

Ontogenetic optimal temperature and salinity envelopes of the copepod *Eurytemora affinis* in the Seine estuary (France)

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ABSTRACT

Temperature and salinity are important factors shaping the habitats of estuarine ectotherms. Their respective effect varies along the life history moments of species with a complex life cycle. Estuarine species, particularly those living in the salinity gradient, are concerned by habitat changes that can reduce their fitness. Consequently, efforts to define the importance of those two environmental variables on developmental stages are required to enable forecasting estuarine species' future distributions. The present study focuses on the main component of the Seine estuary's zooplankton, i.e. the calanoid copepod *Eurytemora affinis*, and aims: (i) to establish the role of temperature and salinity in designing the habitat of *E. affinis* within the Seine estuary; and (ii) to model the habitat of three groups of *E. affinis* defined through the life cycle as follows: all larval instars (N1–N6), the first to fourth juvenile instars (C1–C4), and the pre-adult and adults instars (C5–Adults). For this purpose, data from intensive field studies of zooplankton sampling during 2002–2010 were used. The fine-scale data, i.e., every 10–20 min, on density and abiotic conditions (salinity, temperature) provided inputs for the computation. We established regions in salinity-temperature space where the three groups of developmental instars exhibit higher densities. The computed habitats differ between developmental groups. In general, the preferendum of salinity increases with ontogeny. The optima of temperature are rather constant between developmental stages (~14 °C). Our model can be used to determine *E. affinis* functional habitat (i.e., the spatial relation with structuring factors), to carry out retrospective analysis, and to test future distributions. The present study also emphasizes the need of data from appropriate sampling strategies to conduct habitat definition.

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1. Introduction

Defining the suitable habitat of a species is a fundamental step in adequately projecting the effect of environmental changes on species ranges. Habitat suitability models have been commonly used in the development of predictive biogeography (Guisan and Thuiller, 2005; Elith and Leathwick, 2009). These models rest upon the knowledge of the species' ecological niche, i.e., the range of tolerance of a species to several environmental factors (Hutchinson, 1957). Habitat suitability models build multivariate representations of a species' niche by relating spatial data of species occurrence or density to key environmental variables and then

projecting this niche into future geographic space according to different scenarios (Guisan and Thuiller, 2005). Such models were used on several occasions to assess the potential effect of global change on marine copepod distribution (Helaouët and Beaugrand, 2007, 2009; Beaugrand and Helaouët, 2008). Their use has recently been expended to estuarine copepods with a special focus on the invasion process (Chaalali et al., 2013a, 2013b).

At the interface between the ocean and continents, estuaries are systems with important ecological stakes, but also under numerous abiotic and biotic pressures (Kimmerer and Weaver, 2013). Consequently, estuarine populations represent valuable models to understand the responses to diverse forms of environmental changes. Living in a dynamic ecosystem, such as estuaries, is challenging for zooplanktonic organisms and so is the modeling of these organism dynamics. Those organisms have to face the burden of dispersive and advective losses, variations of abiotic (e.g., salinity) and biotic factors in their environment, and anthropogenic pressure.

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To face such adversity, estuarine copepods have developed behavioral and physiological strategies to maintain the core of their population in a specific area that present the optimal conditions for their development and reproduction. Among the different mechanisms developed by estuarine copepods to maintain their position in an ideal region, one can find a high reproductive rate (Gupta et al., 1994; Devreker et al., 2009), remaining near the bottom to avoid washout by tidal or flood flows (Morgan et al., 1997; Devreker et al., 2008), mechanisms for clinging to the bottom (Shang et al., 2008; Ueda et al., 2010), and tidally-oriented vertical migration (Schmitt et al., 2011; Kimmerer et al., 2014; Chew et al., 2015). At small scale, a range of salinity often defines the optimal habitat. Indeed, salinity alone plays a salient role in the distribution of the estuarine plankton (Laprise and Dodson, 1994; Jassby et al., 1995) and may also contribute to the separation of the habitat of two sibling species (Favier and Winkler, 2014). The habitat can also be differentiated between the different phases of a life cycle (Albouy-Boyer et al., 2016) and the type of reproduction. For instance, in the low-salinity zone, nauplii of the free-spawning copepod *Sinocalanus sinensis* were found downstream compared to adults and juveniles (Suzuki et al., 2012), while egg-carrying copepods, such as *E. affinis* and *Pseudodiaptomus inopinus*, showed the opposite pattern (Devreker et al., 2010; Suzuki et al., 2012).

The second parameter that defines the optimal habitat of copepods is temperature. As euryhaline ectotherms, deviations from isosmotic salinities and temperature rise increase metabolic demand in copepods (Goolish and Burton, 1989; Angilletta et al., 2002; Brown et al., 2004). And in the field, maximal densities of copepods are found when temperature varies within a given range (Mouny and Dauvin, 2002; Mialet et al., 2010).

With the increasing effect of climate change and anthropogenic pressure on the estuarine systems, the optimal geographic area in which the planktonic organisms are able to thrive is subject to change. Increase in flow intensity can change the range of salinity where the center of the population is located (Kimmerer et al., 2014, see their Fig. 6). Additionally, temperature variation and associated water discharge may shift the spatial distribution of copepods as observed in 2005 for *Eurytemora affinis* in the Seine estuary (Devreker et al., 2010). Any prediction of the consequences of those environmental changes requires the current habitat to be defined and to relate such habitat with environmental factors. It is even more essential to have a predictive tool at one's disposal for species that play a salient role in the system they inhabit.

E. affinis is widely distributed in the Northern Hemisphere (Lee, 2000) and is one of the most important estuarine zooplankton species. This species is an important link between primary production and higher trophic levels such as larval fish (Winkler et al., 2003; Moderan et al., 2010). Any change in the population of this copepod may influence the entire estuarine food web dynamics.

In the Seine estuary, copepod species are distributed along the salinity gradient (Mouny and Dauvin, 2002). *E. affinis* is known to tolerate a large range of salinities (Devreker et al., 2007) and to dominate the zooplankton community in the oligo- and mesohaline zones of the Seine estuary (Mouny and Dauvin, 2002) while presenting a limit of distribution in water salinities <18. In the Seine estuary, *E. affinis*' preferendum of salinity varies also with developmental stages, with adults and pre-adults instars more often distributed in the 5–15 salinity zone, and nauplii in the 0–10 salinity zones (Devreker et al., 2010). Prior laboratory studies of post-embryonic development and reproduction suggest that *E. affinis* achieves maximized fitness at a salinity of 15 (Devreker et al., 2007, 2009). *E. affinis* density variability over a tidal cycle is driven by suspended particle matter (SPM), salinity and temperature (Devreker et al., 2010). Devreker et al. (2010) noticed seasonal variation in the size of *E. affinis*' spatial habitat. At the annual scale

the population density is driven by river discharge, chlorophyll *a*, and temperature (Devreker et al., 2010). Field investigations revealed maximum densities of *E. affinis* in the Seine when temperature ranges between 10 and 15 °C (Mouny and Dauvin, 2002). In the lab, Devreker et al. (2004, 2009) found optimal temperature for reproduction and naupliar survival to be around 15 °C, but the temperature range was limited to two values: 10–15 °C. Souissi et al. (2016) confirmed that *E. affinis* of the Seine estuary can be acclimated in the laboratory at a summer like temperature of 20 °C. Low oxygen concentrations act as a “barrier effect” to the expansion of *E. affinis* in the Scheldt (Mialet et al., 2010). Nevertheless, oxygen concentrations in the Seine estuary over the past two decades were above the threshold values of 3 mg/L that constrains *E. affinis* habitats (Mialet et al., 2010; Chambord et al., 2016), i.e. always higher than 5 mg/L (Romero et al., 2016).

Temperature- and Salinity-dependent models were developed for population of *E. affinis* in other temperature estuaries, including the Gironde in France (Chaalali et al., 2013b) and the Nanaimo River Estuary in Canada (Strasser et al., 2011). Unfortunately, both models did not consider the different developmental stages. Despite all the available data (Devreker et al., 2008, 2010), there is no existing habitat model for the different developmental stages of *E. affinis* in the Seine estuary. The aims of the current study are:

- (i) To determine, as an example of practical study, how salinity and temperature shape the habitat of *E. affinis*' developmental stages.
- (ii) To model the habitat of *E. affinis*, for three different groups of developmental stages, in relation to salinity and temperature.

In the present study, the term “habitat” refers to the physical area in terms of salinity and temperatures where the species live. This paper presents the data and the approach used to model the habitat of the different developmental stages of the copepod *E. affinis* in the Seine estuary. Implications of the results for copepod niche modeling are discussed and potential sources of the inter-population variation in this key estuarine species are outlined.

2. Material and methods

2.1. Sampling area

The Seine Estuary is the largest megatidal estuary along the English Channel. It is characterized by an annual maximum tidal range of about 8 m near the mouth at Le Havre, France. The mean annual discharge measured at the Poses dam, in the upstream part of the estuary, is about 480 m³s⁻¹ with a maximum of nearly 2300 m³s⁻¹ and a minimum of 40 m³s⁻¹ (Dauvin, 2006; Massei et al., 2010). All samplings considered in the analysis were conducted in the middle part of the estuary, near the Normandy Bridge (Fig. 1), where the salinity gradient during the tidal cycle shows the largest range (Devreker et al., 2008). Samplings were conducted on board the research vessels *Côte d'Aquitaine* and *Côte de la Manche*.

2.2. Sampling strategy and measurements

For each campaign, a high-frequency Eulerian sampling strategy was employed, with the frequencies being 1 sample collected every 10, 15 or 20 min for a duration varying between 24 and 48 h. Each campaign had the same sampling method and zooplankton sample processing. Details on the method and processing are given in (Devreker et al., 2008). In brief, a 5 L Niskin bottle was used to sample zooplankton every 10 (in 2002), 15 (2004) or 20 (the other dates) min at the sub-surface and near the bottom. Samples were

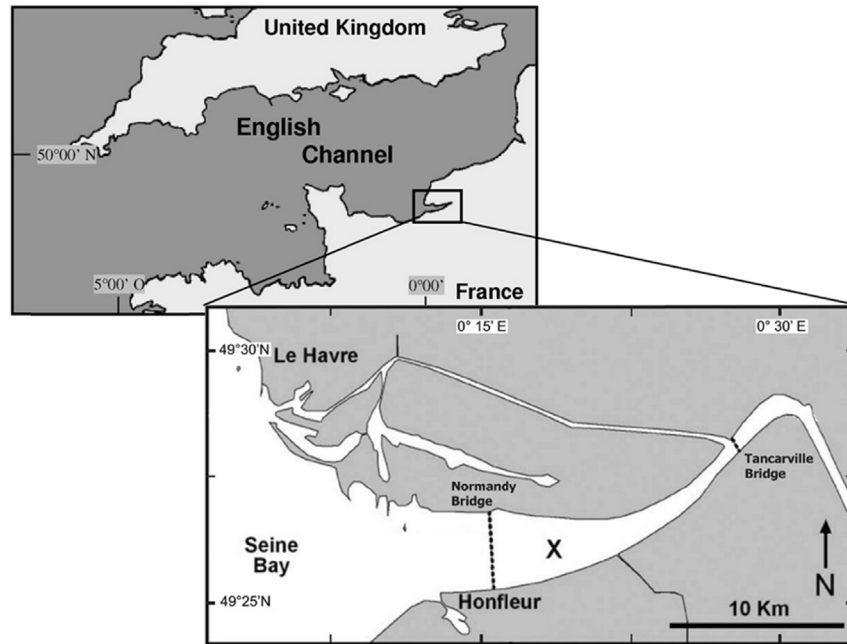


Fig. 1. Maps of the English Channel, and the Seine estuary showing the sampling site near the Normandy Bridge (black cross, 49°26,065 N 00°16,920 E).

filtered through a small 40 μm net, concentrated into a 500 ml container and preserved with buffered formaldehyde. All instars were counted in each sample. We here considered the samples from both the surface and bottom water. A conductivity-temperature-depth sensor (CTD, Seabird SBE 25) provided the temperature, salinity, and depth values for each sample. Salinity was measured using the Practical Salinity Scale.

2.3. Database

With the 18 campaigns combined, we obtained a database covering the 4 seasons over 8 years (2002–2010) and gathered a total of 2001 samples (Table 1).

Developmental stages were pooled in 3 different groups according to their similarity during the tidal cycle (Devreker et al., 2008). The groups of developmental stages were as follows: nauplii (N1–N6), copepodids (C1–C4) and pre-adults with adults (C5–Adults). The last group will be referred to as “adults” group from here on.

2.4. Data analysis

The salinity habitats of *E. affinis*’ developmental stages were defined following several steps. First, classes of salinity were defined to have the most homogeneous distribution of observations (Fig. 2 Step1). The optimal salinity classes (every 2.5 between

Table 1

General information on the temperature measured and the number of samples at the surface and the bottom water for each sampling campaign following tidal cycles. The discharge at Poses dam during the sampling is also provided.

Campaign		Temperature ($^{\circ}\text{C}$)						Discharge (m^3/s)		
		Surface			Bottom			Poses		
Nb.	Date	Mean	Std.	Nb. Obs.	Mean	Std.	Nb. Obs.	Mean	Std.	
1	May 2002	15.37	0.28	72	14.85	0.52	72	511	0.00	
2	May 2004	15.26	0.56	197	14.54	0.85	197	508	0.00	
3	March 2005	4.89	0.23	38	5.02	0.32	38	423	16.53	
4	April 2005	12.32	0.65	42	11.71	1.05	42	428	6.45	
5	May 2005	15.17	0.63	44	14.99	0.84	44	340	1.00	
6	June 2005	17.64	0.77	70	17.08	0.93	70	200	5.5	
7	July 2005	20.96	0.54	68	20.75	0.62	68	203	8.03	
8	September 2005	19.74	0.53	70	19.71	0.57	70	272	13.96	
9	December 2005	8.61	0.06	44	8.68	0.09	44	209	7.65	
10	June 2008	18.08	0.75	45	17.69	0.84	45	450	0.00	
11	July 2008	18.97	0.81	46	18.77	0.80	46	388	72.18	
12	September 2008	16.90	0.29	36	16.79	0.25	36	343	0.00	
13	November 2008	11.99	0.19	37	12.11	0.20	37	545	32.16	
14	February 2009	6.48	0.11	37	6.47	0.08	37	563	0.00	
15	April 2009	13.98	0.91	25	13.64	0.87	26	395	0.00	
16	June 2009	19.68	0.68	39	19.34	0.77	39	186	0.00	
17	June 2010	17.65	0.89	37	17.09	1.10	36	201	14.14	
18	August 2010	19.96	0.19	37	20.16	0.21	38	238	12.73	
Total				1000				1001		

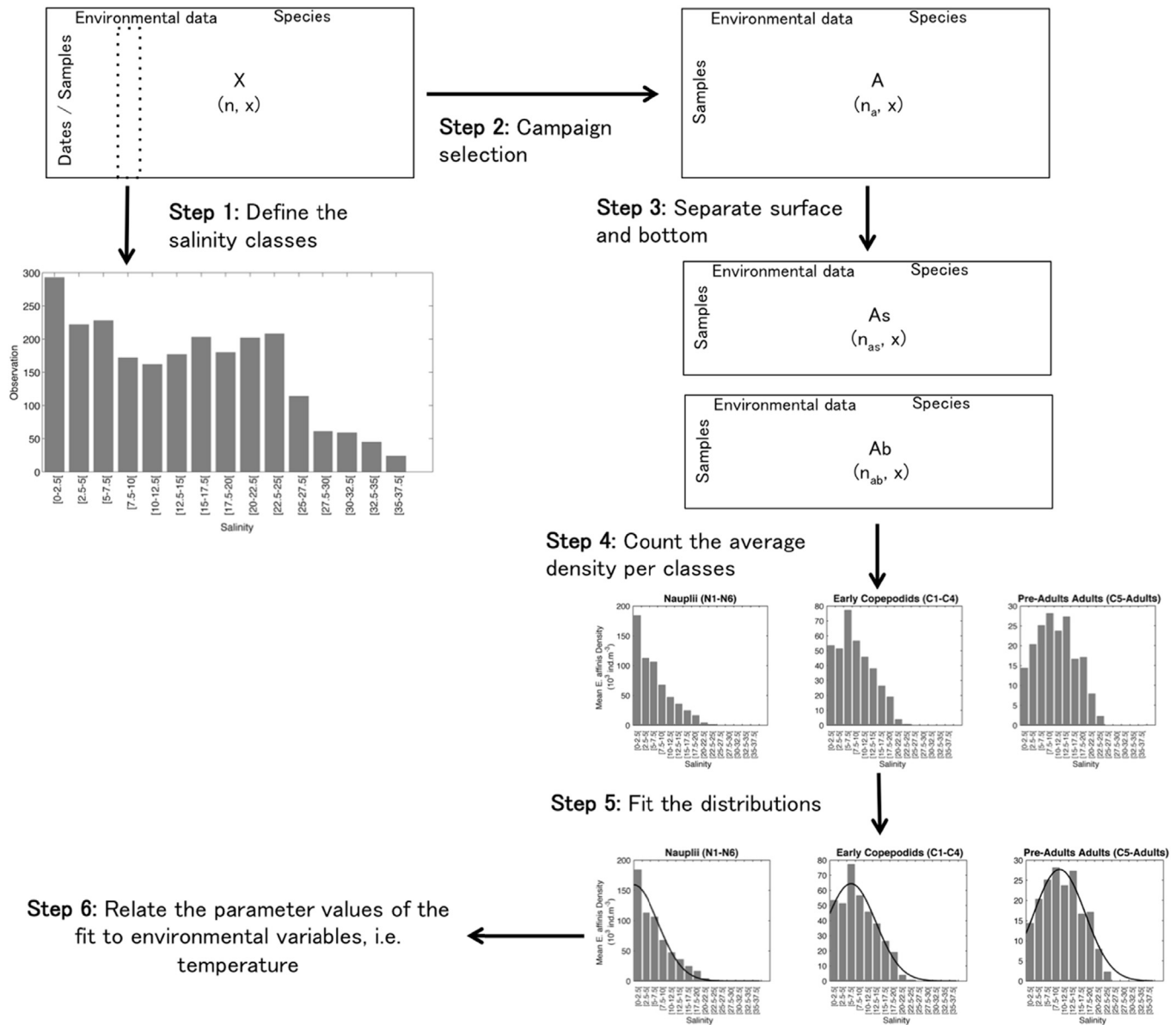


Fig. 2. Diagram of the statistical method used to define the salinity habitat of the species present in the sample collected in the Seine estuary during the different campaign (Step 1–5). The final step (step 6) combines all fits per campaign and link the fit parameter values to the environmental conditions.

0 and 37.5) were similar to those used by Devreker et al. (2010). Each campaign was then extracted from the matrix gathering all data (Fig. 2 Step 2). Bottom and surface sampling were subsequently separated (Fig. 2 Step 3) and the distribution of the mean density of copepods was determined as a function of salinity intervals for both surface and bottom layers (Fig. 2 Step 4). As in Devreker et al. (2008, 2010), the distribution of mean density of copepods as a function of salinity was fitted by a Gaussian function (Fig. 2 Step 5) using the curve fitting toolbox of the software MATLAB R2011 (The Mathworks, Inc.):

$$D_S = a_S e^{-\frac{(S-\mu_S)^2}{2\sigma_S^2}} \quad (1)$$

The Steps 1–5 were repeated for each sampling date. We therefore obtained for each campaign and each depth, three relations between the density and salinity (Eq. (1)), one for each group of developmental stages. Each campaign and depth were

attributed an average temperature. The height (i.e., maximal density value, $a_{S,group}$) and parameters of the Gaussian fits (Eq. (1)), i.e., mean ($\mu_{S,group}$), and standard deviation ($\sigma_{S,group}$) were then related to the temperature (Fig. 2. Step 6). Only the fit exhibiting an arbitrary defined threshold r^2 value > 0.5 were considered for this step of the analysis. Relation with river discharge was also investigated during the study. No relation with river discharge was found. The results of this step are provided in the supplementary materials (Supplementary material 1–3).

The variation of the Gaussian fit parameters was then investigated through the coefficient of variation (CV). When large variations were observed, different fits were tested using the curve fitting toolbox of the software MATLAB R2011 (The Mathworks, Inc.). Otherwise, when the variation was weak or not significant, we considered a constant value for the parameter and fit once again the mean density of copepods as a function of salinity.

Gaussian distribution provided a good fit between temperature

and $a_{S,group}$ (i.e., the maximum density) and $\mu_{S,group}$ (i.e., the optimum salinity). Using the Gaussian distribution, we estimated the habitat of *E. affinis* in relation to both temperature and salinity as follows:

$$\mu_T = a_\mu e^{-\frac{(T-\mu_\mu)^2}{2\sigma_\mu^2}} \quad (2)$$

$$a_T = a_a e^{-\frac{(T-\mu_a)^2}{2\sigma_a^2}} \quad (3)$$

$$D_{S,T} = a_T e^{-\frac{(S-\mu_T)^2}{2\sigma^2}} \quad (4)$$

with T , temperature values and S , salinity values.

We then produced 3D visualization of the habitat for the three developmental stage groups. For that, we took the range of salinity and temperature values measured in the field (T : 4–24 °C, S : 5–25) at the sampling station, and using equation (4) computed the density over these ranges with an increment of 0.1 for both temperature and salinity. The software MATLAB R2011 (The Mathworks, Inc.) was used to plot the density in relation to temperature and salinity providing a visual on how the habitats differ between the three groups. To make a comparison with tracers of water masses, we add a temperature-salinity diagram on the 2D view of these 3D graphs. Finally, we compared the habitats of the three groups using the procedure proposed by Beaugrand and Helaouët (2008). In brief, we first evaluated the breadth of the habitat for densities > first quartile (Case 1), densities > median (Case 2) and, densities > third quartile (Case 3) for each group using Euclidian distance. And in each case, we then examined whether the groups have different habitats applying Multiple Response Permutation Procedures (Zimmerman et al., 1985). The number of permutations was fixed to 10,000 permutations as proposed by Beaugrand and Helaouët (2008). Developmental instar groups were compared two by two for each of the three cases.

3. Results

3.1. Distribution related to salinity

Mean *E. affinis* densities were highest in low salinities (0–17). The densities of each group are higher during spring, and reach their lowest values at the end of summer and in winter for both layers.

The salinity range with the maximum mean density of *E. affinis* (hereafter referred to as “optimal salinity”) varied not only between groups of instars but also as a function of months (Table 2, Fig. 3). Between groups, increase in the optimal salinity with developmental stage appeared as the common pattern for the bottom layer. Nauplii were concentrated in lower salinities, adults in the highest salinities, and copepodids in between (Fig. 3). The pattern was nevertheless disrupted with some instance of all developmental groups gathered in low salinities (Fig. 3 June 2009). In the surface water, no pattern could be identified. This is associated with a 24% of fits with low goodness-of-fit (i.e., $r^2 < 0.5$) for surface data (Table 2).

There was a strong inter-annual variation in the distribution of *E. affinis* in relation to salinity. Between June 2005, 2008, 2009 and 2010 the optimal salinity varied between 0 and 10.09 for nauplii, between 0 and 14.17 for copepodids, and between 0 and 14.68 for adults.

3.2. Relation with temperature

Among the Gaussian fit parameters, the standard deviation (σ) exhibited the least variation between the different campaigns for each developmental group and at both depths (Table 3). Also, except in one case, no significant relation was found between σ and temperature (Spearman's $\rho < 0.5$, $p > 0.05$; Supplementary Material 2).

Therefore, we chose to keep σ constant and perform the fitting once again. For each group of instars and each depth, the value of the standard deviation was set (fixed) as the mean over all campaigns (Table 4).

We combined the data for close temperatures to obtain average mean values for small temperatures ranges. Values obtained for the campaign conducted in March 2005 (Grey stars, Fig. 4) were discarded for the fit, being outliers for most cases (i.e., mean and height for the three groups) and associated with the peculiar condition of anomalously low temperatures in late winter (Devreker et al., 2010). Results of the fits performed on the bottom layer data provided a good relation between temperature and optimal salinity (μ) and maximum density (a). The relation followed a normal distribution with higher optimal salinities obtained for a temperature between 12.5 and 14 °C (Fig. 4).

On the other hand, the fits performed on the surface layer data exhibited low goodness-of-fit with r^2 values only >0.6 in two cases, i.e., the height for copepodid and adults. The results for the surface layer were, consequently, not considered in the following and last step of the habitat definition.

3.3. Computed habitats

In view of the aforementioned results, the habitats were defined for each group of developmental stages, at the bottom layer, and considering only two parameters, i.e., temperature and salinity (Fig. 5). The shape of *E. affinis*' habitat differed between instars' groups. Although they exhibit similar optimum temperature (~14 °C), optimal temperature range (in dark red, Fig. 5) is smaller for the copepodids and bigger for the adults. Copepodids are found at higher levels of salinity than nauplii, but at lower levels compared to adults. The habitats of nauplii had an ellipsoid shape while that of older developmental instars tend toward a more convex polygon, with a center of gravity, and a shape similar to a butterfly wing. The limits of the habitats in terms of salinity move slightly to higher salinities with the developmental stages; starting from a range of salinities of 0–18.5 for nauplii to 1–19 for adults. Thermal limits are consistent between developmental stages ranging between 9 and 20 °C. The density patterns suggest that the habitats of the instars' group overlapped. Differences with the temperature-salinity diagram, i.e., tracers of the water masses, were noticed especially for all copepodids and adults. Nevertheless, the cores of the habitats for all groups are slightly shifted compared to the mixing line, revealing the influence of biological activities. Additionally, the breadth of the habitats decreased with ontogeny, and whatever the case, nauplii, juvenile and adults presented significantly different habitats (Table 5).

4. Discussion

4.1. Niche – habitat – and our approach

Niche modeling is linked to Hutchinson's niche concept (Hutchinson, 1957), which states that species have ecological preferences and are more likely to be found at sites where they encounter appropriate living conditions. Two types of niches can be distinguished, the fundamental and the realized one. The

Table 2
Results of the Gaussian fit of the mean copepod density (ind. m⁻³) as a function of salinity interval in surface and bottom water for each group of instars in the different campaigns. The height (i.e. maximal density value, $a_{s,group}$ in Eq. (1)), mean ($\mu_{s,group}$ in Eq. (1)), and standard deviation (Std, $\sigma_{s,group}$ in Eq. (1)) are provided. Values of r^2 below the threshold values of 0.5 are highlighted in bold grey.

	Campaign	Surface				Bottom					
		Stage	Group	Height	Mean	Std	r^2	Height	Mean	Std	r^2
1	May 2002										
	Nauplii			50.72	10.09	5.97	0.81	172.28	13.02	6.26	0.89
	Copepodids			25.45	5.43	2.84	0.80	166.88	12.29	5.23	0.95
2	Adults			8.90	4.65	1.50	0.94	50.09	10.72	6.32	0.75
	May 2004										
	Nauplii			34.42	0.00	4.32	0.80	159.34	0.00	7.21	0.94
3	Copepodids			20.37	3.46	2.23	0.96	64.45	6.19	7.24	0.94
	Adults			6.13	4.62	2.37	0.97	27.70	9.78	7.49	0.92
	March 2005										
4	Nauplii			19.39	0.00	2.46	0.96	113.73	2.38	6.34	0.96
	Copepodids			8.26	0.00	6.04	0.60	69.41	2.25	7.70	0.98
	Adults			4.35	0.00	1.97	0.05	NaN	NaN	NaN	NaN
5	April 2005										
	Nauplii			10.16	4.60	3.90	0.77	116.69	6.92	6.63	0.78
	Copepodids			20.98	17.25	1.73	0.15	79.33	13.38	6.66	0.75
6	Adults			20.19	17.04	2.09	0.92	32.88	18.21	8.85	0.90
	May 2005										
	Nauplii			9.97	8.93	1.73	0.95	45.35	10.75	4.82	0.97
7	Copepodids			8.54	10.48	2.32	0.97	37.32	12.26	4.42	0.91
	Adults			5.22	9.88	3.01	0.88	17.89	15.27	5.83	0.94
	June 2005										
8	Nauplii			8.25	7.95	5.94	0.55	35.70	10.09	6.69	0.84
	Copepodids			4.59	7.46	3.31	0.60	33.22	14.17	5.57	0.87
	Adults			3.11	7.12	1.39	0.43	11.48	14.68	6.45	0.86
9	July 2005										
	Nauplii			1.22	3.90	12.21	0.56	17.97	5.78	3.12	0.99
	Copepodids			1.62	10.35	3.62	0.92	14.78	4.73	4.70	0.96
10	Adults			0.27	12.04	7.03	0.87	9.01	6.98	2.62	0.99
	September 2005										
	Nauplii			4.64	5.41	2.66	0.50	10.27	7.42	2.77	0.98
11	Copepodids			1.70	6.24	1.92	0.94	4.69	6.87	3.10	0.89
	Adults			0.60	7.56	4.44	0.99	8.04	0.00	5.96	0.98
	December 2005										
12	Nauplii			1.17	0.00	8.15	0.93	3.90	1.88	4.83	0.98
	Copepodids			3.83	5.30	4.95	0.96	9.26	6.60	3.70	0.99
	Adults			0.49	0.00	13.20	0.21	2.25	7.58	2.99	0.98
13	June 2008										
	Nauplii			10.23	0.00	12.21	0.26	65.62	6.69	4.00	0.69
	Copepodids			1.14	7.88	10.18	0.16	31.40	8.74	3.07	0.87
14	Adults			3.08	9.59	3.31	1.00	19.94	9.51	3.38	0.92
	July 2008										
	Nauplii			28.70	0.00	4.87	0.85	59.15	2.82	4.35	0.97
15	Copepodids			4.69	0.00	8.60	0.53	9.37	4.99	4.11	0.96
	Adults			1.96	0.00	8.67	0.82	5.46	4.87	3.95	0.89
	September 2008										
16	Nauplii			4.94	0.00	4.45	0.94	23.65	0.00	4.84	0.98
	Copepodids			8.93	0.00	2.34	0.93	24.76	0.00	4.85	0.99
	Adults			4.12	0.00	1.64	0.99	4.92	3.18	2.59	0.99
17	November 2008										
	Nauplii			1.29	1.25	2.16	0.79	1.21	4.44	7.42	0.91
	Copepodids			3.35	3.02	1.31	0.99	7.40	6.42	3.22	0.99
18	Adults			1.98	3.15	1.45	0.99	2.10	8.53	2.01	0.99
	February 2009										
	Nauplii			7.07	6.05	1.85	0.31	65.01	3.28	2.23	0.68
19	Copepodids			0.42	0.00	29.37	0.06	15.29	2.92	2.71	0.95
	Adults			1.01	6.09	1.54	0.32	3.66	0.00	13.87	0.62
	April 2009										
20	Nauplii			27.86	0.00	13.58	0.38	140.76	6.33	5.04	0.87
	Copepodids			11.00	7.35	4.16	0.99	33.14	9.38	6.86	0.97
	Adults			7.13	11.08	1.23	0.43	27.36	11.65	7.41	0.92
21	June 2009										
	Nauplii			42.24	7.41	2.65	0.99	35.55	0.00	11.31	0.69
	Copepodids			14.25	6.49	3.66	0.70	30.32	0.00	8.72	0.86
22	Adults			6.58	8.32	1.52	0.83	16.31	0.00	9.41	0.88
	June 2010										
	Nauplii			2.05	0.00	10.19	0.33	70.57	0.01	3.23	0.87
23	Copepodids			3.04	8.93	1.16	0.00	8.97	7.60	3.37	0.98
	Adults			3.63	0.00	4.95	0.97	6.29	4.29	5.47	0.94
	August 2010										
24	Nauplii			0.56	1.14	6.72	0.73	30.20	0.00	3.88	0.97
	Copepodids			1.96	0.00	2.78	0.99	7.33	0.73	5.35	0.99

Table 2 (continued)

Campaign	Surface				Bottom				
	Stage Group	Height	Mean	Std	r^2	Height	Mean	Std	r^2
Adults		0.10	8.89	0.61	1.00	1.96	8.45	2.27	0.97

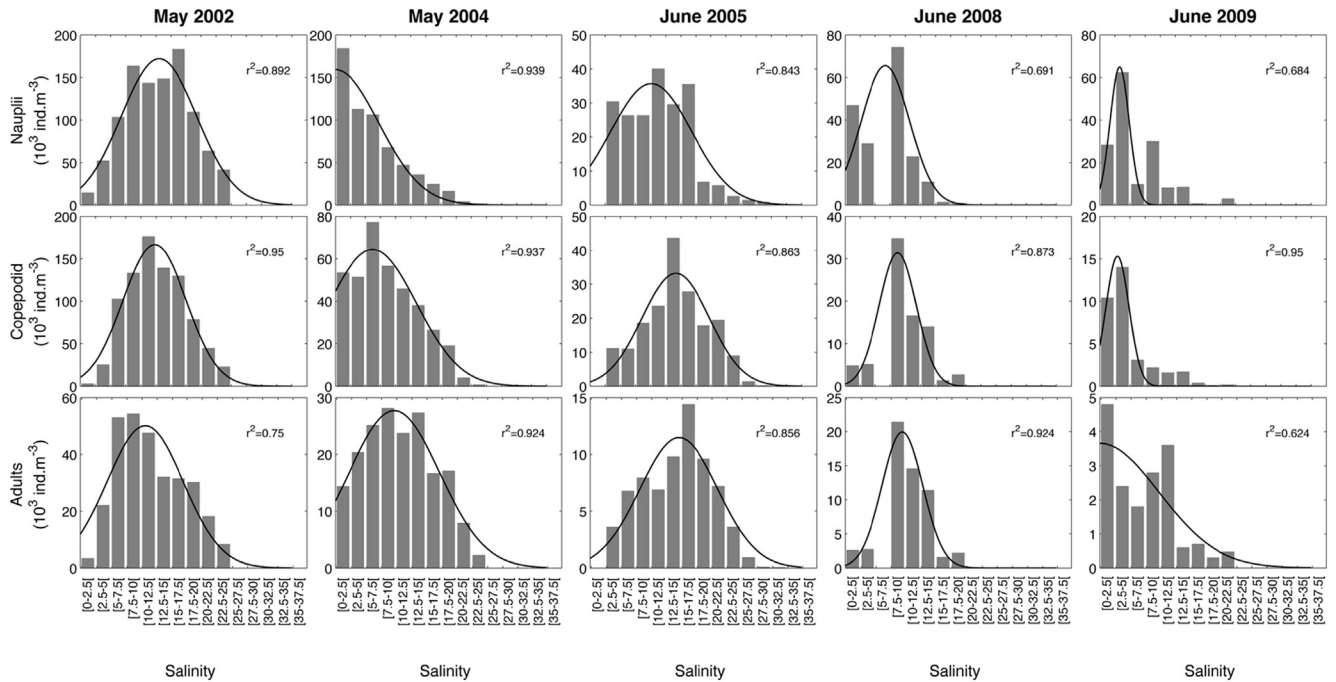
Fig. 3. Examples of Gaussian fit to the mean copepod density (ind.m^{-3}) as a function of salinity interval in the bottom water for each instars group.

Table 3

Coefficient of variation (CV) for the parameters, i.e., height (a), mean (μ), and standard deviation (σ) of the Gaussian fits (Eq. (1)) obtained over the 18 campaigns.

Stage Group	Surface			Bottom		
	Height a	Mean μ	Std σ	Height a	Mean μ	Std σ
Nauplii	1.08	1.04	0.58	0.83	0.90	0.44
Copepodids	0.89	0.71	0.56	1.10	0.67	0.37
Adults	1.10	0.78	0.73	0.92	0.69	0.48

Table 4

The standard deviation (σ) values of the Gaussian fits obtained over the 18 campaigns.

Stages	Depth	Mean σ_T	Std σ_T	Nval
Nauplii	Surface	4.87	2.84	14
	Bottom	5.16	2.26	18
Copepodid	Surface	3.29	1.84	13
	Bottom	4.88	1.79	18
Adults	Surface	3.28	2.40	13
	Bottom	5.33	2.54	17

fundamental niche is resulting from the physiological response to environmental factors; whereas, the realized niche encompasses other processes such as dispersion, competition, and predation.

Different techniques exist to determine the contribution of environmental factors to the definition of the ecological niche of a species and depend on the type of available data (Hirzel et al., 2002, 2006). The estimations of the niches based on observational data

can only provide the realized niche (Pearson and Dawson, 2003). Therefore, one can consider that we only provided the realized niches of three groups of instars of *E. affinis* in the Seine estuary. For Chase and Leibold, a niche should be defined as the environmental conditions allowing a species to have a positive or null growth (Chase and Leibold, 2003). On the other hand, Helaouët and Beaugrand (2009) showed that the use of both the fundamental and realized niches (*sensu* Hutchinson) enables a better understanding of the environmental conditions that allow the growth of the population. The present study did not estimate the egg production rate of *E. affinis*, nor did it investigate the growth rate. To avoid the debate on the proper use of the term “niche”, we opt to use the term “habitat” instead of “niche” in this study, with the habitat being the physical area where the species live. The niche (*sensu* Chase and Leibold) of *E. affinis* from the Seine in terms of salinity and temperature was previously determined with a mechanistic model calibrated on laboratory data (Strasser et al., 2011). Combining mechanistic results, such as those of Strasser et al. (2011), with correlative results, such as ours presented here, has great potential for predicting future species’ ranges and their success in a new habitat (Kearney and Porter, 2009). The combination can be as simple as comparing the predictions from both approaches for a given species (Strasburg et al., 2007), or using the mechanistic approach to refine the space in which to apply correlative predictions (Austin, 2007).

Methods relating species density data from field sampling to environmental factors are based on the use of a variety of regressions analysis. Commonly, normal distributions are used to describe the habitat of copepod species in relation to temperature (Helaouët and Beaugrand, 2009; Fort et al., 2012; Chaalali et al.,

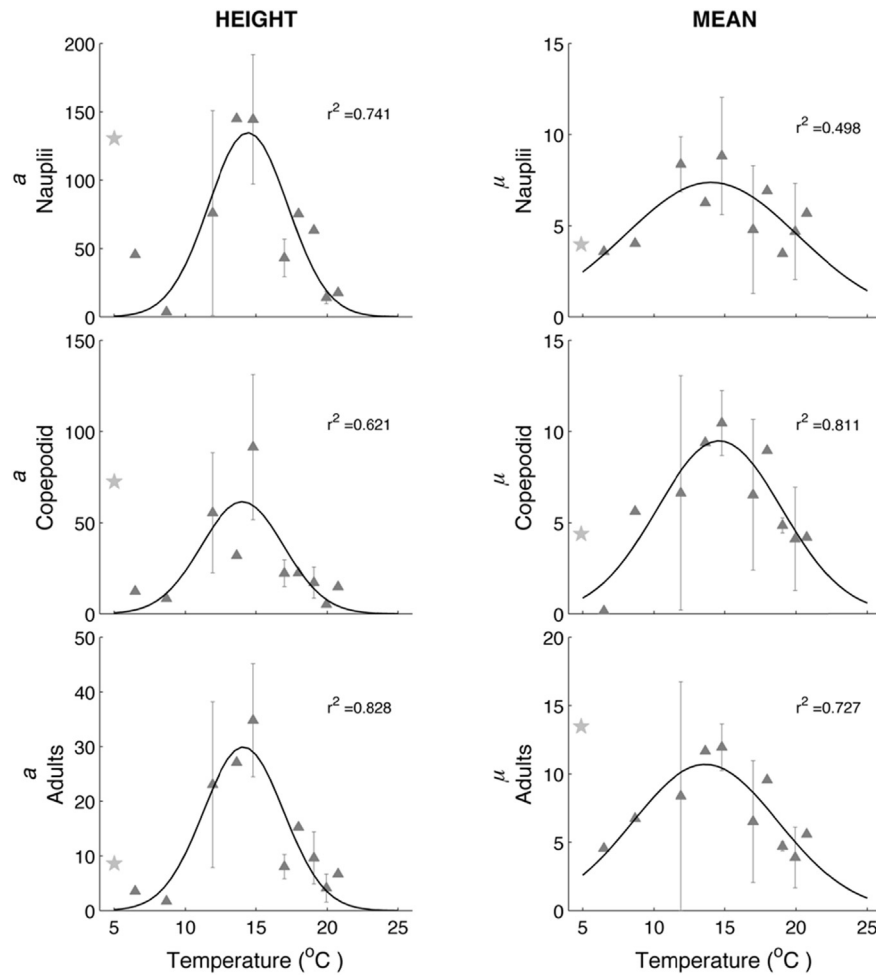


Fig. 4. Relation between temperature and the height (a) and mean (μ) values of the fit performed on the mean copepod density (ind m^{-3}) as a function of salinity interval in bottom waters for each group of instars. Grey stars indicate outliers associated with exceptionally low temperature values (cf. text).

2013a, 2013b). Nevertheless, depending on the copepod species and the sampling protocol, the relation with salinity can be either linear or Gaussian as is the case for, respectively, *E. affinis* and *Acartia bifilosa* in the Gironde (Chaalali et al., 2013b). The exploratory phase of our study revealed that, among the different models tested (i.e., Gaussian, Polynomial 3, Sum of Sine, Exponential 2), the Gaussian model was the most adapted to represent the relations studied here. In our study, the *E. affinis* densities related to salinity exhibited a maximum flanked by two decreasing slopes, a typical characteristic of a Gaussian distribution. The discrepancies between the populations of *E. affinis* from the Seine and from the Gironde have both physiological and behavioral explanations, discussed hereafter.

Identifying the descriptors that determined or limited the presence of a species requires observation with sufficient frequency to permit their analysis. The data analyzed here contained more than 1000 samples for each depth layer. This is an important repository, which after careful screening supported our statistical approach to defining the habitat of *E. affinis*. The high-frequency sampling conducted for all campaigns allowed us to have a similar number of data as other studies on copepod habitats (Chaalali et al., 2013a). Additionally, our data come from different campaigns, but use the same sampling strategy, thus limiting bias and avoiding supplementary steps in the analysis (i.e., homogenisation; Chaalali et al., 2013b). Few studies have investigated all

developmental stages while studying copepod population dynamics in estuaries (Peitsch, 1995; Köpcke, 2004) and none have ever investigated the habitats of all developmental stages despite the previous observation of differences in the breadth of ecological niches between early juvenile and adults copepod (Reygondeau and Beaugrand, 2011). Our study constitutes, therefore, a pioneer investigation on the difference in the habitat occupied by all different stages of an estuarine copepod. This could be a precursor to a future modeling approach taking into account all processes occurring at the population level.

Our approach to defining the habitat is generic and can be applied to any other species. Nevertheless, it is crucial to consider the ecology of the studied organism and have data resulting from an appropriate sampling strategy. In our case, for instance, without any samples from the bottom, we may not have been able to establish any link between environmental factors and *E. affinis* density in the Seine estuary. Indeed the core of its population is found in the bottom layer (Mouny, 1998; Devreker et al., 2008), and restriction to surface sampling would only lead to a truncated view of the species distribution. In fact late developmental stages of *E. affinis*, and particularly adults, have the capacity to increase their jump frequency in turbulent environments, thus allowing them to keep the bulk of the population near the bottom and in a suitable habitat (Michalec et al., 2015). For each campaign, Eulerian sampling for at least an entire tidal cycle was conducted. Our data

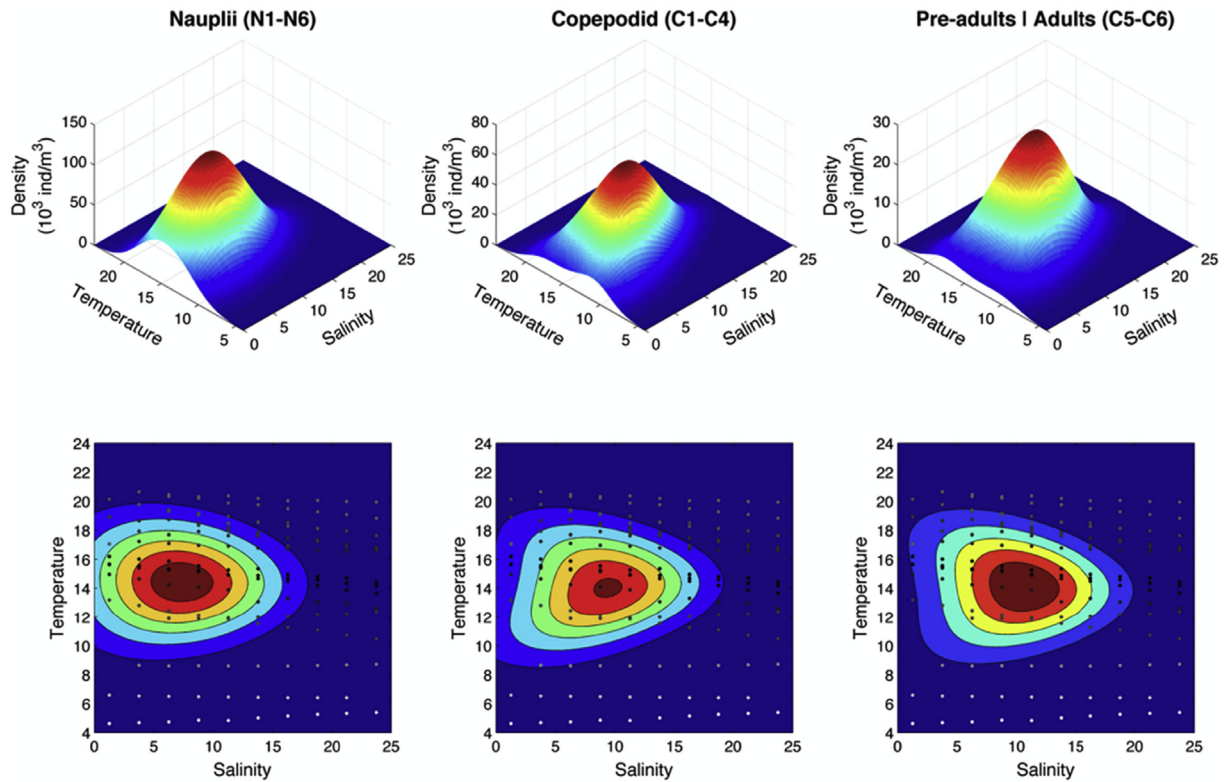


Fig. 5. Top. Simulated habitats of *E. affinis* instars' groups in the bottom waters of the Seine estuary in relation to salinity and temperature. Colors are linked with the density (blue low density, red high density). Bottom. 2D projections of the habitats (color) on classical temperature-salinity graphs (gray scale points). The points represent the measured temperature per classes of salinity for each campaign. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5

Results of the comparison tests based on estimations of the density of the three groups of instars in relation to temperature and salinity. Case 1: density >1st quartile, Case 2: density > median, Case 3: density >3rd quartile. P: probability that the habitats of the three groups are different.

	----- Habitat breadth -----			----- P -----		
	Nauplii	Copepodids	Adults	P _{N,C}	P _{N,A}	P _{C,A}
Case 1	0.2762	0.2672	0.2472	<0.0001	<0.0001	<0.0001
Case 2	0.2106	0.1821	0.1727	<0.0001	<0.0001	<0.0001
Case 3	0.1361	0.1154	0.1110	<0.0001	<0.0001	<0.0001

integer consequently the pattern of variation in population structure between flood and ebb tide (Devreker et al., 2010). Additionally, the high-frequency sampling, performed during each campaign, captured the changes in population dynamics occurring over short timescales (Devreker et al., 2010). The use of Niskin bottles and 40 μm mesh nets allowed the capture of all developmental stages (Devreker et al., 2008) and confer a considerable asset for studying the difference between instars. Finally, the constancy in the sampling protocol and counting method among the different campaigns was undeniably a key point for facilitating the combination of datasets.

4.2. Inter-population differences in *E. affinis*' habitat

Our study provided compelling evidence that *E. affinis*' habitat in the Seine estuary is strongly related to temperature and salinity. This result was expected for such ectothermic species living in an estuary. Indeed, the importance of temperature and salinity as parameters governing both the spatial and temporal changes in estuarine zooplankton have been revealed independently of the

latitude (Bollens et al., 2011; Marques et al., 2011; Palma et al., 2013). We also obtained a relationship between optimal salinity and temperature. Combined effects of these two parameters were previously observed on the physiology of *E. affinis* including larval development (Devreker et al., 2004), protein expression (Kimmel and Bradley, 2001), survival (Gonzalez and Bradley, 1994), and multi-generational responses (Souissi et al., 2016).

On the other hand, considering its dynamic environment, *E. affinis* can be affected by the river discharge in other estuaries (Castel, 1993; Kimmel and Roman, 2004). We did not observe any relation between the river flow and density for *E. affinis* in the Seine estuary (supplementary materials). This could be linked to the fact that, in the Seine estuary, *E. affinis* concentrates at the bottom layer (Mouny, 1998; Devreker et al., 2008), which also explains why we only obtained strong relations for the bottom data. With *E. affinis* near the bottom, the effect of outflow should be limited. Several estuarine species exhibit similar bottom maintenance behavior through active vertical migration (Morgan et al., 1997; Kimmerer et al., 2002; Ueda et al., 2010). In the Seine estuary, the adults and late copepodids of *E. affinis* actively swim to the bottom during the ebb (Schmitt et al., 2011). And this behavior appears to be triggered by turbulence as adults' displacements in the shape of long jumps increase in step with turbulence (Michalec et al., 2015). Moreover, not only is this species migrating toward the bottom, but it is also able to hang onto surfaces as observed in the lab during behavioral experiments (Dur and Michalec, pers. obs.). This active substrate attachment behavior observed in other estuarine species (Shang et al., 2008) is likely to occur in the field with *E. affinis*, as it is an epibenthic species. Linked with this high faculty of late developmental stages to remain in a given area, we have observed a more restrained potential habitat for copepodid and adults. In the

Seine, the flood current is strong on the entire water column with a speed between 1.5 and 2 m/s while the ebb current at the bottom does not reach 1.6 m/s (Kervella et al., 2012). This may lead to “trapping the passive nauplii upstream” corroborating our results on the habitat of nauplii in less saline waters.

The ranges of optimal temperatures estimated in our study are supported by physiological studies conducted on the Seine population. Reproduction (Devreker et al., 2009), growth rate (Devreker et al., 2007), and larvae survival (Devreker et al., 2004) of *E. affinis* were documented to reach their maximum value at 15 °C. Our study gives a range of tolerated temperature between 8 and 20 °C for all stages. In the St Lawrence, the North Atlantic clade of *E. affinis* is found in brackish waters with a temperature of 20 °C during summer (Cabrol et al., 2015). The upper thermal limit of 20 °C is also suitable for culturing *E. affinis* for several consecutive generations (Souissi et al., 2016). Reproduction is affected by temperature <10 °C (Devreker et al., 2009), development cannot be achieved at temperatures <5 °C (Escaravage and Soetaert, 1993), and at temperatures from 20 to 25 °C mortality increases (Ban, 1994; Hammock et al., 2016). This correspondence with physiology was expected from the ecological niche theory (Guisan and Thuiller, 2005; Parmesan, 2005). But in the Gironde estuary, *E. affinis* is found between 2.5 and 32.5 °C (David et al., 2006) despite a similar temperature preferendum (~15 °C). This supports the idea that the thermal sensitivity of ectotherms varies markedly across geographical ranges, often in concert with local conditions (Schmidt et al., 2000; Sinclair et al., 2012).

While governed by the same environmental parameters (i.e., temperature and salinity), *E. affinis* from other estuaries may also present a slightly different salinity preferendum. For instance, the optimal salinity for the population from the Gironde is close to 0 (Chaalali et al., 2013b). And several populations of *E. affinis* are mainly restricted to the low salinity zone (i.e. <4) such as *E. affinis* in the Charente (Moderan et al., 2010) or the North Atlantic clade of *E. affinis* from the St. Lawrence (Cabrol et al., 2015). Our results demonstrate that *E. affinis*' optimal salinity conditions in the Seine estuary range between 5–10 and 8–14 for larvae and later development stages, respectively. These ranges were also shown to be optimal for the growth rate of *E. affinis* from the Nanaimo River Estuary in Canada (Strasser et al., 2011). Juvenile and Adults of *E. affinis* from the Scheldt exhibited a similar range of salinity preferences, peaking at salinity 9 in the 90s (Sautour and Castel, 1995). But since 2007 high abundances were consistently observed in the freshwater part (salinity <0.5) of the Scheldt (Mialet et al., 2010; Chambord et al., 2016). A bit northern, in the Ems estuary, adults and juveniles peaks of abundance were observed at salinity 6 (Sautour and Castel, 1995). The discrepancy in habitat between the Seine and other temperate estuary populations can be attributed to the inter-population differences existing in the *E. affinis* complex for both physiological preferenda (Beyrend-Dur et al., 2009; Strasser et al., 2011) and behavior (Schmitt et al., 2011). For instance, while *E. affinis*' population from the Gironde is found in the oligohaline estuary (David et al., 2005), zero salinity has a negative effect on the survival of *E. affinis* nauplii from the Seine estuary (Devreker et al., 2004). In the Gironde, *E. affinis* is supposed to behave as passive particles and to be consequently entrapped in the vicinity of the estuarine turbidity maximum (ETM; Castel and Veiga, 1990). Similar results were obtained for *E. affinis* from the Chesapeake Bay (Roman et al., 2001). Furthermore, turbidity is high in the Gironde and constitutes the main factor controlling the longitudinal distribution of *E. affinis* (Sautour and Castel, 1995) affecting its egg production (Gasparini et al., 1999) and consequently the population growth.

Our study consolidates the idea that the spatial distribution of estuarine copepod species is constrained by the influence of both

salinity and temperature. While this seems to be the case for species living in the oligo/mesohaline zone (Chaalali et al., 2013a, 2013b), other factors may shape the habitats of a copepod in more saline or fresher water zones. For instance, *E. affinis* from the Scheldt was, in addition to salinity, strongly correlated with oxygen and nitrate concentration (Appeltans et al., 2003; Mialet et al., 2010; Chambord et al., 2016). This revealed the need to carefully consider beforehand the drivers of the habitat of the copepod species in a given estuary.

4.3. Application possibilities

The approach and results on *E. affinis* presented here may have multiple applications.

4.3.1. Functional habitats

One possible future application of our model is to explore the spatiotemporal variation of *E. affinis*' functional habitat in the Seine estuary. Modeled habitats are called ‘functional’ as they represent, in an integrative manner, the area, which plays a role in the life cycle of selected species. The mapping of those functional habitats rests upon the potential habitat, i.e., those defined in the current study, and some tool providing a spatial dimension. The three-dimensional multivariable transport model, calibrated for the Seine estuary (MARS3D; Cugier and Le Hir, 2001; Le Hir et al., 2001), can simulate the variation of salinity on different time scales and represents an appropriate tool for the mapping of salinity within the estuary. The hydrodynamical model MARS3D covers the integrity of the Seine Bay (from Cherbourg to Fécamps) and goes upstream up to the Pose dam. Coupling our current results and the hydrological output of this model (salinity spatialization) will allow the localization, delimitation, and quantification (in terms of volumes) of the functional habitat of *E. affinis* in the Seine estuary. Additionally, the MARS3D model may offer the potential to test different retrospective and prospective scenarios. For instance, this combination of our models with the output of MARS3D could eventually lead to the identification of an upstream displacement of *E. affinis* population in the Seine estuary as observed in both the Scheldt (Chambord et al., 2016) and the Gironde (Chaalali et al., 2013b) estuaries.

4.3.2. Response to anthropogenic forcing

Climate change affects the structure, the dynamics and the functioning of the coastal ecosystems through many physical and biological processes (David et al., 2005; Goberville et al., 2010). Few studies have documented significant changes in copepod distribution ranges in European estuaries. Appeltans et al. (2003) reported a spatial shift in *E. affinis* population from brackish waters towards lower salinities in the Scheldt estuary that coincided with an increase in oxygen concentration in the freshwater zone. Chaalali et al. (2013b), through the definition of its realized niche, provided evidence that the alteration of *E. affinis*' longitudinal distribution in the Gironde estuary between 1975 and 2003 was the result of both changes in temperature and salinity. The niche definition approach's usefulness has also been shown at larger scales. By comparing the realized niches of two *Calanus* species, defined through a correlative approach, Helaouët and Beaugrand (2007) explained the changes in species dominance in the North Atlantic during the 1980s. The differential response to environmental variability associated with the tolerance interval can shed light on the processes involved in species maintenance, decline or override by another species. In the Seine estuary, the mesozooplankton is dominated by *E. affinis* and Acartidae (Mouny and Dauvin, 2002; Devreker et al., 2008), but the marine species *Temora longicornis* can also be found (Mouny and Dauvin, 2002).

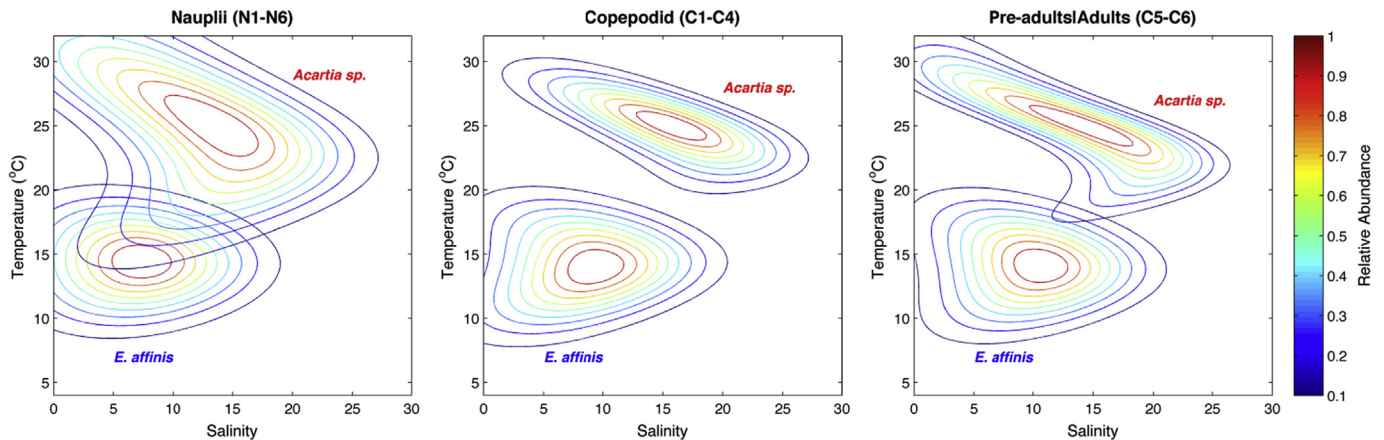


Fig. 6. Example of comparison of simulated habitats of *E. affinis* and *Acartia* sp.'s developmental stages groups in the bottom waters of the Seine estuary with relation to salinity and temperature. Colors are linked with the relative density of each species. This example illustrates the possibility of the approach to define the habitat and highlight the need of appropriate sampling strategy (cf text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The approach of the present study applied to the other abundant species in the Seine estuary, i.e., *Acartia* sp. (Fig. 6) confirmed that this genus is a warm water species preferring higher salinities, compared to *E. affinis* (Cervetto et al., 1999). The habitat of *Acartia* sp. presented in Fig. 6 was obtained from the same database used in the current study. We are here only illustrating the potential of our approach. While the instars of *Acartia* sp. were also counted, only *E. affinis*, the targeted species of the campaign, provide a proper set of data for defining the temperature-salinity-dependent habitats. At the chosen sampling site, *Acartia* sp. only occurs during a short period of the year. Consequently, the results presented in Fig. 6 are to be carefully considered and a more appropriate set of data should be used before conducting any comparative study. This would require the acquisition of data from another sampling station located downstream to that of our study. Downstream sampling station data will also be necessary to define *T. longicornis*' habitat. Once such data is available, we can then use the output from the hydrodynamical model (MARS3D) to compare the functional habitat of the species. Comparing the functional habitat of those species in different scenarios might shed some light on the dynamics of zooplankton in a highly human-influenced environment.

Another of the useful applications of the habitat modeling would be for studying the potential of invasive species. Estuarine ecosystems are susceptible to invasions by non-indigenous copepod species, primarily via ballast water discharges of commercial ships (Cordell et al., 2008, 2009). In some cases, the introduction of invasive species may have contributed to the displacement of native species (Cordell et al., 2008). In addition, anthropogenic influences may contribute to enhancing natural trends and to facilitating the establishment of invasive species (Chaalali et al., 2013a). Comparing the habitats of different species, defined using correlative models such as ours, can reveal the potential for competition between local and invasive species (Bollens et al., 2012). On the other hand, mechanistic models, while being more difficult to develop and implement, offer flexibility and extensibility that might be needed in predicting invasions (Buckley et al., 2010). Better estimates of invasive capacity are possible when combining mechanistic and correlative models (Kearney and Porter, 2009).

4.4. Conclusion

We presented here an approach to defining the habitat of a copepod from sampling data. The approach can be generalized to

other estuaries and species, for which enough data are available, allowing inter-estuarine and inter-population comparisons. We obtained relations defining the habitat of the three main developmental instar groups of *E. affinis* in the Seine estuary in terms of temperature and salinity. In the future, the present work will be developed in its application by combining the obtained relations with the output from the hydrodynamical model (MARS3D) to map the functional habitat of each group of *E. affinis*' developmental stages in the Seine estuary. Our results and approach are valuable for understanding and eventually predicting the sensitivity of aquatic systems such as the Seine estuary and other estuaries to environmental changes.

Author contributions

S.S. and G.D. conceived the project. G.D. performed the analyses. S.S. and G.D. co-wrote the paper.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.ecss.2017.11.008>.

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