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Spatial distribution of the copepod *Centropages typicus* in Ligurian Sea (NW Mediterranean). Role of surface currents estimated by Topex-Poseidon altimetry

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Abstract

A particle-tracking model was used to simulate the dispersion and development of the planktonic copepod *Centropages typicus* during spring in Ligurian Sea. We show that mesoscale current structure, with a coastal jet and eddies, plays a key role in the transport and dispersion of *C. typicus* during its life cycle. Although, in the north, offshore Nice, cohorts can be advected southwestward out of Ligurian basin, more to the south others are retained in the central eddy and may give the start to the spring bloom of this species. However, input of individuals from the south through the Corsican Channel and along the west coast of Corsica may also be important in spring. This study shows that the ambit of *C. typicus* population is larger than the Ligurian Sea. ***To cite this article: J.C. Molinero, P. Nival, C. R. Biologies 327 (2004).***

Résumé

Distribution spatiale du copépode *Centropages typicus* en mer Ligure (Méditerranée du Nord-Ouest). Rôle des courants superficiels estimés par altimétrie (Topex-Poséidon). Nous avons utilisé un modèle lagrangien pour simuler le développement et la dispersion du copépode planctonique *Centropages typicus* en mer Ligure au printemps. Nous montrons que la structure du champ de courant à mesoéchelle, avec un courant de jet côtier et des tourbillons, est importante pour le transport et la dispersion de *C. typicus* pendant son développement. Alors que dans le Nord, au large de Nice, les cohortes sont transportées par le courant vers le sud-ouest, hors du bassin Ligure, elles sont retenues, plus au large, dans le tourbillon central, où peut se produire l'intense développement de la génération de printemps. Cependant, les individus arrivant du sud, soit par le canal de Corse, soit le long de la côte ouest de la Corse, peuvent constituer une contribution importante au stock des *C. typicus* en mer Ligure. Cette étude montre que l'emprise de la population de *Cen-*

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tropages typicus n'est pas limitée à la mer Ligure. ***Pour citer cet article : J.C. Molinero, P. Nival, C. R. Biologies 327 (2004).***

Keywords: copepods; population; Ligurian Sea; Lagrangian model

Mots-clés : copépodes ; population ; mer Ligure ; modèle lagrangien

Version française abrégée

En Méditerranée, l'information sur les échelles spatiale et temporelle des structures et des mécanismes biologiques provient de campagnes de courte durée ou bien de stations côtières. Les premières permettent d'estimer les échelles spatiales sur un instantané du milieu marin, tandis que les secondes fournissent des séries temporelles qui contiennent aussi des propriétés spatiales, en particulier lorsque le courant côtier est rapide.

Les observations faites dans la mer Ligure montrent que le courant cyclonique engendré par la formation de l'eau profonde méditerranéenne en hiver est rapide près des côtes et relativement lent au centre du bassin. Un front hydrodynamique limite les deux régions.

On a constaté que le développement du copépode *Centropages typicus* est synchrone dans tout le Nord du bassin occidental de la Méditerranée. Le maximum d'abondance, qui peut atteindre 2500 individus m^{-3}, se situe en avril. Cette espèce épipélagique est donc soumise au transport et à la dispersion par les courants superficiels.

L'altimétrie satellitale, fournie par Topex-Poséidon, permet d'établir le champ de courant avec un pas d'espace de 1/8 de degré. Nous avons utilisé le champ de courant du 10 avril 2001 fourni par MF-SPP pour simuler les trajectoires d'individus de *C. typicus* pendant leur développement. La trajectoire est calculée par interpolation des quatre vecteurs vitesse les plus proches. La turbulence due aux instabilités et aux tourbillons de taille inférieure au pas d'espace du champ de courant est prise en compte par une composante aléatoire normale d'écart type 200 $m\,j^{-1}$, correspondant à un coefficient de diffusion turbulente de $0{,}462 \cdot 10^5\ cm^2\,s^{-1}$. Compte tenu de la température de la mer à cette époque de l'année, nous avons adopté 28 jours comme temps de développement de l'œuf à l'adulte et 24 jours pour la durée de vie de la femelle adulte.

Le champ de courant utilisé pour les simulations de trajectoires illustre bien la circulation cyclonique en mer Ligure (Fig. 1). Près de la côte, le courant est rapide, mais sa vitesse est plus grande au nord, le long de la Riviera, qu'au sud, le long de la côte corse. Dans la partie centrale, le courant est faible et des tourbillons apparaissent. Le tourbillon majeur, situé au nord, est particulièrement bien défini. Les autres sont localisés dans des régions de courant faible. Le gradient de courant permet de situer le front qui limite l'eau côtière et celle du tourbillon majeur, bien que la résolution du champ de courant ne permette pas de le localiser avec précision.

Les trajectoires des copépodes pendant leur développement montrent des différences selon le lieu de ponte (Fig. 2). Les individus issus d'œufs pondus au large de Nice sont rapidement transportés vers le sud-ouest, hors de la mer Ligure. Ceux qui sont issus d'œufs pondus au large de la Corse arrivent au stade adulte dans la zone côtière de Nice.

La dispersion engendrée par la diffusion turbulente horizontale montre que des individus issus de la même région peuvent être transportés dans différentes parties de la mer Ligure (Fig. 3). On constate aussi que des individus situés au large de Nice peuvent continuer leur développement dans le tourbillon majeur. Les copépodes du tourbillon majeur ont une forte probabilité de rester dans ce tourbillon, qui constitue une zone de rétention pour l'espèce.

Les trajectoires issues de la zone côtière au nord-ouest de la Corse montrent que les individus peuvent terminer leur développement au large de Nice ou dans le tourbillon majeur. On peut aussi faire l'hypothèse que les individus issus de la mer Tyrrhénienne arrivent dans l'eau côtière du Nord de la mer Ligure. Le champ de courant, bien que conservant ses caractéristiques cycloniques, peut évoluer dans le temps, par exemple sous l'influence du forçage atmosphérique. La zone de rétention mise en évidence peut se déplacer ou se modifier.

Cette étude suggère qu'en quelques générations des *Centropages typicus* peuvent traverser la mer Ligure. Elle montre aussi que l'emprise de la population de cette espèce dépasse la mer Ligure. On peut s'attendre à une homogénéité génétique dans toute la partie nord de la Méditerranée occidentale. C'est probablement le cas pour toutes les espèces planctoniques dont le cycle biologique se déroule dans la couche superficielle de la mer.

1. Introduction

Mesoscale structures in the ocean appear to be the relevant scale for biological processes and variables. In the Mediterranean, most of the information about the spatio-temporal variability of copepods abundance has been obtained either from short time cruises or from coastal stations [1–5]. While the former provide the spatial scale from a synoptic snapshot, the latter give records merging time and space scales, especially when the current velocity along the coast is strong.

The current pattern in the Ligurian sea shows a cyclonic gyre that is promoted by the deepwater formation during winter and is forced by water runoff along the coast in autumn and spring [6]. Along the north coast, water is flowing from east to west. The average velocity in the coastal jet is from about 10 $cm\,s^{-1}$ along the coast to 50 $cm\,s^{-1}$ 20 miles offshore [7]. A hydrodynamic front sets the limit between coastal waters flowing rapidly (North Current [8]) and central waters where the currents are weak [9]. The density gradient in the frontal zone is stronger during winter and early spring, and the vertical component of the water velocity governs the phytoplankton bloom of the Ligurian Sea via the input of nutrients.

The development of *Centropages typicus* is more or less synchronous in all observation sites in the northern basin of western Mediterranean [10]. The annual cycle shows a main peak during spring when the adults' abundance can reach up to 2500 $ind\,m^{-3}$. *C. typicus* becomes a dominant species and can reach 70% of the total copepod abundance [11].

C. typicus is an epipelagic species. It is usually collected in the upper 100 m [12] and most of the population is located in the upper 50 m [11]. The hydrodynamic characteristics of the Ligurian Sea suggest that these copepods are transported on long distances during their life. However, two hypotheses about the spatio-temporal variability of this species can be considered:

(*i*) there is a resident population in the Ligurian Sea; the short and long-term variations depend on the specific forcing and the events occurring in the Ligurian Sea;
(*ii*) *C. typicus* is continuously imported into Ligurian Sea; hydrodynamic forcing outside the Ligurian Sea or at its boundaries set the time-space properties of *C. typicus* abundance.

However, in the last hypothesis, the picture depends on the generation time. This study is a simple investigation on the distances travelled by a copepod during its development and on the effect of the pattern of currents.

Individual-based models have been used to study the interaction between biological properties of living particles and hydrodynamic processes (for instance: effect of vertical mixing and transport of phytoplankton cells in the light gradient [13], exchange of individuals between patches of benthic organisms by means of larval transport over the Georges Bank [14], changes in development properties during vertical transport or migration [15,16], or horizontal transport [17,18]).

Altimetry provides current fields with a spatial definition that allows the estimation of the trajectory of a buoyant particle. A recent approach has used satellite altimetry (Topex-Poseidon data) to estimate the transport and dispersion of spiny lobsters larvae around Hawaiian Islands [19]. In this paper we investigate the spatial scale of a cohort development in the Ligurian Sea by using a current field from April which provides the mesoscale structure, computed from Topex-Poseidon altimetry.

2. Material and methods

2.1. Copepod life cycle

The generation time of the species, that is development time from egg to reproductive adult, estimated from laboratory experiments, is close to 25 days at a temperature of 15 °C (egg to N6: 11 days, C1 to adult: 14 days [20–22]). The lifespan of a female is from

13 to 22 days. We consider here that the durations of the larval (naupliar stages) and juvenile (copepodite stages) periods are of the same order of 14 days (total: 28 days) and the adult lifetime is 24 days. Overall, the generation time is close to the estimation given by Huntley and Lopez [23] for the temperature of 14 °C. As we analyse in this work the development of the species during early spring, we consider that it is not limited by the food availability.

2.2. *Velocity field and particle tracking*

The current field in the Ligurian Sea used here was taken from Topex-Poseidon data records for 10 April 2001, in the framework of the Mediterranean Forecasting System Pilot Project.

Files giving the two components of horizontal current on a 1/8 of a degree grid were obtained from the MFSPP database. The current velocity in a given location (x, y) was computed by linear interpolation from the four surrounding grid points. The distance travelled during one time step (0.1 day) was computed from the two components of current velocity, the east–west component, $u_{(x,y)}$, and the north–south component, $v_{(x,y)}$. In order to take into account the sub-grid turbulence that can affect the trajectory of the particle, a random component of transport (r_x, r_y) was added to the displacement during a time step:

east–west component (zonal component)

$$X_{(t+\mathrm{d}t)} = x_{(t)} + u_{(x,y)}\,\mathrm{d}t + r_x$$

north–south component (meridional component)

$$Y_{(t+\mathrm{d}t)} = y_{(t)} + v_{(x,y)}\,\mathrm{d}t + r_y$$

$$\text{with} \quad r_x = n_x(2K\,\mathrm{d}t)^{0.5} \text{ and } r_y = n_y(2K\,\mathrm{d}t)^{0.5}$$

where n_x and n_y are random numbers from a normal distribution $N(0, 1)$ and K is the eddy diffusion coefficient.

The characteristic length taken into account here is the grid size (1/8 of a degree, $1.4 \cdot 10^4$ m). From the Okubo relation [24], we estimated K as $0.462 \cdot 10^5\ \mathrm{cm^2\,s^{-1}}$. Thus the standard deviation (rms) of the trajectory will be 200 m. It has been shown that on the vertical, strong gradients of density induce a non-isotropic dispersion [25,26]. However, considering that the horizontal gradients of density are not so strong as vertical ones, we assume here that the eddy diffusivity is isotropic.

3. Results

In the current field of 10 April 2001, the main pattern is cyclonic, with the strong coastal current that represents the North Current [8], also designated as Liguro-Provençal current. Its velocity reaches 20 to 40 $\mathrm{cm\,s^{-1}}$ (Fig. 1). This strong circulation is able to transport the copepods on long distances during their development. At that time of the year, water enters the Ligurian Sea in the east from the Tyrrhenian Sea through the Corsican Channel and in the south from the western basin along the western coast of Corsica. Some eddies appear superimposed to the cyclonic pattern in the steady water of the central area. One of them, more active, is located off Nice. These eddies are potential retention areas for *C. typicus* populations and the coastal current seems to be a conveyor belt for the individuals that live closer to the coast.

Fig. 2 gives the trajectories of individuals during their development, assuming that eggs are laid in each one of the locations on the Villefranche–Calvi transect, in the absence of dispersion. The result of the strong coastal current is to wash the cohort produced in Nice area and to bring in this area adults born close to Corsica in one (24 days) or two genera-

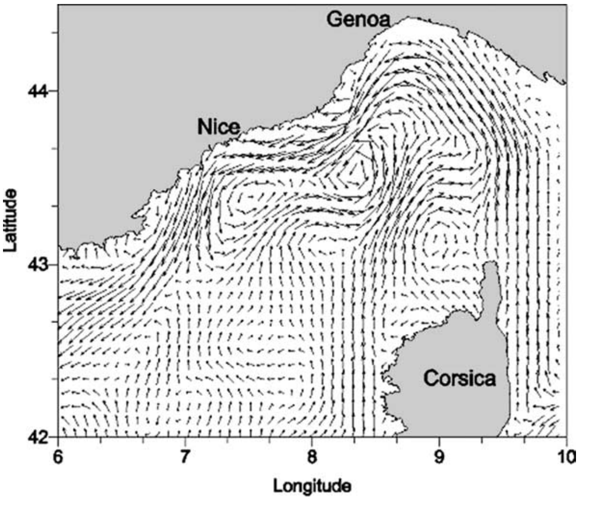


Fig. 1. Geostrophic surface current, 10 April 1999, estimated from Topex-Poseidon satellite altimetry. Current velocity is in the range 0.06–0.67 $\mathrm{m\,s^{-1}}$. The cyclonic current field is the typical pattern of the Ligurian Sea. The water flowing through Corsican Channel is merging to the flow entering Ligurian Sea in the South to give the North Current. Several eddies are generated in the centre of the Ligurian Sea.

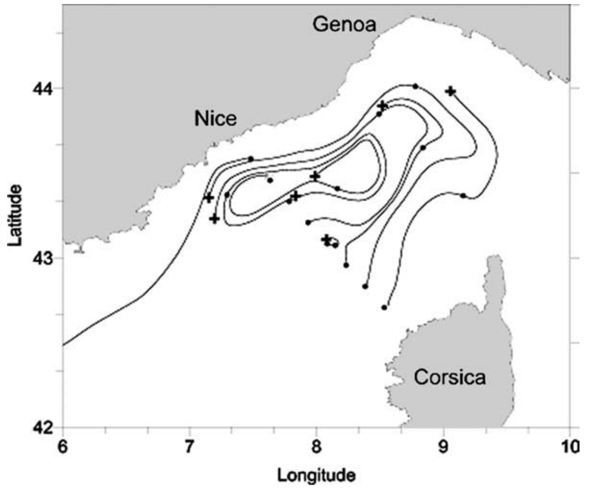


Fig. 2. Simulated copepod trajectories during their growth from egg to adult. The starting points are situated at different sites of a Nice–Corsica transect. Three steps in the life cycle of copepods are represented by symbols on the trajectories: egg (dot), nauplius VI stage (second dot) and adult stage (cross).

tions (48 days). Eggs laid in the northern coastal zone will complete their larval development (N1–N6) about 100 km downstream and out of the Ligurian Sea. On the contrary, eggs laid offshore in the major eddy will become adults in the same area and may stay there for several generations.

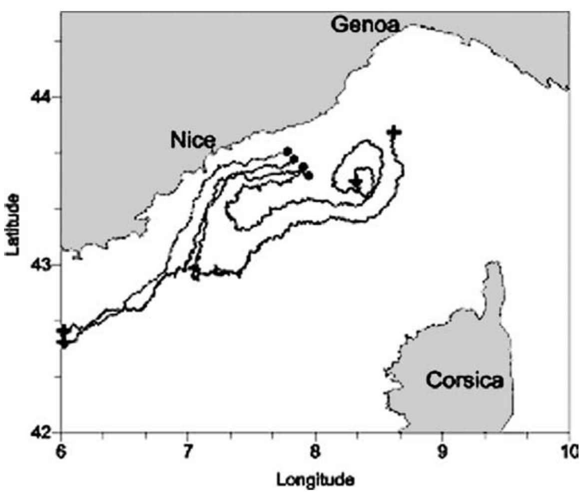
What emerges immediately from these results is, firstly, that the fate of eggs will depend on the location of the female, and secondly, that *C. typicus* can invade the basin in one-generation time. The random dispersion due to the sub-scale eddy diffusion allows the individuals to escape from an eddy or to be trapped by it. Under this condition, the issue of a trajectory is not certain. Three different situations are shown in Fig. 3. Groups of eggs are laid (*i*) in the coastal area off Nice (Fig. 3a), (*ii*) in the Nice offshore water, in the major eddy (Fig. 3b), and (*iii*) around the northern part of Corsica (Fig. 3c). The results show that eggs laid in the coastal waters close to Nice cannot give a large contribution to the local *C. typicus* population. The retention time is close to zero. On the contrary, as the current pattern in the central area provides a retention structure, cohorts produced there can stay and numbers can increase locally. The retention time appears to be larger than the generation time. It should also be noted that *C. typicus* in the coastal area off Nice could originate from different locations: either from the southwest, along Corsica, or from northern Tyrrhenian Sea. The southwestern individuals appear to contribute in the sub-population of the central eddy (Fig. 3c).

Fig. 3 suggests that individuals at different developmental stages can be found in coastal and offshore waters. Using the copepodites/adults ratio, Molinero [11] suggested, from observations along a transect off Nice, that cohorts of different ages can be found in coastal and offshore waters at the same time, with a dominance of adults close to the coast and of copepodites offshore. The difference in the residence time can explain the difference in the timing of the cohorts.

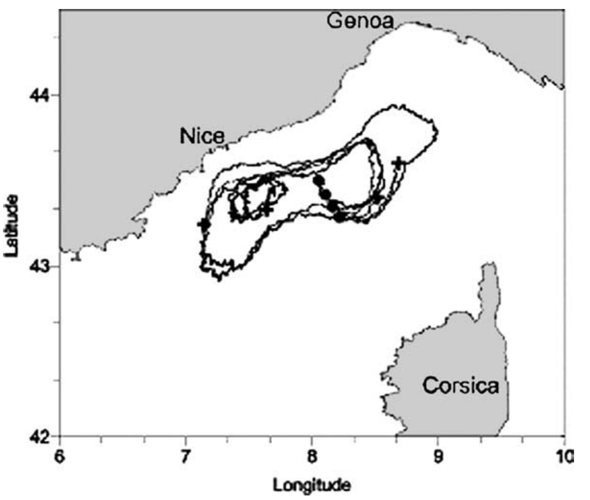
The rapid development of *C. typicus* during April all over the Ligurian Sea showed by Pinca and Dallot [3] depends on a dispersion mechanism. This is suggested by the dispersion of the progeny of a single *C. typicus* female during its life. We simulated the trajectory of a female just moulted in the southern part of the Villefranche–Calvi transect, with a life span of 24 days. The estimated track of the female shows that it may die in the coastal area off the French Riviera. The potential area covered during one generation can be approached by following the tracks of individuals issued from the eggs produced each day. Fig. 4 shows the trajectory of one egg from the clutch produced daily (average 30, [27]). Some of the individuals follow the female trajectory, others can escape and either disperse in the northeast or enter the major cyclonic eddy. As a consequence of both transport and dispersion, an important part of the Ligurian Sea can be seeded by this *C. typicus* female in one-generation time.

4. Discussion

The pattern of currents velocity in the Ligurian Sea provided by Topex-Poseidon altimetry gives a convenient frame to study biological characteristics previously described locally. Most of the hydrological properties of the Ligurian Sea already known are depicted on the velocity map: the cyclonic circulation, with strong currents along the coast, especially in the north; the velocity gradient between coastal waters and central ones and the inflow of water through the Corsican Channel. This synoptic view shows that several eddies are coexisting in the slow moving water and that the



(**A**)



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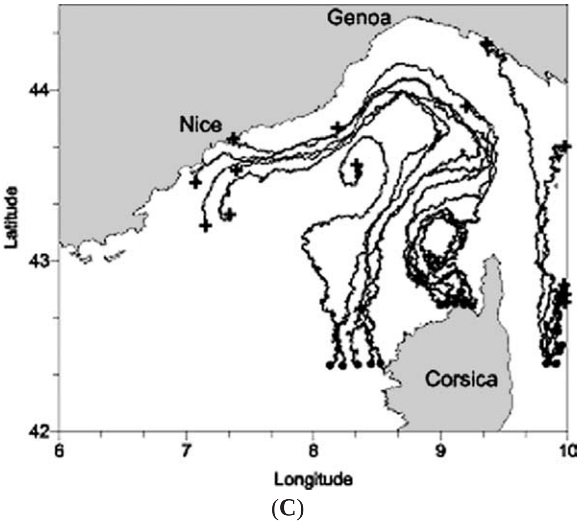

(**C**)

Fig. 3. Simulated individual trajectories of copepods *Centropage typicus* developing form eggs laid in different areas of Ligurian Sea (egg laying location: large dots; start of adults stage: cross). **A**: Coastal waters in North Current. The individuals close to the coast are exported out of Ligurian Sea. The more offshore ones can enter an eddy and continue their development there. **B**: Offshore water. Eggs released in the area influenced by the eddy structure can complete their development in the same area. **C**: Southern waters: most of the individuals are reaching the North current water and will be transported out of the Ligurian Sea during adult life.

major flow of water coming from the south along the southwest coast of Corsica can proceed north and generate an eddy on the northern part of Corsica. This pattern was depicted by trajectories of surface buoys [28]. However, the productive frontal structure [29] cannot be precisely situated, because the grid size of the currents map is too large, although the gradient of current between two adjacent grid cells can suggest its location, especially along the north coast. The inflow of water from the Tyrrhenian Sea appears to be important, so that zooplankton species transported may affect the Ligurian communities along the Italian coasts. Vignudelli et al. [30] suggested that the benthic fauna of the Ligurian Sea could be affected by the transport of larval stages through Corsican Channel in relation to NAO index variation.

The simulated trajectories of copepods show that the whole Ligurian Sea is the relevant scale for the

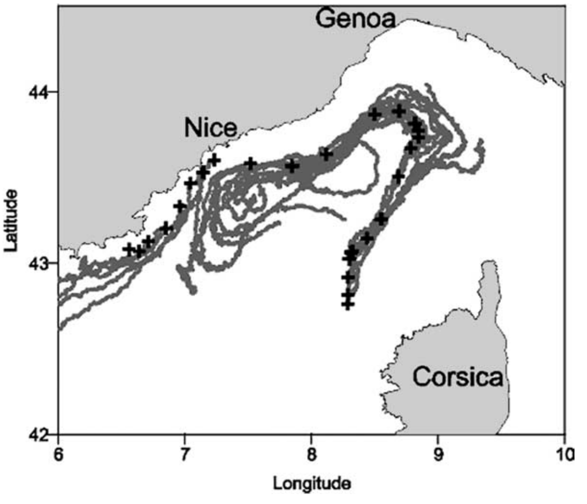

Fig. 4. Area covered by the offspring of a female during its life when spawning (24 days). Crosses show the position of the female each day when a clutch of eggs is laid. Trajectories show the position of one larva (nauplius stage) issued from each eggs clutch. The coupling of copepod life cycle and hydrodynamics (transport and turbulent diffusion) plays an important role in the spreading of *Centropages typicus* population all over Ligurian Sea in spring.

C. typicus population. From estimations of geostrophic current velocity on a Nice–Calvi transect, Gostan [7] made a crude estimation of 15 days as the time necessary for a particle to flow from Corsica to Nice. From Fig. 1, the duration of the travel from north Corsica to Nice can last for 24 to 48 days, depending on the starting place.

Cohorts of *C. typicus* can evolve independently in the coastal current and the main offshore eddy. This may explain the difference in the copepodites/adults ratio observed on a transect off Nice [11]. However, exchanges of individuals between these two regions can occur through instabilities of the frontal structure, meandering of the front, small scale eddies or filaments produced by eddy deformation [31].

The study of trajectories of living organisms is useful to understand the interaction between current patterns and biological properties. Most previous studies have used a current field generated by a simulation model. Tremblay et al. [14] estimated the recruitment location of *Placopecten magellanicus* larvae from different populations on the Georges Bank with a current field produced by a finite-element spatial model [32]. Miller et al. [17] used the same current fields to describe the distribution of the life stages of *Calanus finmarchicus* on the Georges Bank and in the Gulf of Maine. The results depend on grid size and physical processes considered in the physical model. Our study is based on surface topography, which is under the direct influence of the current fields. The forecasted trajectories of copepods are only dependant on grid size.

Our results suggest that, starting with a small number of females in March, *C. typicus* may cover the whole Ligurian Basin in one- or two-generation time. This explains both the maximal abundances observed off Nice in spring [11,33,34] and the wide spatial distribution of *C. typicus* in the Ligurian Sea in April [3].

The productive areas where copepods reach adulthood (fronts, limit of eddies) will be at the origin of strong cohort production. Sinclair [35] has developed the concept of retention structure for early life stages of fish. It appears that eddies are such retention structures. The size of the favourable ones is related to the development time of the species considered. A similar situation has been described for retention and transport of fish larvae in the Gulf of Alaska [36]. The hypothesis of match between life cycle and hydrological structures is underlying the Lagrangian modelling of fish larvae in the North Sea [37]. We can hypothesize that during winter a small number of individuals are confined in the offshore eddies where they take benefit from the phytoplankton bloom developing on the fronts. They can produce the first spring cohorts that will spread over the entire Ligurian Sea, as suggested in Fig. 4. Another scenario for the spreading over the Ligurian Sea suggested by the current field is that possibly this species develops earlier in the south and is transported into the Ligurian Sea through Corsican Channel flow and west Corsica inflow.

Altimeter data are a useful tool to study spatial properties of pelagic populations. Our results suggest that *C. typicus* is not isolated in the Ligurian Sea for several generations and we suggest that *C. typicus* as well as other small copepod species living in surface waters of the northwestern Mediterranean have a single genetic pool.

5. Conclusion

Due to the cyclonic current pattern of Ligurian Sea, pelagic species are not isolated for many generations.

In the coastal waters, they are transported rapidly. In the central area, several mesoscale eddies can be retention structures that slow down the transport through the Ligurian Sea. The current field computed from Topex-Poseidon altimetry was useful to compare the time scales of water transport and copepod development. Although the current pattern can change in time according to the forcing by atmosphere through the wind field and the pressure gradients between adjacent basins, the cyclonic landscape will persist. By this approach, we suggest that the spring generation of *Centropages typicus* spreading over the Ligurian Sea can originate from different areas and we emphasize the role of the central eddy as a retention structure.

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