periods, the effects of ocean waves on flow and larval dispersal are assumed to be negligible and have not been taken into account in the simulation. For an energetic event such as a winter storm, wave effects should be included in simulations using for the hydrodynamic part CROCO coupled to the spectral wave model WAVEWATCH-III (Tolman et al., 2016), with the 3D wave forcing of MacWilliams et al., (2004) based on the vortex force formalism.

3. Results

3.1. Neap tide period

The dispersal of *Ampelisca* is simulated for 17 June, from 21h00 GMT (start) at the beginning of the diel migration to 21.20 (end), introducing alternating periods of 5 min presence near the bottom and 5 min near the surface. Fig. 4 show the distribution of the 1 000 *Ampelisca* individuals at 21h05 and 21h20, respectively.

20 min after start time, only a few *Ampelisca* are left inside the PN area, their numbers increasing from 17 at 21h06, to 34 at 21h10, then 54 at 21h15 and finally 58 at 21h20. These results illustrate that, for short times spent in the water column, only limited numbers of *Ampelisca* are dispersed (less than 6 %), which means that 94 % of *Ampelisca* remain inside the PN habitat. An automatic counting method permitted to account the number of *Ampelisca* in the Pierre Noire domain.

In a second step, the dispersal of *Ampelisca* is simulated from 21h00 GMT on June 17 (start) at the beginning of the diel migration to 6h00 on 18 June GMT (end of the night and end of diel migration), introducing alternating periods of 5 min presence near the bottom and 5 min near the surface over a total duration of 9 h.

During the night, the *Ampelisca* individuals are dispersed in two main directions, to the west and northeast. A total of 334 *Ampelisca* leave the PN area at the end of the night (Fig. 5; Table 3). At mid-low-tide 2.00 on June 18, more than 48 % of *the Ampelisca* leave the PN area. Then, at the end of the simulation, 67 % are again present in the PN area, showing a return of about 15 % of the *Ampelisca* population after a transport
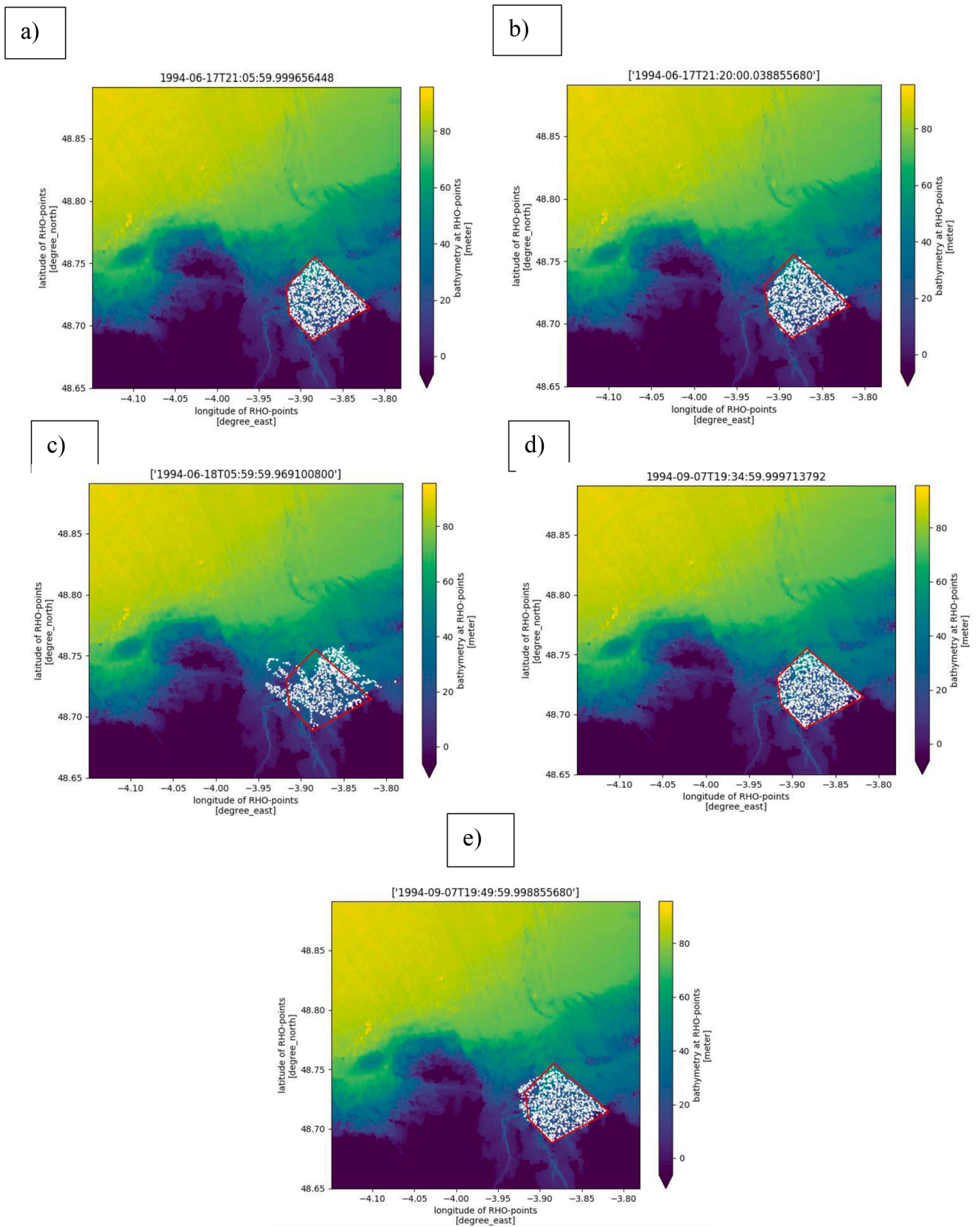
Fig. 5. a) Map of *Ampelisca* positions (white circles) at 21.05 for 17 June 1994; b) at 21.20; c) at 6.00 for 18 June 1994; d) Map of Ampelisca positions (white circles) at 19.35 on 7 September 1994; and e) at 19.50. The red polygon represents the boundaries of the *Ampelisca* positions at the start time of 21.00 on 17 June 1994 (i.e., start time).

Table 3
Number of *Ampelisca* present inside the Pierre Noire habitat for the night of 17 June 1994 at 21h00 GMT to 6h00 GMT on 18 June 1994.

GMT hours	Number of *Ampelisca* in the Pierre Noire habitat
21h05	984
22h00	824
23h00	688
00h00	564
01h00	525
02h00	516
03h00	529
04h00	536
05h00	545
06h00	666

outside the zone (Table 3).

3.2. Spring tide period

The simulations of 17 and 18 June 1994 correspond to a neap tide situation (slow currents, with maximum speed less than 1 m.s^{-1}) and wind speeds less than 5 m.s^{-1}. This illustrates a period of weak agitation and slow currents during the breeding of *Ampelisca* in June (Dauvin and Zouhiri 1996). Therefore, in a second step, the dispersal is simulated for an equinoctial spring tide in September 1994 (7 and 8 September; maximal current speed about 2 m.s^{-1}), also corresponding to the breeding season of the bivoltine species (two broods per year, such as with *A. tenuicornis* and *A. typica* (Dauvin et al., 2021). The wind was slightly above 7 m.s^{-1} during the night of 7 to 8 September 1994. Similar simulations as applied in June were replicated during 20 min and through the night for the September period.

In a first step, the dispersal of *Ampelisca* on September 7 is simulated from 19.30 (start) to 19.50 (end), introducing alternating periods of 5 min at the bottom and 5 min on the surface. In 20 min, only a few *Ampelisca* leave the area and their numbers increase from 9 at 19.35 to 49 at 19.40, then 65 at 19.45 and finally 84 at 19.50 (Fig. 6). Again, these results illustrate that, for short times spent in the water column, few amphipods are dispersed (less than 10 %), which means that 90 % of *Ampelisca* remain inside the PN zone, but the loss is nevertheless about twice that found in June.

In a second step, the simulations start at 19h30 GMT on 7 September and end at 7h30 GMT on 8 September, when the night duration is 12 h compared with 9 h in June. To follow the dispersal of *Ampelisca* during the night of September 7 to 8, several successive situations are set up with alternating periods of 5 min at the bottom and 5 min on the surface throughout the duration of the simulations. Only situations at the following times are represented here: 23h30 GMT, 2h30 GMT, 5h30 GMT and 7h30 GMT (Fig. 6).

These simulations show a very large dispersal of *the Ampelisca* individuals. After 5 min, at 19.35, the *Ampelisca* remains inside the PN area (Fig. 6). At 23.30, there is a strong dispersal following the direction of the current, preferentially to the west according to the tidal currents (Fig. 6). At 2.30, dispersal continues towards the west, with the most westerly swarm of *Ampelisca* being transported to the south while a small proportion is transported to the northeast (Fig. 6). At 5.30, there is a reversal of the currents and a certain number of *Ampelisca* return to their initial position in the PN area, while there is no more transport to the northeast (Fig. 6). Finally, at 7.30 or after 12 h in the water column, the dispersal is once more important with transport to the west and northeast (Fig. 6).

Table 4 reports the number of *Ampelisca* remaining within the PN area hour by hour. At low tide, only 11 % of the *Ampelisca* remains in the PN area, and therefore a very large proportion has left (89 %). 12 h after release, i.e., at 7h30, 73 % have left the PN area and 27 % remain, which illustrates a certain return of the *Ampelisca* to their initial position (16 %).

4. Discussion and perspectives

Our study simulating *Ampelisca* dispersal represents the first application of the ICHTHYOP model to a benthic organism that spends a very short time in the water column. The observations of Dauvin and Zouhiri (1996) serve as a basis for the simulations using ICHTHYOP and CROCO numerical modelling during a neap tide corresponding to the reproductive swarming period (17–18 June 1994) of *Ampelisca* in the PN fine sand community of the Bay of Morlaix. This community covers a very small surface-area (6 km^2) and comprises a very dense *Ampelisca* population which persist along the time (Dauvin, 1987; Poggiale and Dauvin, 2001; Dauvin et al., 2021).

Ampelisca swim near the bottom at dusk just after sunset and become very abundant in the suprabenthic layer in the early hours of the night (Table 1). Even though males outnumber females in the water column (Dauvin and Zouhiri 1996), our simulations do not test the male/female differences. Most of the *Ampelisca* males are pelagic and only low numbers of males are found in the benthic samples (Sheader, 1977). The pelagic life of males is short and they die after mating which takes place in the water column (Ruppert et al., 2004). After mating, the females return on the sea bed where they construct their tubes, spawning their eggs into their marsupium. In the Bay of Morlaix, the duration of embryo development is about one month (Dauvin, 1987). The juveniles come out of their mother's tube and then build their own tubes nearby without a larval dispersal phase.

To compare this neap tide situation during periods of low agitation despite the lack of available observational data, we simulate the nocturnal dispersal during a period of equinoctial spring tide at the end of summer 1994 (7–8 September), with a longer night of 12 h as against 9 h, again with light wind conditions comparable to those recorded in June. The differences in dispersal between these two periods can then be attributed almost exclusively to differences in current velocity: less than 1 m.s^{-1} in June and more than 2 m.s^{-1} in September.

There is good evidence that forcing by tidal currents is related to the dispersal of *Ampelisca* in the Bay of Morlaix for both periods (June and September) during variable durations in the water column ranging from 5 min to 12 h. The number of *Ampelisca* transported outside the fine sand PN zone increases with the duration of their presence in the water column and the maximum current speed. In our simulations, we consider the *Ampelisca* individuals as passive particles without any horizontal proper movement. Therefore, they are passively driven horizontally by tidal currents and wind effects. With a mean speed of vertical displacement of 10 cm.s^{-1} similar to other marine amphipods, this speed is between 5 and 10 % of the horizontal current speeds in June and September 1994, and we assume that an hypothetical horizontal *Ampelisca* displacement is insignificant in comparison with the tidal forcing currents. However, they can migrate vertically, so we positioned the Ampelisca swarm in the bottom water layer (up to 3 m above the sea bed) and then near the surface (down to 3 m below the sea surface) for alternating successive periods of 5 min.

The dispersal of *Ampelisca* occurs in two main directions, to the west and to the northeast of the PN fine sand habitat. The dispersal results from tidal current activity and is much stronger in September (Fig. 6) during a period of spring tide than in June during a period of neap tide. The strong tides in September lead to significant losses, with a maximum of 88 % of Ampelisca leaving the PN zone as against 40 % in June. This swimming behaviour throughout the night appears incompatible with the long-term sustainability of populations at the PN Station: high populations of *Ampelisca* have been maintained in the PN fine sand community over several decades (Dauvin et al., 2021). It is therefore very likely that diel migration of *Ampelisca* in the water column is of such short duration that it allows the sustainability of these dense populations.

However, enhanced transport of *Ampelisca typica* has been observed by Macquart-Moulin et al. (1987) due to its advection during diel migration associated with Mistral winds blowing for several days on
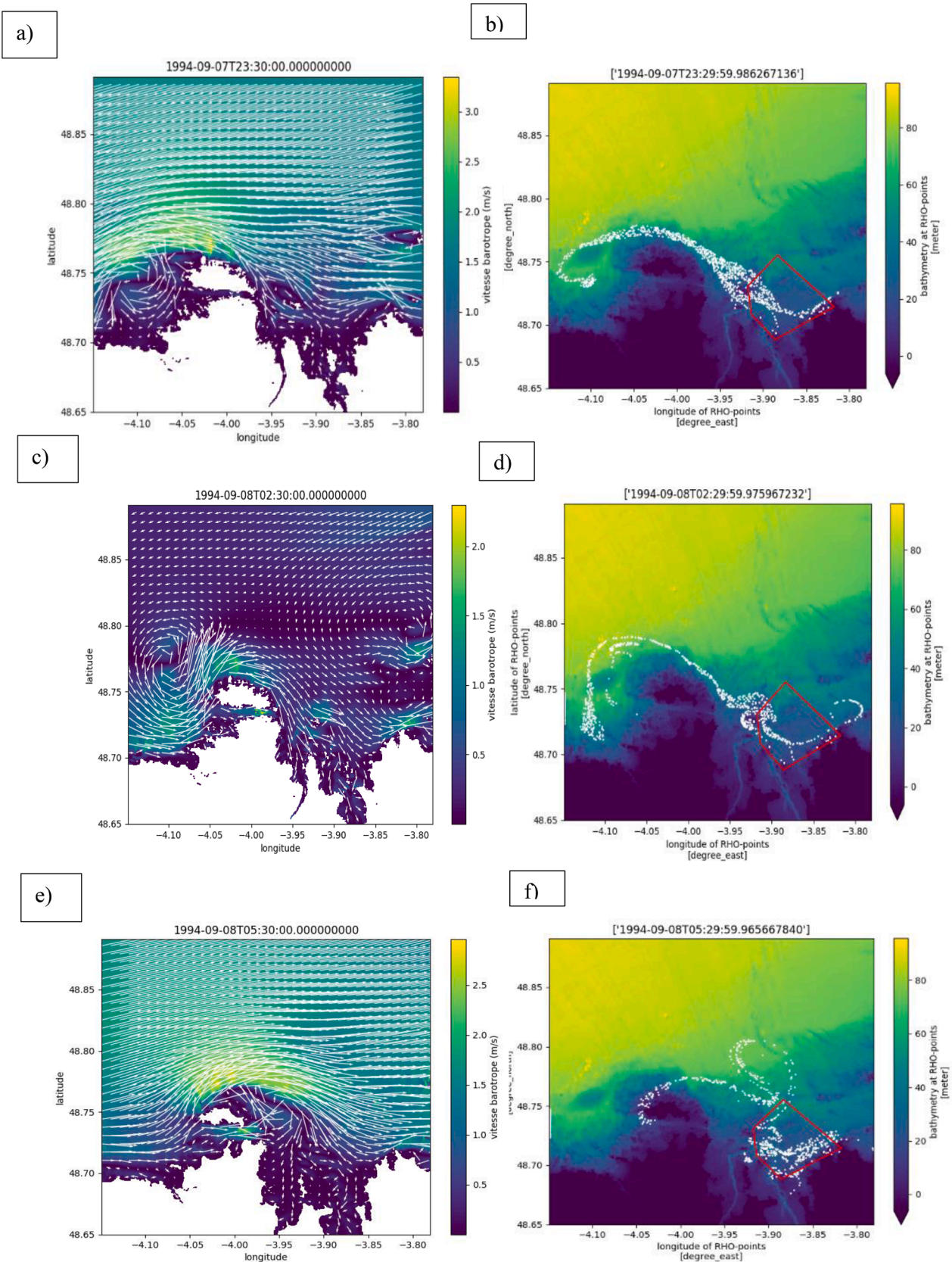
Fig. 6. Successive maps of the *Ampelisca* positions on 7 September 1994 at (b) 23h30 GMT, (d) 2h30 GMT, (f) 5h30 GMT and (h) 7h30 GMT on 8 September 1994 with associated barotropic tidal currents at the same moments (a, c, e, g). The red polygon represents the boundaries of the initial position of *Ampelisca* at 19.30 on 7 September 1994 (i. e. start time).
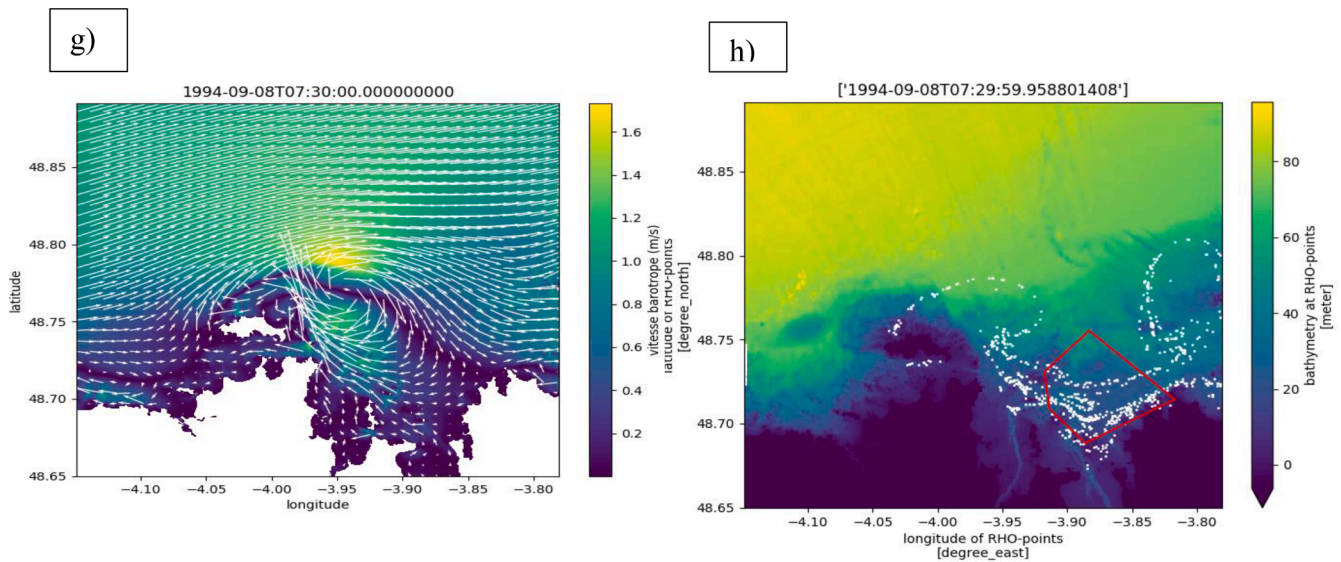
Fig. 6. (*continued*).

Table 4
Number of *Ampelisca* present inside the Pierre Noire habitat for the night of 7 September 1994 at 19h30 GMT to 7h30 GMT on 8 September 1994.

GMT hours	Number of *Ampelisca* in the Pierre Noire habitat
19h35	984
20h30	784
21h30	562
22h30	342
23h30	206
01h30	114
02h30	156
03h30	296
04h30	338
05h30	384
06h30	361
07h30	271

nearshore and offshore zones in the Marseille area (North-western part of the Mediterranean Sea). This phenomenon can disperse *A. typica* over long distances from shallow waters to deeper areas offshore outside the initial habitats and thus causes significant losses from the coastal population.

The simulations were run for 20 min, with the presence of *Ampelisca* alternately near the bottom and then near the surface for 5 min, indicating that *Ampelisca* remains mainly in the PN zone during short migrations in the water column. The loss is more marked during spring tide than neap tide, and represents less than 10 % of the individuals.

However, our study does not simulate the behaviour of males compared to females. The former is more adapted to a pelagic (and therefore dispersive) life and die after the fertilization phase in water. It is more efficient for the permanency of the population, that the females rapidly return to their benthic habitat to rebuild a tube rather than make several migrations in the water column up to the surface during the night and then construct a new tube at each diel migration. In addition, a brief presence in the water column reduces the risk of being consumed by fish that feed on small crustaceans such as amphipods and *Ampelisca* which emerge from the benthos at dusk and dawn (Dauvin et al., 2000).

Our study does not simulate active vertical swimming activity (i.e. displacement of about 10 cm.s^{-1}). Such behaviour had been used to simulate the migration dynamics of juvenile salmonids in the San Fransico Bay and its tributary rivers (Sridharan et al., 2023). Similar movement rate of the fish relative to the water over a short timescale (a few minutes) should be used for the *Ampelisca*.

Furthermore, the high abundance of *Ampelisca* corresponds to muddy fine sand and fine sand habitats in a weakly dispersive hydrodynamic regime (Dauvin et al., 2021). After the Amoco Cadiz spill and the disappearance of *Ampelisca* on the PN station, as other fine sand habitat enclaves favourable for *Ampelisca* populations in North Brittany, the recolonization was slow (a decade). It was effective, bearing witness to the arrival of individuals probably from the south of Brittany. Ten years after the oil spill, *Ampelisca* populations again dominate the abundance of the Morlaix Bay site (more than 30,000 individuals per m^2 in the early 1990s) (Poggiale and Dauvin, 2001; Dauvin et al., 2021).

In conclusion, our results suggest that the ICHTHYOP model can be used to simulate the dispersal of *Ampelisca* during its diel migration and that short-lived vertical migrations in the water column are clearly more consistent with the sustainability of the dense benthic populations of the PN fine sand community in the Bay of Morlaix. Moreover, the colonisation processes of these insular *Ampelisca* populations remain and the following question arises. Is the distance between fine sand enclaves compatible with a gradual recolonization of the Bay of Morlaix owing to the residual drift from southern Brittany to northern Brittany due to the dispersed individuals outside the fine sand communities during the diel *Ampelisca* migration for the PN station (see Tables 3 and 4).

In the future, it would be interesting to use the same hydrodynamic and larval dispersal models to simulate the movements of these amphipods and clarify the process of gradual recolonization of species distributed in isolated habitats.

CRediT authorship contribution statement

Jean-Claude Dauvin: Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Conceptualization. **Assia Zarrouki:** Formal analysis. **Martial Boutet:** Validation, Software, Formal analysis. **Anne-Claire Bennis:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declared that there is no competing interest.

Data availability

Data will be made available on request.

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