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Article

Decapod Crustacean Larval Communities in the South Adriatic: Spring Composition, Horizontal and Vertical Distribution Patterns

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Abstract: An oceanographic cruise from southern Adriatic to the northern Ionian basins, during 2013 spring period, allowed us to describe spatial abundance and distribution of decapod crustacean larval assemblages with a multidisciplinary approach. Seventeen locations on the Apulian and Albanian shelves and offshore waters, including the Strait of Otranto, were sampled by BIONESS electronic multinet. In May 2013 a swarm of zoeae (11 Brachyura taxa, mostly at first instar, with *Xantho granulicarpus* at 87%) was recorded in the neuston of the Italian side. Decapod larvae were concentrated in the first 20-30 m surface layer, strongly linked to the thermocline and generally above the DCM, suggesting that they are involved in surface water circulation. The migratory behavior of decapod larvae in coastal stations is quite regular between 20 and 60 m depth and daily time independent. In offshore stations, migration is compatible with the day-night cycle, where a minimum WMD value is evident at about 20m at night. The availability of four satellite-tracked surface drifters in the same area and period of the larvae presence, represented a possibility to discuss the geographic dispersal of larvae linked to the surface circulation in successive days. Only one drifter crossed the south Adriatic passing from the Italian to the Balkan neritic area, employing about 40 days. The actual genetic homogeneity of many Brachyura coastal species populations on the opposite sides of the Adriatic Sea, suggests the existence of a genetic connection which should not rely exclusively upon larvae circulation and needs to be fueled by additional strategies of biological communication.

Keywords: ecological connectivity; larvae of Brachyura; spatial distribution; diel vertical migration; Adriatic Sea

1. Introduction

The existence of planktonic stages, generally larvae, in the life cycle of marine benthos species, has been considered as the main responsible of the observed geographic distribution and/or genetic inter-population connectivity, mainly for sessile neritic species [1-2]. To interpret the Supply Side Ecology [3-4] founded on larvae abundance and dispersal community dynamics and population connectivity along shorelines. However, only so called “teleplanic larvae” justify high dispersal possibility for the species [5]. More every stage of life has survival rates and persistence times in the planktonic stage (the Pelagic Larval Duration, PLD) which do not allow them to disperse on large

spatial scales. In laboratory conditions, the PLD of *Brachyura* larvae (zoea) has been observed to be inversely correlated with water temperature [6-11].

The debate over degree to which marine larvae produced in a local population are likely to return to that population (self-recruitment, or retention), or migrate to another population (export), is open [12]. Moreover, hydrodynamic models and genetic structure data indicate that the average scale of dispersal can vary widely even within a given species, at different locations in space and time [12-14]. Dispersal prediction of larvae requires knowledge of the processes regulating larval dispersal and the spatial and temporal scales over which it occurs. Estimates of marine larval dispersal, which ranges from a few meters to hundreds of kilometers [15-19], are well correlated with PLD for many organisms, including Decapoda, even though exceptions do exist [20-22]. Furthermore, larval behavior significantly affects the dispersal: e.g., larvae occupying very near-bottom waters typically perform a short distance dispersal [12].

Small basins could be attractive by coast to coast exchanges for species propagules represented by planktonic larvae, more than large oceanic areas, also because generally corresponding to a more extended presence of the shelf and of their conditioning of water circulation [23]. The South Adriatic Sea could be interesting from this point of view because it is only 76 km wide in its narrower point (Otranto-Cape Linguetta), thus suggesting an enhancement of connectivity between benthic communities of the opposite sides. Bray et al. [24] already predicted that larvae of coastal benthos in the Adriatic Sea are able to pass from the East to the West side of the basin following the surface currents, with Apulia (the South-West coast of the Basin) acting as a sink area.

Among Crustacea, Decapoda *Brachyura* represents a good candidate for studies on the dispersal capability of coastal benthos by means of larvae. These larvae (zoeae and megalopae) are reported as typical of the uppermost layer of the sea water (neuston) [25], although perform daily vertical migrations, and this fact makes possible the prediction of their traveling routes inside surface currents. Dos Santos et al. [26] well described a general tendency, among Decapoda larvae, to persist in the vicinity of their birth sites, with larvae of coastal species accumulated in coastal sites and those of the neritic species with a larger spatial distribution.

Inter-annual, cross-shore and alongshore differences on decapod larvae distribution have been established as closely affected by local hydrodynamic conditions of adult sites [27], suggesting the existence of a strategy driven by the necessity to persist in the same area of adults, more than to disperse elsewhere by currents. Studies of Torres et al. [28-29] suggest that larvae of coastal/neritic species, living in shallow waters, perform daily vertical migrations (involving the neuston) smaller than those of mesopelagic and/or deep bottom species. From the standpoint of dispersion studies, the two-dimensional space represented by the sea surface is the migration field for those larvae which stay in the surface layer, at least for a part of each day (generally nighttime). The frame is accomplished by the extension of the vertical migration behavior that typically this plankton shows, with a pulsating presence, during the day, in different water layers which possibly move at different speeds and/or in different directions [26].

Despite the high number of studies investigating decapod larvae abundances in coastal and shelf areas [e.g. 28,30-32], such studies remain scarce in slope and offshore areas [e.g. 29,33-35]. Concerning the Mediterranean Sea, most of these studies on decapod larvae abundances were carried out in the western part [e.g. 28-29, 34-38] for summer and autumn-winter periods. Referring to Adriatic Sea, very few specific studies on larvae decapod larvae distribution have been done [39-41], while other few references in some zooplankton papers have been made [42-43]. During the same spring oceanographic cruise the spatial variation of the biodiversity patterns of both neuston and pelagic polychaetes has already been the subject of two articles [44-45], while drifter tracks are also available [46].

Thus, this study aims at understanding the spatial abundance and distribution of decapod crustacean larval assemblages among seventeen coastal-shelf and offshore locations spanning from the southern Adriatic to the northern Ionian basins, during 2013 spring period. Particularly, the study aimed to assess the fine scale vertical distribution and migration behaviour of decapod larvae, in relation to environmental conditions. Here the attention has been focused on the swarm of Decapoda

larvae which recorded in neuston of stations “Penna Grossa” (PGR) and S13 [44]. This natural experiment is useful to clarify what role, if any, larvae play in the geographic distribution of species, and if they somehow represent the best connection device between the populations inhabiting the opposite sides of a small marine basin like the Adriatic Sea [24,47].

2. General environmental Patterns in the Region

The Southern Adriatic Sea is enclosed between the Italian and the Balkan coast. It is characterized by a wide depression more than 1200 m deep [48]. South of the Gargano Promontory, the Italian coast is low and exhibits a wide and sandy shelf, whereas the eastern coast is generally irregular with several river mouths and a shelf that narrows from north to south, where the Strait of Otranto connects the Adriatic to the Ionian Sea.

The South Adriatic Sea is affected by two coastal currents of surface waters: (i) the Western Adriatic Current (WAC), that flows south-eastward along the Italian coast and brings the Adriatic Surface Waters (ASW) relatively less salty and nutrient-rich waters due to fresh inputs in the North Adriatic stretch (mainly Po river) [49], and (ii) the Eastern Adriatic Current (EAC) that enters the basin along the Balkan coast and carries north-westward Ionian Surface Water (ISW, relatively warmer and saltier) [50]. EAC forms the South Adriatic Gyre (SAG), a permanent topographically-constrained cyclonic circulation feature in Southern Adriatic, characterized by positive vorticity whose strength is modulated by large-scale climate-driven patterns [51]. Particularly, in periods characterized by an Ionian cyclonic circulation phase (as at the beginning of 2013, [52]) the higher vorticity of the local wind forcing, correlated with more frequent southerlies over the Southern Adriatic, has a dominant effect in sustaining the SAG strength.

In April ([53], fig. 3d) and May 2013 wind fields in Southern Adriatic showed dominant components towards East (1.0 m sec^{-1} , westerlies) and North (0.33 m s^{-1} , southerlies) [54], with evident influence on the monthly averaged SAG pattern and transient connectivity at surface in the region, as highlighted in the model reanalysis [55] (Figure 1).

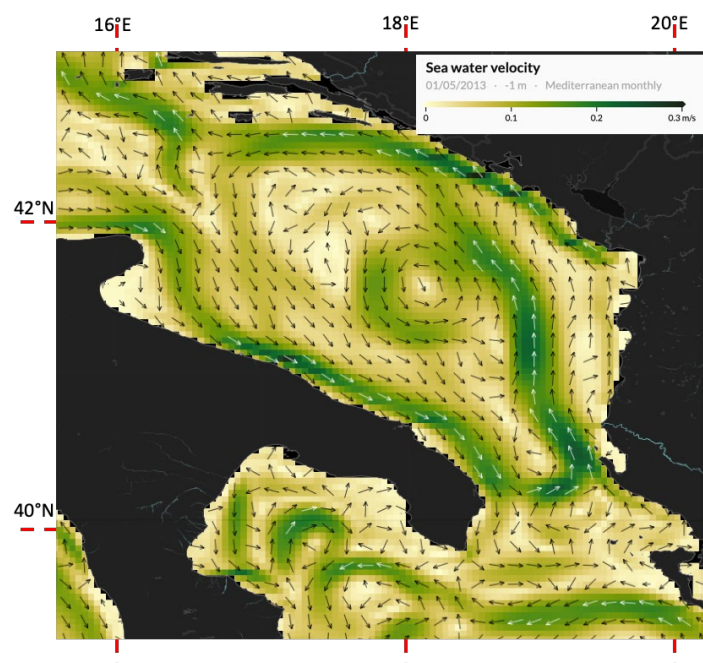


Figure 1. May 2013: estimated monthly averaged water velocity at surface in Southern Adriatic (model reanalysis, modified from CMEMS). Main circulation patterns (WAC, EAC, SAG) can be recognized.

3. Materials and Methods

An oceanographic cruise between the Italian Apulian and Albanian-Greece coasts in the southern Adriatic Sea (Figure 2) was carried out aboard *R/V Urania* from 8 to 21 May 2013 in the framework of the EU FP7 CoCoNET project [56].



Figure 2. Map of the study area with spanning locations of BIONESS multinet and Neuston net (red and blue dots, respectively).

3.1. BIONESS Sampling

To investigate the horizontal and vertical distribution of zooplankton, of decapod larvae particularly, seventeen locations on the Apulian and Albanian shelves and offshore waters, including the Strait of Otranto, were sampled (Figure 2). The samples were collected in late spring using a BIONESS (Bedford Institute of Oceanography Net and Environmental Sampling System [57], a multiple-opening and closing-net sampler equipped with ten nets (200 μm mesh size) with a mouth area of 0.25 m^2 . By a multi-parametric probe (SBE 911 plus, Seabird Electronics) and a fluorescence sensor (Seapoint Chlorophyll Fluorometer, Seapoint Sensors) mounted on its frame, data of depth (m), temperature ($^{\circ}\text{C}$), salinity and Chl a ($\mu\text{g l}^{-1}$) were processed with Ocean Data View (ODV) software to obtain on board real time vertical profiles. Flow velocity and filtration efficiency were monitored by internal and external flowmeters (GO2031H). The BIONESS was towed at a speed of 1.5-2 m s^{-1} and slowly towed along an oblique path, allowing very detailed resolution of the zooplankton vertical distribution. During each tow, a maximum of nine depth intervals was sampled. During the first downcast, the thermocline, pycnocline, halocline, and Deep Chlorophyll Maximum (DCM) layer thickness were analyzed, in order to decide upon the sampling layers. A total of 136 zooplankton samples were collected in several layers between the surface and few meters above the seabed, along a 0–1100 m water column (Table 1). Five 20 m thick layers (0–20 m, 20–40 m, 40–60 m, 60–80 m, 80–100 m) in the first 100 m were sampled, followed by wider up to the maximum reached depth. Filtered water volume varied between 25 and 108 m^3 , with volume increasing, generally, with depth. On board, each sample was preserved in 4% borax-buffered formaldehyde and seawater solution. Sam

pling details are shown in Table 1. Sunrise and sunset times were 05:49 and 20:45 (GMT + 2:00).

Table 1. BIONESS sampling data.

Station	Local date	Position		Local Time		Bottom depth	Max sampled depth
	May 2013	Lat. N	Long. E	Start	End	(m)	(m)
S1	09	42°09.994'	15°39.966'	20:23	21:37	99	90
S3	10	42°09.985'	16°38.059'	14:05	15:47	178	170
L41	10	41°59.952'	16°59.872'	18:38	20:21	580	550
S7	11	42°10.049'	18°32.310'	15:28	16:46	190	180
S10	11	41°29.780'	18°22.453'	23:48	02:07	1123	1096
S8	12	41°29.971'	18°50.127'	04:47	06:35	324	310
S15	13	41°02.365'	18°31.554'	05:36	07:38	939	900
S16c	13	40°53.072'	18°57.210'	11:48	13:09	317	300
S22	14	40°05.222'	19°21.708'	18:03	20:25	965	900
S21	14	40°05.008'	19°08.001'	22:17	00:28	972	900
S23	15	39°40.001'	19°22.009'	18:01	20:29	1172	1100
S24	15	39°40.004'	19°08.008'	22:14	00:23	1089	1000
S25	16	39°39.917'	18°22.140'	04:26	05:59	261	210
S20	16	40°05.012'	18°50.071'	14:50	16:41	738	700
S19	17	40°26.801'	18°32.195'	10:19	11:42	127	100
S14	17	41°02.305'	17°52.030'	18:02	19:51	699	600
S11	18	41°29.991'	17°34.972'	07:10	09:25	1137	1060

3.2. Neuston Collection

A neuston net (1 x 0.5 m rectangular mouth opening and a 200 µm mesh size), equipped with lateral buoys to float on the sea surface with the upper border at 5 cm above the sea level, was used to collect neuston in a total of 27 stations (Figure 2). The net was towed at the speed of 1 kn. The presence of a flowmeter at the center of the mouth allowed to measure the volume of filtered water at each sample collection. The filtered volume (m³) for each sample was calculated by approximately correcting the value by an average of 90% of the net mouth surface (on the basis of the non-complete submersion of the net mouth). At each sample collection, the neuston was immediately stored in 50 ml Falcon tubes with 95% ethanol (final concentration, 80-90%). At each station, abundance data represent the average of two neuston collections. For more sampling details see Liparoto et al. [44]. Environmental parameters on Brachyura larvae swarm sites were shown in Table 2. Temperature, salinity and dissolved oxygen (CTD) vertical profiles were obtained by a multiparametric probe incorporated into a carousel of 5L Niskin bottles. Due the mostly superficial presence of Brachyura larvae, only surface water characteristics (over the thermocline) were used to calculate its pelagic life duration (PLD).

Table 2. Hydrological parameters (salinity, temperature, dissolved oxygen) of the sea water in the South Adriatic Sea at stations Penna Grossa (PGR), and S13, and as average values of the whole basin.

Station	Local date	Position		CTD Surface			CTD Bottom		
	May 2013	Lat. N	Long. E	S	T (°C)	O ₂	S	T (°C)	O ₂
PGR	17	40°45.67	17°47.00	38.33	18.44	5.07	38.86	14.79	4.89
S13	17	41°02.30	17°35.04	37.20	19.69	5.12	38.80	13.89	4.93
Average, 30 stations	---	---	---	37.89	18.97	5.11	38.84	14.35	4.87

3.3. Laboratory Analysis

In the laboratory, a qualitative–quantitative analyses of both mesozooplankton and neuston samples were performed. BIONESS sub-samples, ranging from 1/10 to 1/25, were analyzed for species identification and specimens counts, depending on the total sample richness, while identification of rare species was carried out on the entire sample. For the neuston, mesozooplankton and decapod larvae were sorted and quantified. At the stations PGR and S13 (Table 2), Brachyura larvae (zoeae and megalopae) were found as dominant on the remaining zooplankton community [44]. Such abundant populations were chosen for the study of Brachyura dispersion and, consequently, the larvae were identified at higher taxonomic levels using the guides given by [58-62]. Larvae derived

from BIONESS collections where roughly identified as Decapoda, containing not only Brachyura but, in less extend, also Anomura and shrimp larvae. BIONESS samples were not collected in PGR and S13 coastal stations (those interested by the Brachyura swarm), but their results have been used to have a general picture of decapod larvae abundance (ind. m⁻³) and distribution in the whole south Adriatic basin.

3.4. Statistical Analysis

To assess the vertical partitioning of the decapod larvae by daytime and nighttime abundances, the Weighted Mean Depth (WMD) was calculated according to the equation: $WMD = \frac{\sum(n_i \times z_i \times d_i)}{\sum(n_i \times z_i)}$, where n_i is the number of ind. 100 m⁻³ in the i layer, d_i is the depth of a sample i (centre of the depth interval), and z_i the thickness of the layer [63-64]. Based on the vertical profiles of temperature and salinity at each station, the thickness of the thermocline and halocline layers were visually estimated. Likewise, the depth at which the fluorescence reached the maximum was considered as the Deep Chlorophyll Maximum (DCM) depth. Then the correlations between these parameters and the abundance of decapod larvae in the seventeen stations were tested using the Kendall rank-based test, which does not rely on any assumptions on the distributions of the dependent and independent variables.

3.5. Surface Drifters

Lagrangian, i.e. water-following, instruments are best suited to study transport and dispersion in the marine environment [65-66]. A total of 26 CODE drifters (for a description see Pisano et al., [67] or Zambianchi et al. [46]) have been employed to reconstruct the surface water circulation in the south Adriatic, during the period of the cruise. Their 2-D motion has been tracked by satellite, for a maximum period of 6 months (corresponding to the maximum duration of the batteries). The present study only took into consideration the tracks of 4 drifters transiting in the same area of Brachyura larvae swarm (stations PGR and S13) at the same period of their localization, i.e. from 2 days before to 10 days after their collection (Table 3). Based on the water temperature, a PLD of 40 days has been established for the larvae (zoeae, mostly of the first instar) found in May 2013 at stations PGR and S13, (surface water temperature 18.44 and 19.69 °C; average of the whole basin, 18.97°C, and never more than 21.15 °C in the other stations).

Table 3. Identification code of the drifters entering the box-area containing the stations where Brachyura larvae were abundant in the neuston (date of collection, 17 May 2013). Only drifters entering the delimited area in the period 15-27 May have been considered.

Drifter	Drifter code	Date (May 2013)	Position	
		Entrance in the box-area	Lat. N	Long. E
A	300234011313880	25	41.361	17.484
B	300234060849380	15	41.361	17.884
C	300234060240900	27	40.661	17.884
D	300234011313890	20	40.661	17.484

CODE drifter motion represents the uppermost 1 m of the sea surface circulation; their GPS positions were accurate to a 10 m order of magnitude and were transmitted/recorded every 15 min. Raw data were edited to remove spikes and errors and are available at <http://www.coconet-fp7.eu>. An area (rectangular box) has been individuated around the two selected stations (PGR and S13), considering them as the starting points for the larvae drift. The selected box-area had size of 0.7° Lat N x 0.4° Long E (Table 3).

4. Results

4.1. Hydrographic conditions

A different vertical structure of the water masses between Apulian, offshore and Albanian stations, characterized the oceanographic conditions of the mid-May late spring sampling period. Temperature and salinity profiles (Figure 3), show an evident stratified temperature and a marked thermocline between 20 and 40 m that separates the upper layer from the underlying layers, with a difference of about 4-5° C between the upper (warmer) and the lower (colder) layer. A marked halocline was evident deeper (18-26 m) on the Italian side than on the Albanian one (5-15 m). Horizontal and vertical variability of thermohaline characteristics evidenced some marked differences both among stations and along the sampled water column.

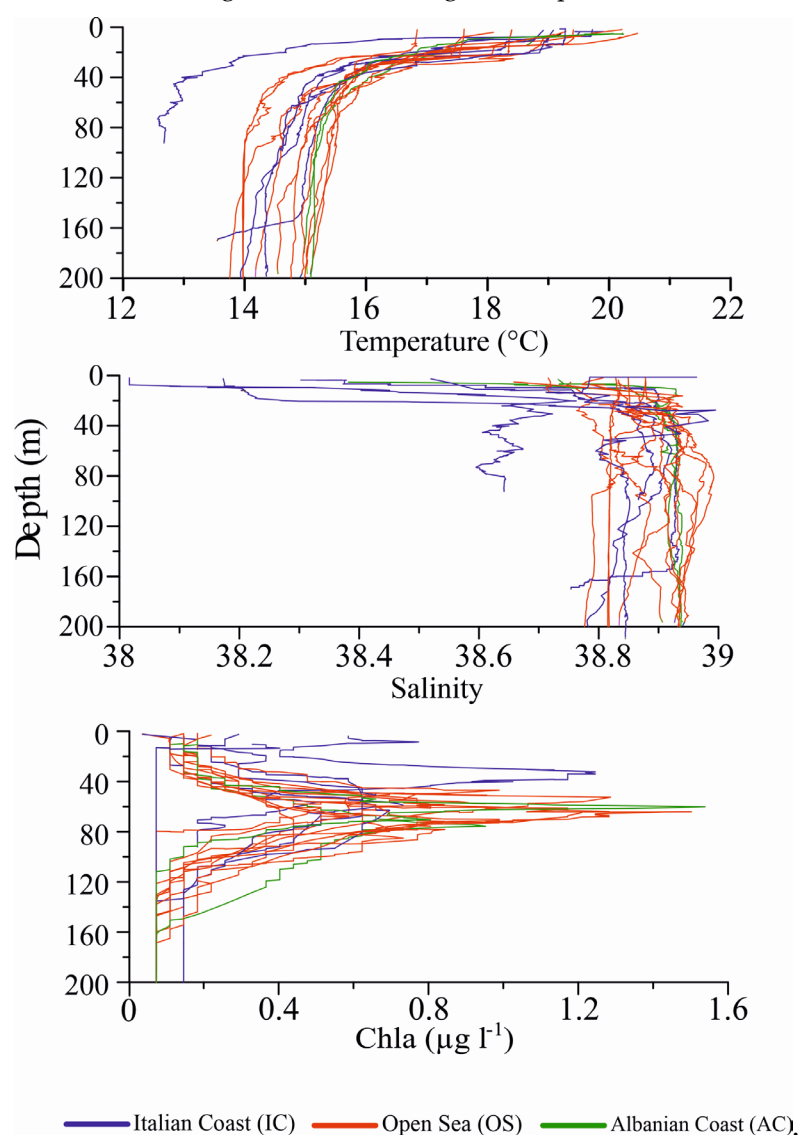


Figure 3. Potential temperature, salinity and fluorescence vertical profiles at all sampled stations, from surface down to 200 m (IC: S1, S3, S25, S19, S14 stations; OS: L41, S10, S15, S16c, S22, S23, S21, S24, S20, S11 stations; AC: S7, S8 stations).

Fluorescence profiles showed maxima in the layer between 50 m and 80 m in depth for all the stations (Figure 4), except for St. S1 that showed highest chlorophyll *a* concentration at about 35 m (1.17 mg m⁻³). A different depth of the DCM among sites was detected. Generally, in the areas close to the coast and in Otranto Channel this maximum was found at about 60 m, but with very different

max chlorophyll *a* values: 0.696 mg m^{-3} , 1.54 mg m^{-3} and 1.12 mg m^{-3} , in the Apulian and Albanian sides and Otranto Channel, respectively.

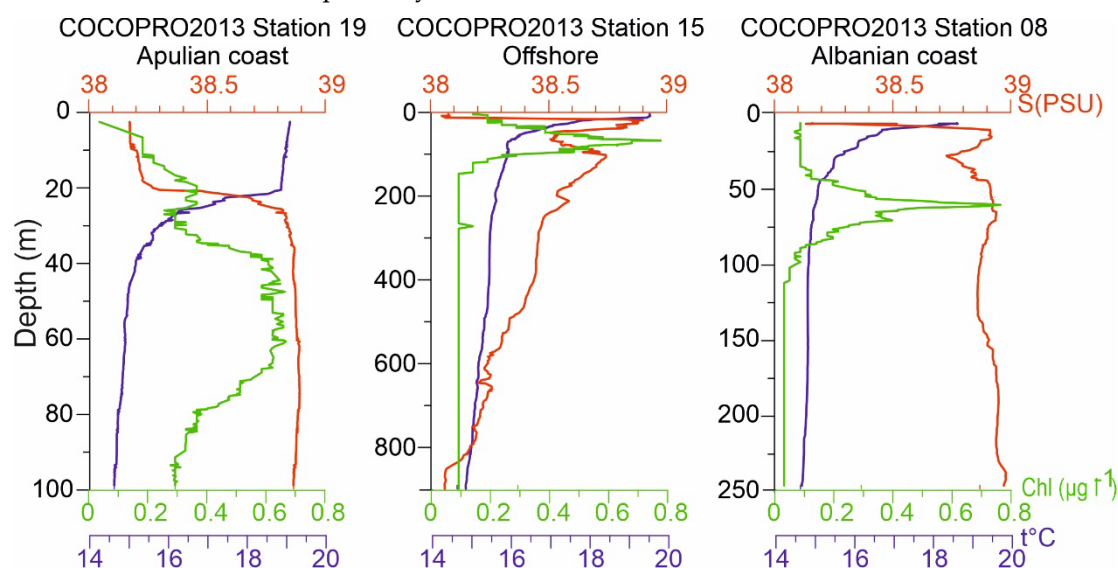


Figure 4. Vertical profiles of Temperature ($^{\circ}\text{C}$), Salinity, and Chl *a* ($\mu\text{g L}^{-1}$), at stations S19, S15, S08 in the CoCoNet cruise 2013 as representatives of Italian, central South Adriatic, and Balkan coast, respectively. Please note that depth scales vary.

4.2. Zooplankton and Decapod Larvae Spatial Distribution

The total zooplankton mean abundance was $442 \pm \text{SD } 258 \text{ ind. m}^{-3}$. Copepods were the most abundant taxon representing from 72 to 91% of the total zooplankton, with a mean abundance of $401 \pm 236 \text{ ind. m}^{-3}$. Zooplankton abundance and biomass (Dry Mass) were higher on the Italian ($408 \pm 811.7 \text{ ind. m}^{-3}$ and $9.7 \pm 15.5 \text{ mg m}^{-3}$, respectively) than Albanian coasts ($219 \pm 53.0 \text{ ind. m}^{-3}$ and $5.4 \pm 2.7 \text{ mg m}^{-3}$). Spring holoplankton accounted for the main part of the zooplankton (85-98%). At the chlorophyll maximum depth, between 20-40 m and 60-80 m, abundance peaks of the most representative species occurred.

Meroplankton percentage increased along the Albanian coasts, mostly due to bivalve and polychaete larvae. Crustacean decapod larvae represented less than 0.7% of the zooplankton community and about 7.2% of the meroplankton. Decapod larvae densities were higher along the coastal and continental shelf waters, rather than in offshore pelagic waters (Figure 5). In the integrated 0-100 m layer abundance values were highly variable (0.44 to $88.89 \text{ ind. m}^{-2}$ in the stations 23 and 19, respectively). In decreasing abundance order, follow the stations S7 ($45.16 \text{ ind. m}^{-2}$), S22 (26.11), S14 (16.89) and S3 (16.22). In four stations (L41, S16c, S20, S21) no decapod larvae were found.

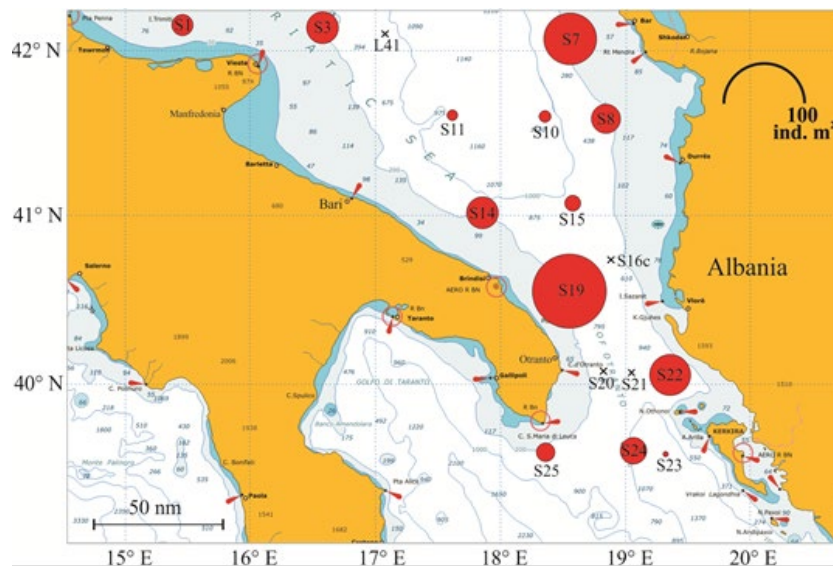


Figure 5. Representation of decapod larvae abundance. Values come from the integration of 0-100 m surface layer, and they are referred to a water column of 1 m² basis and 100 m of depth. Stations PGR and S13 (interested by a swarm of *Brachiura* larvae) were not interested by the BIONESS collection.

Decapod larvae vertical distribution is shown in Figure 6. Among the nine stations with a depth greater than 700 m, only in two (S22 and S23) very few decapod larvae were found in the layers between 400 and 800 m depth. More than 95% of the larvae occupied the 100 m surface layer. Higher larvae concentrations occurred in the 0-20 m in station 19 along the Italian coast (about 436 ind. 100 m⁻³) just over the thermocline, and in the layer 20-60 m in the S7 on the Albanian side (113 ind. 100 m⁻³) below the thermocline and over the DCM. In the other stations the concentration of decapod larvae was lower than 70 ind. 100 m⁻³.

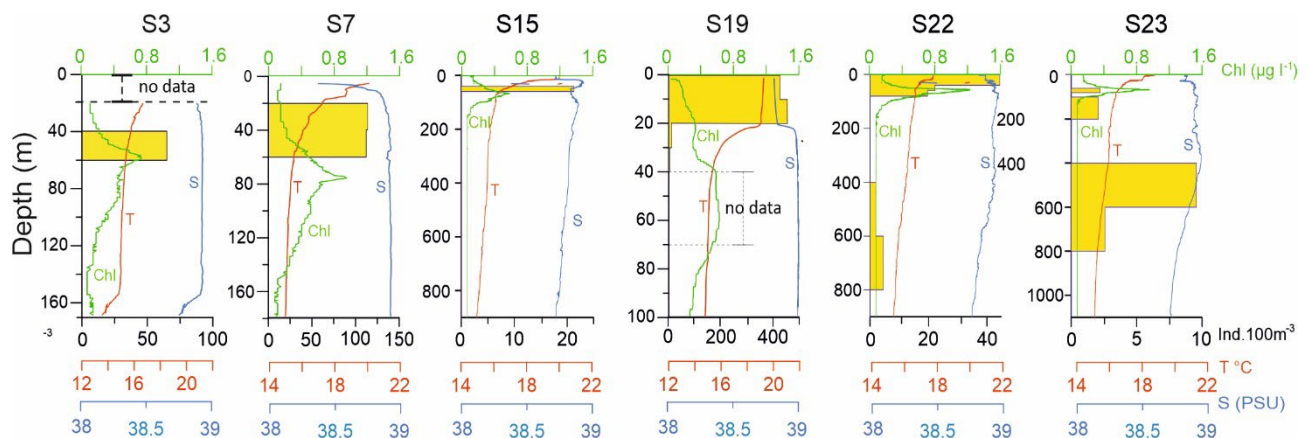


Figure 6. Vertical distribution of crustacean decapod larvae in six selected stations. .

4.3. Diel Vertical Migration

To examine temporal changes in the vertical distribution of decapod larvae abundance (%), in the absence of daily vertical catches in a fixed station, ten coastal and offshore BIONESS samples were chosen, and sorted according to the daily sampling time (Figure 7). Decapod larvae showed clear diel vertical migration, that did not appear to be affected by the difference among inshore and shelf stations physical conditions.

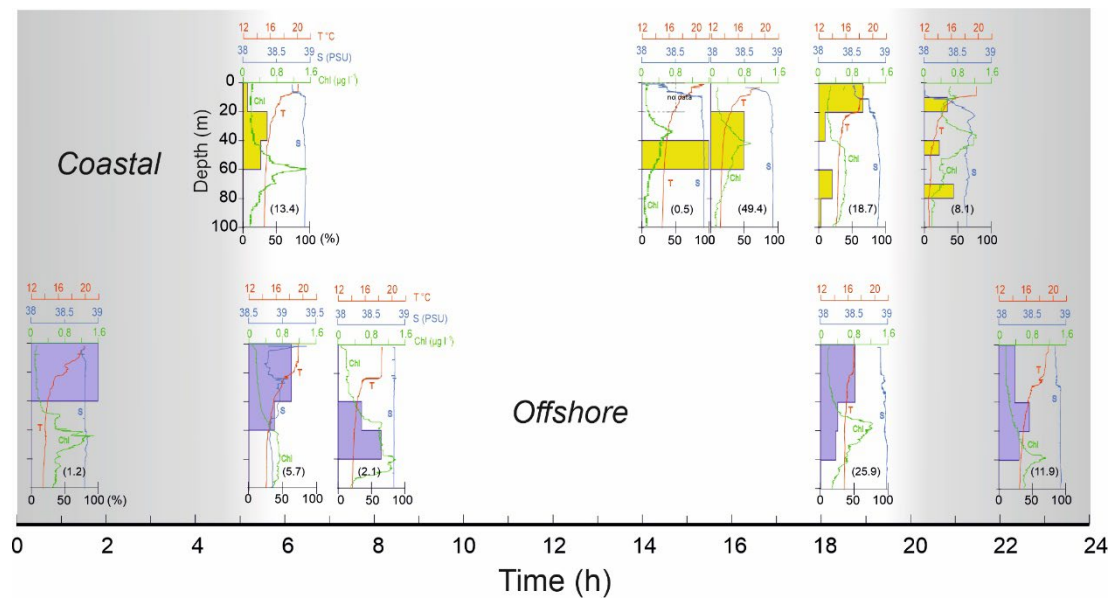


Figure 7. Vertical distribution of decapod larvae (as percentage of total numbers) from the BIONESS hauls at coastal and offshore five stations selected according to the daily sampling time. Numbers in brackets are average abundance in ind. m^{-3} for the entire water column at each sampling time.

In the morning, between 07:00 and 08:00 h, about one hour after sunrise, the whole community of decapod larvae is distributed between 40 and 80 m depth, with the greatest percentage between 60 and 80 m. At the beginning of the afternoon, between 14:00 and 16:00 h, the community remains between 40 and 60 m, even if a part is distributed up to 20 m. Between 18:00 and 21:00 h, in the period prior to night, their distribution is almost bimodal, with the highest percentage in the first 20 m (coastal) and up to 40 m (offshore) and low number of individuals up to at 80 m. Between 22:00 and 24:00, at the beginning of the nocturnal period, the community occupies almost the whole water column between surface and 80 m depth, with about 50% between 60 and 80 m. Between midnight and 02:00 h, their distribution entirely occupies the layer between the surface and 40 m. Before sunrise, between 05:00 and 06:00 a migration to the deeper layers is evident and ends after sunrise. Figure 8 shows the WMD trend both in coastal (bottom 100 m depth) and offshore stations (bottom 600 m depth). It seems that the migratory behavior of decapod larvae in coastal stations is quite regular between 20 and 60 m depth and daily time independent. In offshore stations, on the other hand, migration is classically compatible with the day-night cycle, where a minimum WMD value is evident at about 20m at night which gradually becomes deeper up to late afternoon (about 19.00-20.00 h) when the migration towards the surface layers begins.

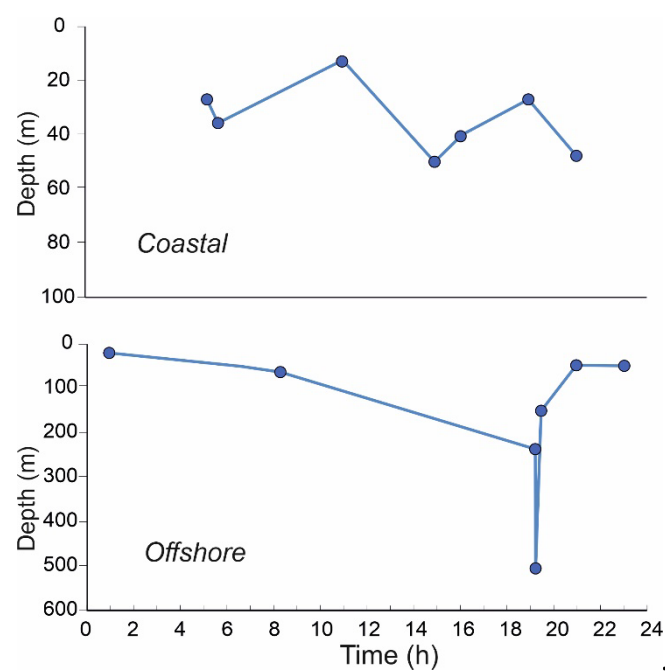


Figure 8. Vertical profiles of decapod larvae WMD values in coastal and offshore stations, according to the daily sampling time.

4.4. Vertical Larvae Distribution in Relation to Environmental Variables

Decapod larvae abundance appears significantly and inversely correlated to the thermocline layer thickness ($\text{Tau} = -0.51$, Kendall rank-based test, $p < 0.01$), and is therefore lower in offshore waters than in coastal waters (Figure 9). However, this abundance is not significantly correlated either with the DCM depth or with the halocline thickness ($p > 0.05$ Kendall rank based test).

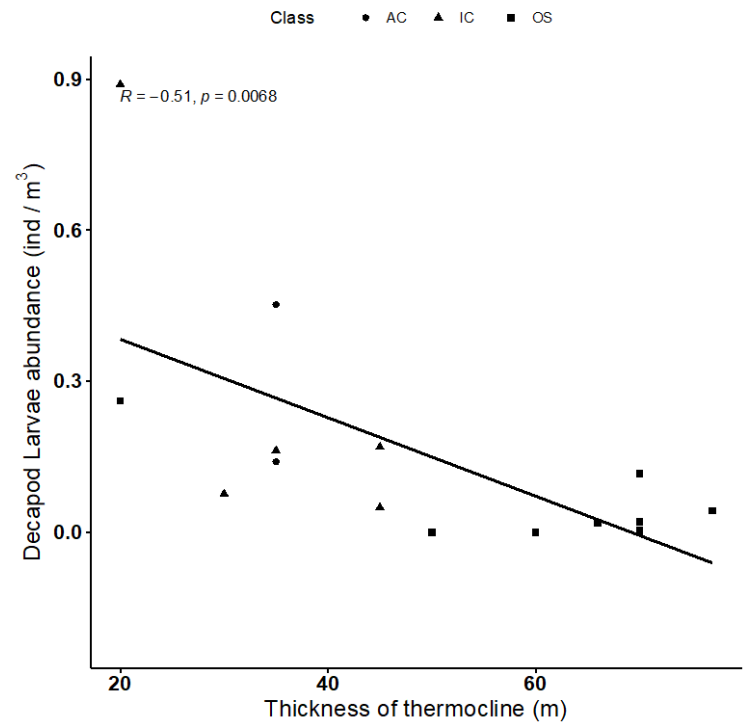


Figure 9. Relationship between decapod larvae abundance and thermocline thickness in each station (AC – Albanian Coast, IC – Italian Coast, OS – Open Sea).

4.5. Neuston Collection

Decapod larvae have been collected in the neuston of many stations of the South Adriatic in the same cruise (see Liparoto et al. [44]). Among Decapoda (Table 4), Brachyura larvae (zoeae and megalopae) were considerably abundant (about 0-50 cm below the sea surface) of isolated coastal stations. In May 2013, their abundance ranged between 0 and 3.75 ind. m⁻³ in the whole neuston collection, but PGR and S13 (Italian side of the basin) showed concentrations of 93.02 and 231.00 ind. m⁻³, respectively. In the same station S13 the highest number of Natantia larvae was recorded (593.97 ind. m⁻³). In total the average mean of the four groups of Decapoda was 34.82 ind. m⁻³ ± 150.29. Average abundance values of decapod larvae obtained by fifteen neuston stations, twenty-three mesozooplankton (WP2) stations and seventeen multilayered (BIONESS) collections, gave results of 1.87 and 0.34 ind. m⁻³ in neuston and water column, respectively.

The detailed analysis of data from the two rich neuston stations (S13 and PNG) allowed the recognition of Brachyura (Table 5) as the main components of the whole decapod assemblage. The identified larvae were mainly zoea-I instar belonging to a total of 11 species, largely (87%) represented by *Xantho granulicarpus*.

Table 4. Decapod larvae abundance (ind. m⁻³) in the whole neuston collection.

Station	Natantia larvae	Brachyura larvae	Decapoda macrura	Anomura larvae
S20	0.04	0.00	0.00	0.00
S21	0.00	0.39	0.11	0.00
S22	0.88	0.30	0.00	0.00
S23	0.79	3.73	0.00	0.00
S24	0.46	0.64	0.00	0.00
S25	0.15	0.15	0.00	0.67
Pennagrossa	6.30	93.52	0.00	0.00
Tremiti	0.89	5.38	0.00	0.00
L41	0.00	0.00	3.65	0.00
Sazan	0.00	0.45	0.00	0.00
Bar	0.23	2.38	0.21	0.50
Ulcinj	31.60	0.00	0.00	0.00
Budva	0.00	0.12	0.00	0.00
Gram	0.06	0.00	0.00	0.00
Plazh Ari	0.00	0.00	0.00	0.00
S.Andrea	13.54	3.68	0.70	0.00
S13	533.97	258.21	3.06	0.00
S19	0.42	0.46	0.00	0.00
S16c	0.05	0.01	0.00	0.00
S14	0.07	0.92	0.00	0.00
S07	0.15	0.61	0.00	0.00
S11	0.00	0.02	0.00	0.00
S15	0.00	0.00	0.00	0.00
S03	0.00	0.11	0.00	0.00
S08	0.65	0.17	0.08	0.00
S10	0.00	0.00	2.80	0.00
S12	0.32	1.12	0.00	0.00
S17	0.21	0.12	0.00	0.00
Mean	21.10	13.30	0.38	0.04
SD±	100.72	51.11	1.00	0.15

Table 5. Larvae identified in the two cruises and relative instars (Z1–Z6 = zoea stage, instars 1-6; M = megalopa stage; undet. = not determined). Reported numbers indicate percentages on the total of larvae.

Family	Species	Cruise (May 2013), stations PNG and S13								
		Z1	Z2	Z3	Z4	Z5	Z6	undet.	M	tot
Leucosiidae	<i>Ebalia nux</i> A. Milne-Edwards, 1883	0.9								0.9
Epialtidae	<i>Acanthonyx lunulatus</i> (Risso, 1816)	1.2	0.7							1.9
Pirinelidae	<i>Pirimela denticulata</i> (Montagu, 1808)	0.5		0.5						1.0
Geryonidae	<i>Geryon longipes</i> A. Milne-Edwards, 1882	0.2								0.2
Portunidae	<i>Carcinus aestuarii</i> Nardo, 1847			0.2						0.2
Goneplacidae	<i>Goneplax rhomboides</i> (Linnaeus, 1758)		0.5							0.5
Xanthidae	<i>Xantho granulicarpus</i> Forest, in Drach & Forest, 1953		86.7							86.7
Polybiidae	<i>Liocarcinus</i> sp.							0.5		0.5
Pilumnidae	<i>Pilumnus</i> sp.		0.2							0.2
Grapsidae	<i>Pachygrapsus marmoratus</i> (Fabricius, 1787)	0.2								0.2
	<i>Brachyura</i> undet.							7.3	0.2	7.5

4.6. Transport by Surface Currents

The basin- and sub basin-wide circulation described by CODE drifters deployed in the framework of the May 2013 cruise, has been discussed in two recent papers [68-69]. Lagrangian surface trajectories accurately depict an overall cyclonic circulation, dominated by a northwestward coastal current along the Balkan coast, commonly reported as EAC (East Adriatic Current) and a southeastward one along the Italian coasts (WAC, or West Adriatic Current). West-East connections are guaranteed by three cyclonic recirculations localised in correspondence of the three morphologically distinct sub-basins of the Adriatic Sea (northern, central and southern).

In consideration of the approximate PLDs evaluated as above described, we considered the backward and forward destiny of surface drifters passing by stations with high concentration of larvae, for a drifting time of 40 days (as often done in physical-biological studies [70-71]). As mentioned in the Materials and Methods section, we broadened this high concentration points into a 0.7° Lat by 0.4° Lon rectangular region (Figure 10). The drifter trajectories passing through the box (and so possibly the zoeae tracks) are characterized by a local southeastward direction off the Apulian coasts, roughly following the WAC. Two of them (drifters A and B) eventually turn eastwards, following the southernmost branch of the SAG, but only B reaches the continental shelf (i.e. depths less than 200 m) on the opposite side of the basin, whereas A is trapped by higher bathymetry (Figure 10).

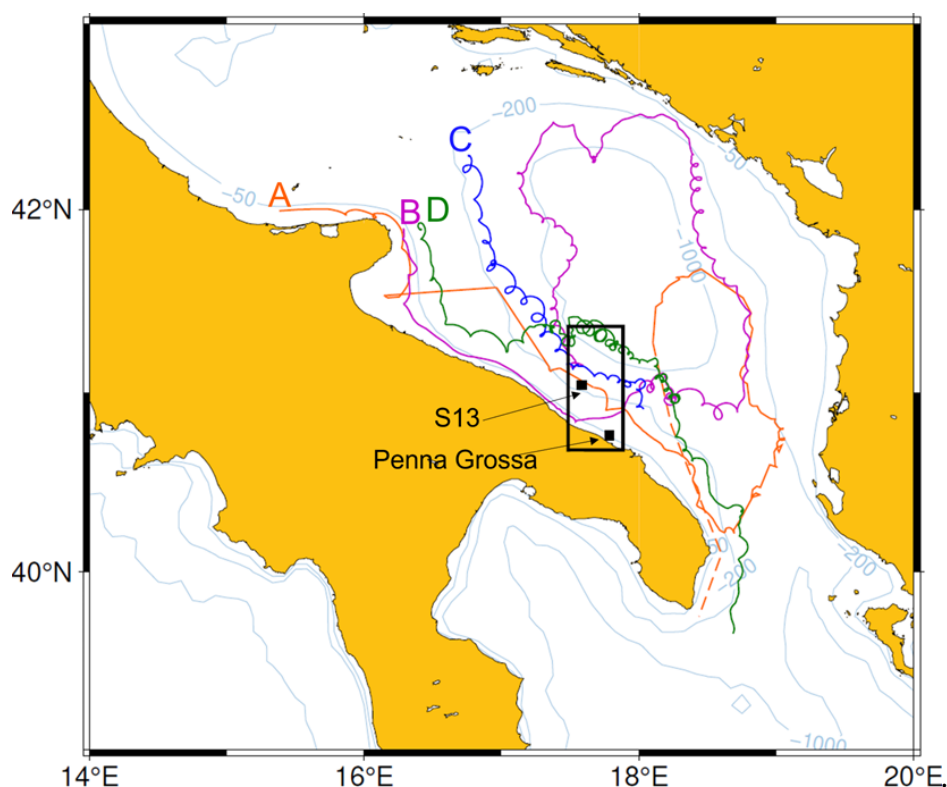


Figure 10. Trajectories of 4 drifters passing close to PGR and S13 stations (black squares in the rectangular area) at the time of the *Brachyura* larvae swarm. Trajectory starting points are marked by the corresponding drifter names (letters A to D). Dashed lines refer to poorly sampled tracks segments.

4. Discussion

The vertical profiles of temperatures in May 2013 show a thermocline between 20 and 40 m depth and generally above the DCM. Larvae of decapods (collected with BIONESS in the whole basin) appeared strongly linked to such a layer, suggesting that they are involved in surface water circulation. Among Decapoda, larvae of *Brachyura* are reported as typical components of the neuston [25], and well persisting in the first 50 m if deriving from coastal benthic species [26]. Also in the present study, multilayer samplings carried out over the whole studied area, suggested that Decapoda larvae preferred the uppermost water layers (0-40 m). The aggregation of such a rich plankton component at the sea surface justifies a prediction of their horizontal distribution with time, based on surface drifter movements. The availability of a set of surface drifters deployed during the same cruise when zooplankton and neuston have been collected, allowed us to assess the destiny of surface water masses and indirectly the destiny of their content in terms of larval populations. In fact, although possible exceptions exist, water masses above the thermocline can be considered as homogenous from the oceanodynamic point of view. Our assessment has been tuned on a definition of the PLD derived from the literature (even though for different species). The maximum PLD relative to the larval stage/age and to the sea surface temperature of May 2013 resulted to be 45 days (mainly zoeae). Surface drifters transiting through the area containing the sampling stations were followed backward and forward in time for a total of 40 days, in order to reconstruct a possible larvae dispersal path. Even though PLD is not known for the species found in abundance during the considered period (*Xantho granulicarpus*), literature data suggest as possible a cross of the South Adriatic Sea from west to east. The species mainly represented in the samples of the present study is common along the Mediterranean coastline and inter-population genetic connections among crab species is documented. It is known that the littoral crab *Pachygrapsus marmoratus* is genetically uniform in the whole Mediterranean Sea [72] even if compared populations are separated by thousands of kilometers. Schiavina et al. [73], however, established that coastal crabs of different

species are genetically related and grouped in three areas of the Adriatic Sea: North, Central, and South, independently from their collocation on the Italian or Balkan coastline. This mirrors the circulation of the Adriatic, which can be summarized in an overall cyclonic circuit, further subdivided, both morphologically and dynamically, into three sub-basins and three corresponding cyclonic re-circulations. In terms of transport of passive particles, an asymmetry has been observed in the zonal exchange, with a preferential East to West surface connection with respect to the opposite, West to East one [68]. This is witnessed by the successive results by Bray et al. [24] who assessed a preferential transfer of larvae from the eastern to the western coast, with the southwestern coast (i.e. the Apulian one) functioning mainly as a sink area. Fraser et al. [74] demonstrated that for many coastal taxa transoceanic transport and landfall occur thanks to passive rafting of adults on buoyant objects, more than larvae drift. On this basis, Trembl et al. [75] predicted that for 95% of coral reef species, the larval settlement occurs within 155 km of source population and/or within 13 days.

To obtain an indication of the vertical distribution of *Brachyura* larvae the multilayer samplings of the BIONESE were used as a reference, although they did not interest the stations rich in *Brachyura* larvae. Larvae of BIONESE samples in general appeared as scantily concentrated confirming the exceptionality of the result coming from PGR and S13 stations. From the analysis of the whole sample set collected, it is evident that decapod larvae swarm interested heavily only and just stations PGR and S13. The present study shows that *Brachyura* larvae generated at level of the stations PGR and S13 mostly disperse alongshore in South-East direction. The West-East coast connection for neritic crab species based on larvae dispersal is possible, but weak, because based on only $\frac{1}{4}$ of the individuated dispersal paths, and because the survival rate of *Brachyura* larvae after 40 days should be very low. It is possible that *Brachyura* use other solutions than planktonic larvae to disperse in large geographic areas. Discontinuous geographic presence of corals in isolated Pacific atolls has not been justified with larvae dispersal, but with rafting of the benthic phase on buoyant pumice [76]. The geographic distribution of Hydrozoa in the Mediterranean Sea does not correspond to the existence and duration of the planktonic stage (the medusa) in the life cycle of each species [77]. The role of no planktonic stages in the geographic distribution of neritic benthic organisms, and in the connectivity of distant populations, has been investigated in further depth taking into consideration viable fragments (the so called asexually produced propagules). These are sometimes more abundant than larval stages in coastal plankton [78-80]. Additionally, also resting stages might allow species to perform long travels and/or to be relatively insensitive to ecological barriers [81]. Whatever the nature of the propagules, their dispersal mechanisms represent an open question, the main problem being a quantitative assessment of the phenomenon. Such alternative dispersal strategies justify species distribution and genetic flow between populations, more than that attributable to larvae.

5. Conclusions

The present study proposes a general framework for *Brachyura* larvae circulation (*Xantho granulicarpus*, in detail). The PLD obtained from literature data, based on larval age and on water temperature, and the study of drifter motion in the southern Adriatic suggested that zonal coast to coast crossing from Italian to Balkan side by larvae is possible in the studied period and at the investigated latitude, but it appears as not sufficiently reliable to ensure inter-population connectivity. Particularly, most drifters (here considered as proxies for larvae in the surface layer) moved mostly along shore (southeastwards) and crossed the basin in only one case among 4, in agreement with Carlson et al. experimental and numerical findings [68]. Finally, the high mortality which affects crab larvae, further should reduce the drifting survivors down to a negligible number. All these considerations suggest that the recorded huge swarm of *Xantho granulicarpus* larvae on the Apulian side of the southern Adriatic, is probably not enough to justify a genetic connectivity of the two opposite populations, and to push for alternative solutions for maintaining such a connectivity.

The genetic connection of Adriatic benthic populations has been ascertained (see the case of Fratini et al. [72]). This notwithstanding, the limited possibility of *X. granulicarpus* larvae to cross the south Adriatic during their PLD, reduces their importance in the framework of genetic connection of

opposite side populations, and confines them mostly to the renewal of very close (adjacent) populations. Weersing and Toonen [82] already found that in the marine environment average PLD is poorly correlated with connectivity calculated on the genetic structure of populations. This was confirmed, among others, by a successive study by Tremblé et al. [75] where the different role of PLD in local- and broad-scale connectivity is discussed and suggested that 95% of the connectivity based on larvae occurs within the first 13 days and 155 km from the source population. The present study, conducted directly in the field, adds information to many others, with newly considered species, areas, and/or seasons. Connectivity of Brachyura populations results not reliable if exclusively linked to planktonic larvae, and other distributional strategies are probably available for every species.

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