Distribution of echinoderm larval populations in the geostrophic frontal jet of the eastern Alboran Sea

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ABSTRACT

A survey of selected echinoderm larvae and postlarvae was conducted during Almofront-1 cruise in the eastern Alboran Sea (Mediterranean Sea). In the study zone, surface waters from the Atlantic current enter *via* Gibraltar forming a hydrologically complex area with associated eddies and gyres. The distribution pattern of echinoderm larvae is described and related to specific biological and physical frontal processes responsible for larval retention or dispersal. In the part of Alboran Sea, influenced by Mediterranean waters, echinoderm larvae and postlarvae were quite scarce in comparison to the stations localised in the Atlantic jet and sites under influence of Atlantic waters where species richness and larval abundance were higher. The Anticyclonic gyre which originates in the Atlantic current could act as a hydrodynamic trap maintaining larvae near the African coast where recruitment is possible.

RÉSUMÉ

Distribution des larves d'échinodermes dans un jet frontal géostrophique de l'est de la mer d'Alboran.

La distribution des larves et post-larves d'échinodermes méroplanctoniques est décrite dans la partie est de la Mer d'Alboran (Méditerranée S.E). Les pêches examinées ont été effectuées au cours de la campagne Almofront-I dans une zone où les eaux de surface du courant Atlantique entrant en Méditerranée par le détroit de Gibraltar forment un système de jet frontal géostrophique. La répartition spatio-temporelle des larves a été étudiée en relation avec quelques processus biologiques et hydrodynamiques de cette région capables de favoriser la rétention des larves ou leur dispersion. Dans la zone située sous l'influence des eaux méditerranéennes les larves et post-larves sont peu diversifiées et peu nombreuses. Dans le courant et les sites sous l'influence des eaux atlantiques la diversité et l'abondance larvaire sont plus grandes. Le tourbillon anticyclonique qui provient du courant atlantique semble constituer un piège hydrodynamique maintenant les larves et post-larves près de la côte Africaine où peut se faire le recrutement.

INTRODUCTION

Oceanographic processes governing the evolution of water masses have therefore a control in the spatial distribution and in the faunistic composition of the plankton at the corresponding scale (Haury et al., 1978; Greenblatt, 1982; Legendre and Demers, 1984; Boucher et al., 1987; Sinclair, 1988). Concerning marine invertebrates, the majority of them possess pelagic eggs and larvae. These larvae are produced during well-defined periods, and due to their limited means of locomotion, generally display a passive behaviour relative to the movement of water masses. The success of planktonic larval life depends on the transport to suitable areas for later development and subsequent recruitment. Some work has emphasised the importance of hydrodynamical structures as fronts and gyres on larval dynamics and consequently on recruitment (Yamamoto and Nishizawa, 1986; see review of Young and Chia, 1987; Hill, 1990; Davis et al., 1991; Farell et al., 1991; Le Fèvre and Bourget, 1992). However, processes involved in larval retention and dispersal are best understood for shallow coastal waters, such as estuaries, bays or reefs (Cronin and Forward, 1982; Epifano et al., 1984; Banse, 1986; Emlet, 1986; Epifano et al., 1988; Black and Moran, 1991; Benzie et al., 1994). Few studies have examined the transport of meroplankton in the open sea (Pearce and Phillips, 1988; Pedrotti and Fenaux, 1992; Hill, 1991).

The purpose of this paper is to relate the influence of mesoscale hydrodynamical structures (gyres and fronts) associated with the Atlantic current flowing into the Medi-

terranean sea on echinoderm larvae distribution. Extensive experimental and field investigations were carried out during Almofront-1 cruise in the Eastern Alboran Sea (Mediterranean Sea) in order to study the physical and biological processes associated with a strong geostrophic frontal jet at the boundary between the surface inflow of Atlantic and the resident Mediterranean water (Prieur et al., 1993; Prieur and Sournia, 1994). Our study is a spatio-temporal survey of echinoderm larvae and postlarvae; their distribution pattern was described and compared to biological features and hydrological structures capable of influencing larval retention or dispersal.

MATERIALS AND METHODS

The cruise Almofront-1 was carried out from 24 April to 26 May 1991 on board R/V L'Atalante (Prieur and Sournia, 1994). It was divided into two legs. In leg A, a grid of 83 stations 11 km apart were sampled with a CTD (conductivity, temperature, depth recorder) in the Alboran Sea to locate the jet and associated eddies and to map the mesoscale hydrological structures of the Eastern Alboran Sea (Fig. 1 A). To determine the internal structure of the frontal jet, physical data were also collected by four Tow-yo sections across the frontal jet using a towed ADCP (Acoustic Doppler Current Profile) and up-and-downing CTD equipped with a oxygen and fluorescence probes (Prieur et al., 1993). According to Prieur et al. (1993), two major structures were noted north of the jet front system: 1- an
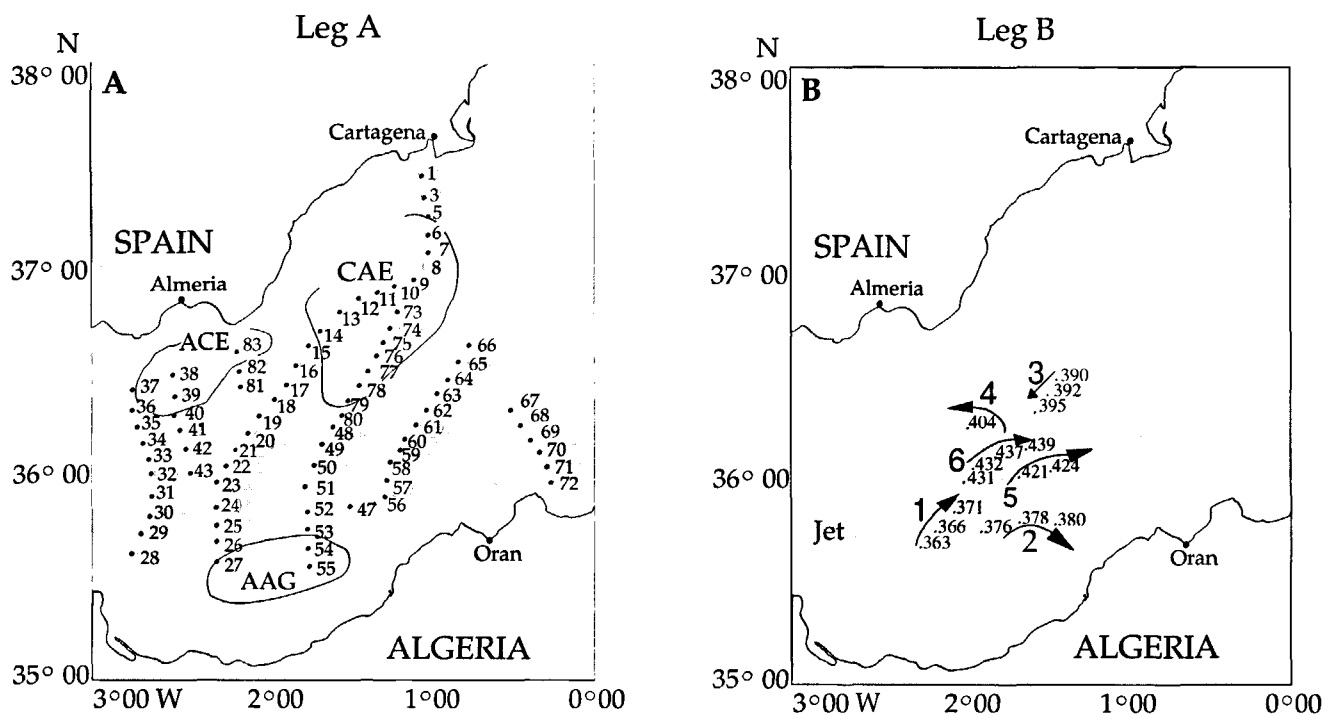

Figure 1

Alboran Sea (SW Mediterranean Sea) with the location of the Atlantic jet. A : the 83 CTD-rosette stations of the synoptic survey during Leg A, the 18 stations where zooplankton were collected are shaded. ACE (Almeria Cyclonic Eddy), CAE (Cartagena Anticyclonic Eddy) and AAG (Atlantic Water Anticyclonic Gyre). B: localisation of the zooplankton hauls at the six sites of the Leg B across the frontal system and position of zooplankton tows around sites. Arrows indicated the position and drift of the sediment traps which were followed for positioning stations (modified from Prieur and Sournia, 1994).

anticyclonic eddy South of the Cartagena CAE (Cartagena Anticyclonic Eddy) and, 2- a weak eddy ACE (Almeria Cyclonic Eddy) both at 200 m depth (60 and 30 km in diameter respectively). To the south, the anticyclonic gyre AAG (Atlantic Anticyclonic Gyre) recirculates Atlantic water (Fig. 1 A).

During the leg B, 6 well-established hydrological sites were determined across the frontal jet structure by following the surface buoy of drifting sediment traps lines (Prieur *et al.*, 1993). Sites were characterised hydrodynamicaly using data from ADCP and CTD and ranked according to the depth of the isopycnal 1028.00 kg m^{-3} which decreases from the South to the North as follows: site 2 was located in the south of the jet in the Atlantic water (AAG), site 1 was located in the right of the main jet of inflowing Atlantic water, site 5 in the left side of the Atlantic jet, site 6 was located on the left edge of the jet in the boundary of the front, site 4 was located outside of the jet in Mediterranean water and characterised by a divergence and site 3 was situated northward of the jet in an antyciclonic eddy and was the most influenced by Mediterranean oligotrophic waters (Fig. 1 B).

During leg A, zooplankton were sampled in 18 of 83 CTD stations with a WP2 triple net (500 μm, 200 μm and 80 μm mesh size, Ø 57 cm, SCOR UNESCO, 1966) (Fig. 1 A). Vertical hauls were taken between 200-0 m. In leg B, zooplankton samples were taken at each hydrological site by a multiple opening closing BIONESS multinet device (500 μm mesh size and 1 m^2 sampling area, Sameoto *et al.*, 1980) and a modified small net BIONESS (200 μm mesh size, Ø 30 cm) filled inside each 500 μm net. Oblique hauls were made in nine depth intervals between 550 m and the surface. In each site zooplankton were also sampled with a WP 2 triple net over two depth rages: 100-0 and 200-100 in 16 stations (Fig. 1 B). Since the 500 μm net retained only the postlarvae of ophiuroids (Fenaux *et al.*, 1994), we present here only the results obtained with the 200 μm mesh size nets. After each collection, samples were immediately fixed in 4 % formaldehyde.

The different volumes filtered by the nets were calculated. The volume filtered by the WP2 net in a layer of 200 m depth was 48 m^{-3} (Wieghardt, 1953; Tranter, 1967). For zooplankton collected with a BIONESS 200 μm mesh size, the volume of sea water filtered was calculated for each depth intervals using a flowmeter situated at the center of the net and another one outside the net (*cf.* Tab. 2). Due to different sampling apparatus for collecting zooplankton, the abundance of plankton in the results were expressed as individuals collected per 100 m^3 of sea water. In order to compare larval abundance between the two legs, stations made during leg A were ordered from the South to the North according to the depth of the isopycnal 1028.00 kg m^{-3} which gives the relative positions of different hydrological sites sampled in leg B (*see* Prieur *et al.*, 1993). In the laboratory entire samples were counted and organisms identified under a dissecting microscope according to Fenaux (1968; 1969) and Pedrotti (1990; 1993). Amongst four classes of Echinoderm possessing pelagic larvae, Ophiuroids were identified down to species level. Among the two ophioplutei abundant in our samples, *Ophiopluteus bimaculatus* has not been assigned to well-defined species,

and its name corresponds to the larval name given by Müller (1852); and *O. compressus* according to Tyler and Fenaux (1994) is presumably the larva of *Ophiura carnea*. The majority of Echinoid larvae were identified down to species level. In the Order Spatangoida, *Echinocardium cordatum* and *Brissopsis lirifera* were identified. Few larvae of Holothuroids and Asteroids were identified to species. Some auricularia were identified as the larvae of *Holothuria forskali*, and some bipinaria were identified as *Luidia sarsi*. Brachiolarian stages of *Asterias* species were present in the samples.

RESULTS

Larval distribution obtained in the two legs with the WP 2 net up to 200 m showed the same patterns of abundance. Data indicated that echinoderm larvae were more abundant in stations localised in the Atlantic Waters (AAG) and in the Atlantic jet than in stations under influence of Mediterranean waters (Fig. 2, 3, 4).

In stations located in Atlantic waters the most important group were ophiuroids followed by holothuroids (Fig. 3 A, B). Late-stages and postlarvae of *Ophiopluteus compressus* (*Ophiura carnea*, *see* Tyler and Fenaux, 1994) and *O. bimaculatus* represented more then 40 % of the total number of larvae found in leg A and B (Fig. 3 C and D). Concerning echinoids, late-stages and postlarvae of *Paracentrotus lividus*, *Genocidaris maculata* and spatangoids dominated.

In the jet zone during leg A, at station 24, young-stages of the two ophioplutei *Amphiura filiformis* and *O. compressus* represented 100 % of larvae found. During leg B, (sites 1
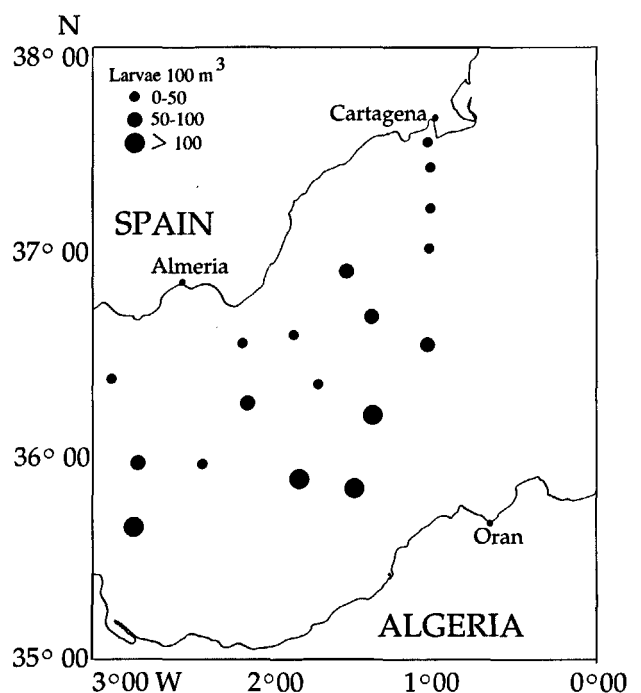

Figure 2

Distribution and abundance of total number of echinoderm larvae in 18 stations of the synoptic survey during Leg A in the Alboran Sea.
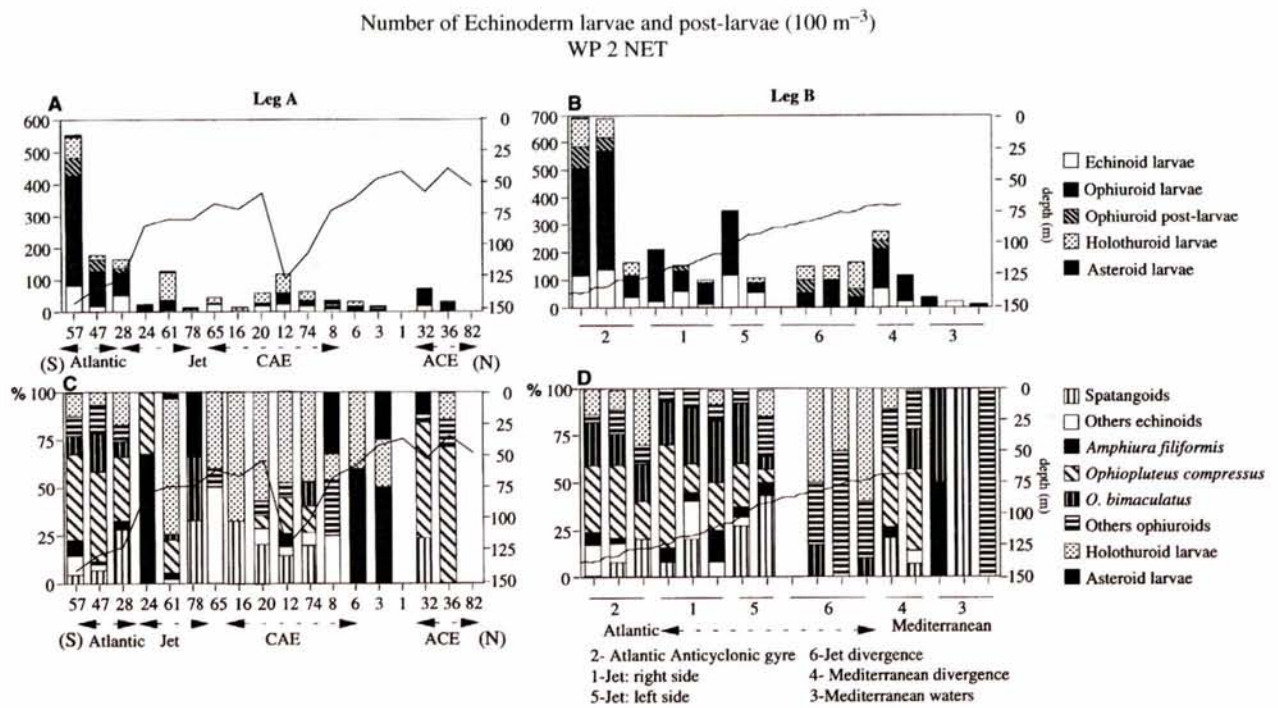
Number of Echinoderm larvae and post-larvae (100 m^{-3})
WP 2 NET

Figure 3

Number of larvae and postlarvae of the four classes of echinoderm (ind. 100 m^{-3}) from 200-0 m sampled with a WP2 net in different stations of Alboran Sea. A: during the synoptic survey of Leg A. B : in stations around the different hydrological structures during leg B. C and D: percentage of the principal larval species found during leg A and B. Stations were sorted according to the decreasing depth of the 1028.00 kg m^3 isolines which give the virtual positions of different sites across the front and forms the interface between Atlantic and Mediterranean Waters (see Prieur et al., 1993).

and 5) young-stages of *O. compressus* and *O. bimaculatus* represented about 50 % of the total number of larvae found. Concerning echinoids young *Paracentrotus lividus* and young and old spatangoids were found (Fig. 3 C and D).

At station 61 during leg A and in stations made in site 6 (Jet divergence) during leg B, young holothuroids larvae represented more than 50 % of species found.

At site 4 in the Mediterranean divergence, old *O. compressus* represented 43 % of larvae found in the 200-0 layer (Fig. 3 D). At stations located in the CAE during leg A, holothuroids larvae represented more than 50 % of species found, followed by late-stages of the spatangoid *Echinocardiun cordatum* (20 %) (Fig. 3 C). At stations made in the ACE, *O. compressus* of different ages comprised more than 60 % of the total echinoderm larvae found. In the other stations under influence of Mediterranean Waters larvae were scarce, in stations 3 and 6 young larvae of *A. filiformis* represented 50 to 60 % of the total echinoderm larvae found, the other larvae present were young auricularia and bipinaria (Fig. 3 C). Spatangoid larvae were present in the CAE and at site 3 located in the Mediterranean waters, nevertheless they were absent from coastal stations of Mediterranean waters (Fig. 3 A). Postlarvae were more numerous in Leg B than in Leg A.

Vertical distribution

In samples taken using the BIONESS net, during leg B, the Atlantic site (Site 2) showed the highest abundance and diversity comprising seven identified Echinoidea species,

six Ophiuroidea larvae and three groups of larvae, auricularia and penctactula of Holothuroidea and bipinaria of Asteroidea (Tab. 1). Sixty-seven per cent of the total numbers of individuals were concentrated in the first 25 m, lar-
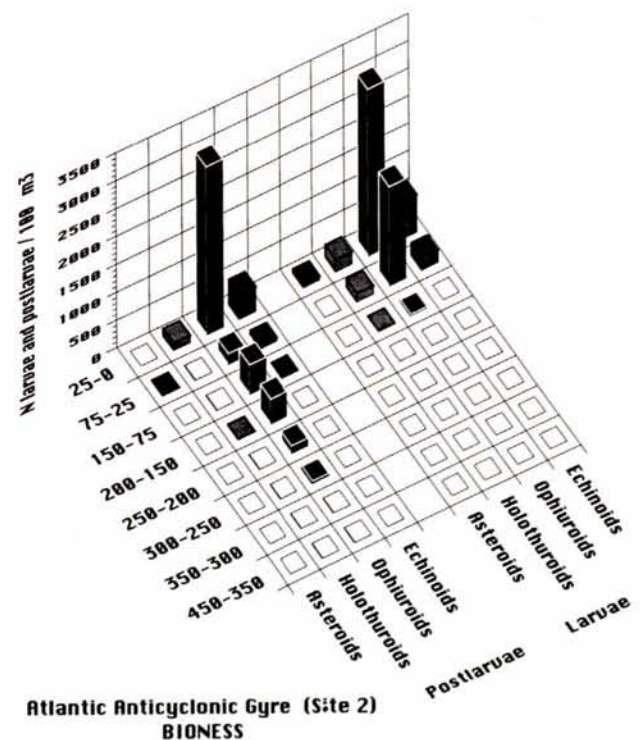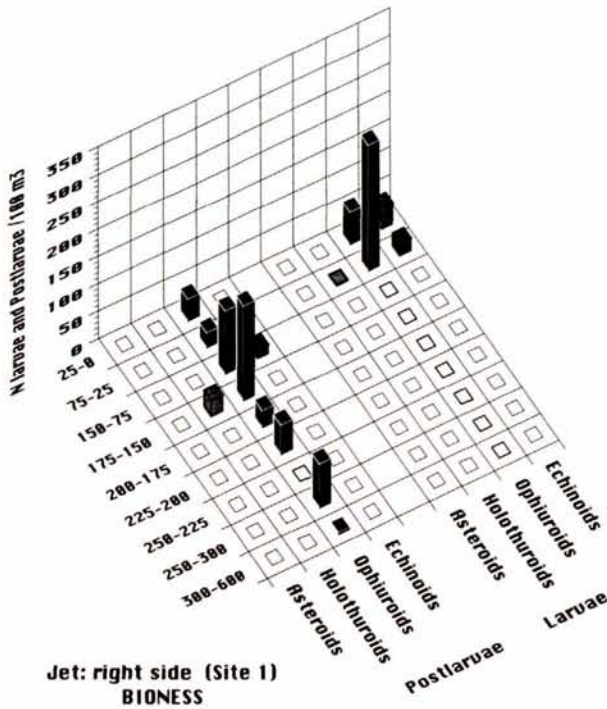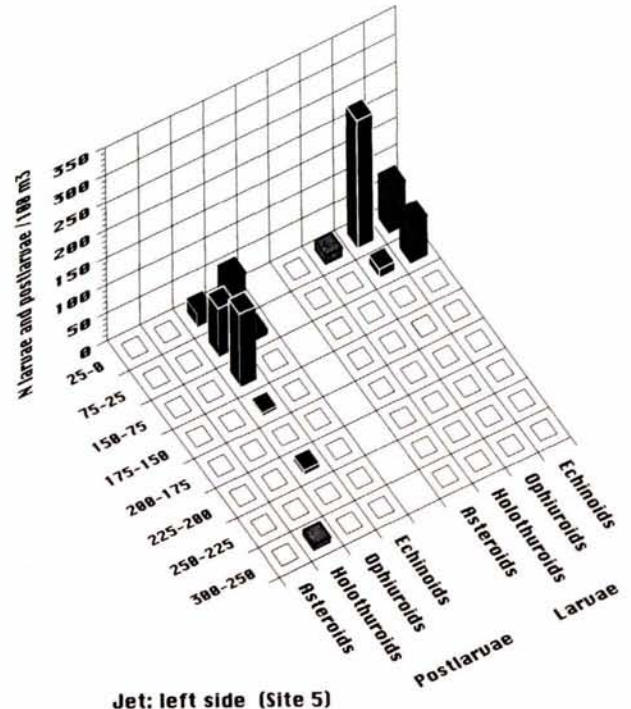

Figure 4 (A)

A
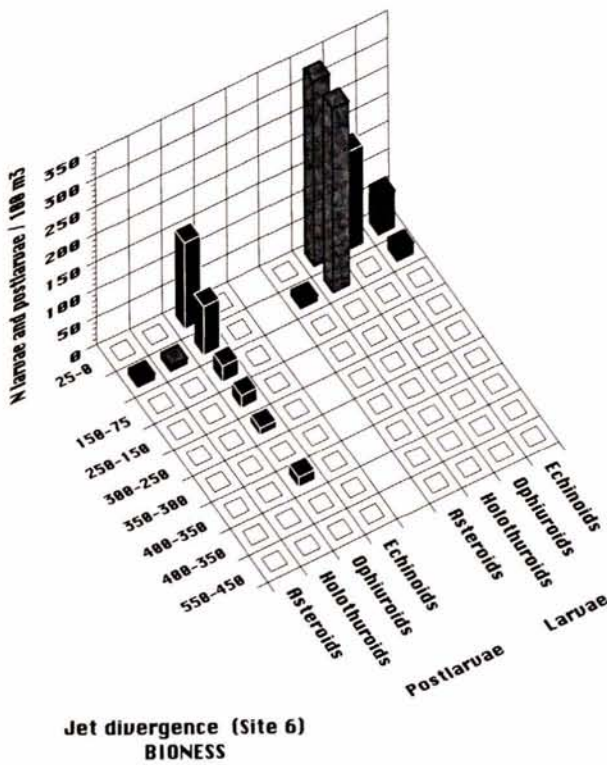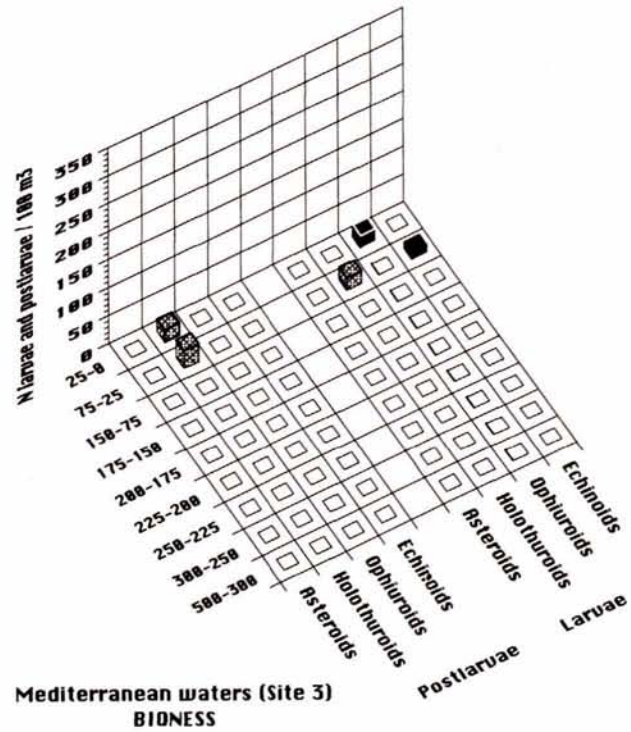
Figure 4 (B, C, D, E)

(A, B, C, D and E) Number of larvae and postlarvae of the four classes of echinoderm (ind. 100 m⁻³) at different depths sampled with a BIONESS multinet device in different hydrological sites during the leg B in the Alboran Sea. (Note that in figure 4A (site 2), the number of larvae and post-larvae is 10 times higher than in the other sites).

vae were present down to 150 m and postlarvae in deep layers down to 300 m (Tab. 2 and Fig. 4 A). Ophiuroids were present at greater concentrations than other echino-

derms. Late-stages of *Ophiopluteus compressus* and their postlarvae composed more than 73 % of the total number of individuals. They were present in greater concentrations

Table 1

Echinoderm larvae and postlarvae found in different hydrological sites in the Eastern Alboran Sea during Almofront 1 (April/May 1991).

Species	Site 2	Site 1	Site 5	Site 6	Site 4	Site 3
Classe Echinoidea						
Regularia						
O. Diadematoida						
S. O. Stirodonta						
Arbacia lixula (Linnaeus)	L					
S. O. Camarodonta						
Genocidaris maculata Agassiz	L - PL	L				
Sphaerechinus granularis (Lmrck)	L		L		L	
Paracentrotus lividus (Lmrck)	L - PL	L		L		
Echinus sp Lamarck	L	L	L			
Irregularia						
O. Spatangoida						
Brissidae			L			
Brissopsis lyrifera (Forbes)	L				L	
Spatangoidae	L - PL	L	L			
Echinocardium cordatum (Pennant)	L	L		L	L	
Classe: Ophiuroidea						
O. Ophiurae						
Amphiura filiformis (Müller)	L - PL	L - PL	L - PL	PL	PL	L
Ophiothrix fragilis (Abildgaard)	L - PL	L - PL	L - PL	L - PL	L - PL	
Ophiura albida Forbes	L	L	L			
Ophiura ophiura (Lmrk)				PL		
Ophiura carnea Lutken *	L - PL	L - PL	L - PL	PL	L	L
Ophiopluteus bimaculatus	L - PL	L - PL	L - PL	L - PL	L	L
Classe: Holothuroidea						
auricularia	L	L	L	L	L	L
pentactula	PL	PL	PL			
Classe: Asteroidea						
bipinaria	L		L	L		

Ophiopluteus compressus

below 25 m, in the upper layer of 25 m *O. bimaculatus* (37 %) and *Ophiothix fragilis* (23 %) were the most abundant species (Tab. 2). Amongst seven species of echinoids present, late-stages and postlarvae of *Paracentrotus lividus*, *Genocidaris maculata* and late-stages of *Brissopsis lyrifera* were the most abundant.

At the right side of the jet (Site 1), nine species of echinoderms were identified, and auricularia and penctactula of Holothuroidea were also found (Tab. 1). Larvae were principally found in the upper 75 m and postlarvae down to 600 m (Tab. 2, Fig. 4 B). Ophiuroids were also present at higher concentration than the other echinoderms, they represented more than 73 % of the total number of individuals. In superficial layers, *Ophiopluteus bimaculatus* represented 57 to 61 % of larvae found, while in deeper layers postlarvae of *O. compressus* were the only species found (Tab. 2). Larvae of *Paracentrotus lividus* and Brissidae were present but in lower concentrations.

At the left side of the jet core (Site 5) larvae were abundant in the upper 75 m and postlarvae down to 300 m (Tab. 2, Fig. 4 C). *Ophiopluteus bimaculatus* composed 80 % of the total number of larvae found, and their postlarvae were present between 25 to 150 m depth. In a deeper layer 100 % of postlarvae were from holothuroids (Tab. 2).

In the jet divergence (Site 6) the fauna was quite different from the others sites. In the superficial layer of 75 m, holothuroid larvae composed 44 to 70 % of the total number of larvae (Tab. 2, Fig. 4 D). In deeper layers postlarvae of *O. compressus* represented 40 to 66 % of postlarvae. The other postlarvae were *Amphiura filiformis* and *Ophiothrix fragilis* (Tab. 1). At this site only young echinoid larvae were present, postlarvae were absent (Tab. 1). Data from BIONESS are missing for site 4. The last site under influence of Mediterranean Waters (site 3) was the site with less abundance. Species richness was lower than at the other sites. Five species were found (Tab. 1). Species were concentrated in the first 75 m; some larvae of *Ophiopluteus compressus* were found in the upper 25 m and pentactulae of holothuroids between 75 to 25 m (Tab. 2, Fig. 4 E).

DISCUSSION

Presence of echinoderm larvae in the Alboran sea

Echinoderms present in the Alboran Sea were reported by Tortonese (1980), Sibuet (1974) Rodriguez and Ibanez (1976) and Rodriguez (1980). Rodriguez found 17 species of Asteroidea, 13 Ophiuroidea and 16 Echinoida along the Spanish South Mediterranean coast from 0 to 300 meters depth (Tab. 3). Except for the echinoid *Psammechinus microtuberculatus* which is a Mediterranean species according to Tortonese (1965) and *Ophiopluteus bimaculatus* which has been described only in planktonic samples from the Mediterranean waters (Mortensen, 1921; Fenaux, 1968;

Table 2

Number of larvae(L) and postlarvae (PL) (100 m⁻³) in different hydrological sites of Alboran Sea sampled by the BIONESS net (except site 4 where data are from WP2 net).

Depth (m)	Abundance 100 m⁻³	Filtered vol. m⁻³	Nb. of species	Predominant stage %	Predominant specie %
Site 2					
25-0	7540	19	13	59% larvae	37% O.bimaculatus
75-25	2400	39	11	89% larvae	55% O.compressus
150-75	597	59	7	95% postlarvae	87% O. compressus
200-150	459	41	4	100% postlarvae	87% O. compressus
250-200	139	58	2	100% postlarvae	85% O. compressus
300-250	39	73	1	100% postlarvae	100% O. compressus
350-300	0	46	0	——	——
450-350	0	44	0	——	——
Site 1					
25-0	140	20	4	71% larvae	57% O. bimaculatus
75-25	290	44	9	89% larvae	61% O. bimaculatus
150-75	131	49	3	100% postlarvae	80% O. compressus
175-150	200	14	4	100% postlarvae	43% O. compressus
200-175	31	13	1	100% postlarvae	100% O. compressus
225-200	53	15	2	100% postlarvae	50% O. compressus
250-225	0	18	0	——	——
300-250	80	30	2	100% postlarvae	83% O. compressus
600-300	4	102	1	100% postlarvae	100% O. compressus
Site 5					
25-0	408	25	7	80% larvae	49% O. bimaculatus
75-25	180	51	6	60% postlarvae	20% O. bimaculatus
150-75	130	80	3	100% postlarvae	81% O. bimaculatus
175-150	7	100	2	85% postlarvae	50% O. bimaculatus
200-175	0	49	0	——	——
225-200	8	48	1	100% postlarvae	100% O. bimaculatus
250-225	0	46	0	——	——
300-250	10	42	1	100% postlarvae	100% pentactula
500-300	-	203		——	——
Site 6					
25-0	734	18	5	78% larvae	44% auricularia
75-25	469	41	5	77% larvae	70% auricularia
150-75	29	70	2	100% postlarvae	40% O. compressus
250-150	23	104	2	100% postlarvae	66% O. compressus
300-250	13	64	1	100% postlarvae	100% O. compressus
350-300	0	71	0	——	——
400-350	18	45	2	100% postlarvae	50% O. compressus
450-400	0	75	0	——	——
550-450	0	35	0	——	——
Site 4					
200-0	198	48	8	92 % larvae	43% O. compressus
Site 3					
25-0	42	19	2	50% larvae	50% O. compressus
75-25	63	38	3	100% postlarvae	83% pentactula
150-75	0	69	0	——	——
175-150	0	102	0	——	——
200-175	0	67	0	——	——
225-200	0	60	0	——	——
250-225	0	44	0	——	——
300-250	0	33	0	——	——
500-300	0	54	0	——	——

Pedrotti, 1990; 1993), the other larvae and postlarvae found are common in both Atlantic and Mediterranean fauna (Tortonese, 1980). According to Tortonese (1980) six Atlantic species apparently exist only in the south-western zone (NW Africa, Alboran Sea): three Crinoidea (*Antedon bifida moroccana, Leptometra celtica, Neocomatella europaea*), two Ophiuroidea (*Amphiura incana* and *Neocnus incubans*) and an Asteroidea *Henricia abyssalis*.

While we do not find in the Alboran Sea echinoderm species considered to be indicators of Atlantic water, the presence in the Atlantic jet of *Ophiopluteus bimaculatus*, described only for planktonic samples from the Mediterranean waters, suggests that adult forms may be a common to Mediterranean and Atlantic Ocean fauna. The presence of greater abundance of ophiuroid postlarvae in leg B than in leg A, is probably due to the aging of the population.

Table 3

Echinoderms of Alboran Sea (except Holothuroidea and Crinoidea) according to Rodriguez (1980), (L) larval species found in the Almofront samples (legs A and B).

Ophiuroidea	Echinoidea	Asteroidea
Acrocnida brachiata	Arbacia lixula (L)	Astropecten aranciacus
Amphipholis squamata	Brissopsis lyrifera (L)	A. jonstoni
Amphiura chiajei	B. atlantica mediterranea	A. irregularis pentacanthus
Amphiura filiformis (L)	Brissus unicolor	A. platyacanthus
Astrospartus mediterraneus	Centrostephanus longispinus	A. bispinosus
Ophiacantha setosa	Echinus acutus (L)	Anseropoda placenta
Ophiactis balli	E. melo	Asterina gibbosa
Ophiocoma nigra	Echinocyamus pusillus	Allopatiria ocellifera
Ophioderma longicauda	Echinocardium cordatum (L)	Chaetaster longipes
Ophiothrix fragilis (L)	Echinocardium mediterraneum	Coscinasteria tenuispina
O. quinquemaculata*	Genocidaris maculata (L)***	Echinaster sepositus
Ophiura ophiura (L)	Psammechinus microtuberculatus	Luidia ciliaris
Ophiura albida (L)	Paracentrotus lividus (L)	L. sarsi (L)
Ophiura carnea (L) **	Sphaerechinus granularis (L)	Marthasterias glacialis
	Stylocidaris affinis	Ophidiasterophidianus
	Spatangus purpureus	Sphaerodiscus placenta
	Schizaster canaliferus	Tethyaster subinermis

* conspecific with *Ophiothrix fragilis* (Guille, 1968).
** absent in the list of Rodriguez but found in the gulf of Lion, Balearic is. (Tortonese, 1979) and in the sea of Banyuls-sur-Mer (Guille pers. com.) refered as *Ophiopluteus compressus*.
*** absent in the list of Rodriguez, but found in our samples.

Horizontal distribution of larvae in relation to the hydrological structures

In the Eastern Alboran Sea (SW Mediterranean Sea), Almofront-1 cruise coincided with the spring reproduction period of many echinoderms of the Mediterranean Sea (Fenaux, 1968; Pedrotti, 1993). During the cruise a zonal front and an associated eastward flowing jet were found in the southerly position at 35° 45' N extending from Cape Tres Forcas (3° 00 W) to Oran (1° 00 W) along the 1000 m isobath. Our results show that the pattern of larval distribution are consistent with the presence of the Atlantic water front, in view of the fact that species richness and larval abundance were higher in the waters of Atlantic origin than in Mediterranean waters.

The sites under influence of Mediterranean waters (site 3, ACE and CAE) are characterised by a lower larval abundance and species richness. Similar observations have already been made for mesopelagic macrozooplankton and micronekton (Baussant et al., 1993). This site is an oligotrophic site, characterised by the lowest biomass of zooplankton (Thibault et al., 1994) and a lower productivity (Prieur et al., 1993). North of the frontal zone, despite the presence of an anticyclonic eddy (CAE), no transport of larvae coming from the other sites was observed. However, due to the large area sampled and the weaker larval concentration it is difficult to relate patterns of larval distribution with hydrological structures.

In the sites within the Atlantic jet, results from larval distribution indicated that species richness and abundance were higher than in sites under influence of Mediterranean water. Even if the permanence of the inflow of Atlantic water and the geostrophic front is establish (Tintoré et al., 1988), we can not assert that larvae were transported within the current from Atlantic Ocean. Considering 0.5 m s^{-1} the mean surface velocity of the current, larvae

will require about 20 days to reach the studied zone. This could be true for more aged larvae, however, in the Atlantic jet, younger larval populations were principally found, in contrast with stations located in the Mediterranean waters and in the AAG, where older larval population dominated. The circulation associated with the jet inflow is at the origin of two anticyclonic gyre (Tintoré et al., 1988). The inflowing jet initiates the western Alboran gyre in the basin west of Cape Tres Forcas, and before enters the eastern Alboran sea, the inflow adopt a southerly position along the Moroccan coast (Heburn and La Violette, 1990). Young larvae (aged of few days) within the jet were probably originated from adjacent coastal areas west of Cape Tres Forcas.

The site 2, south of the jet, showed the highest abundance and species richness. It is possible that larvae from the jet were accumulated in this site. Moreover, this site is located in an Anticyclonic gyre AAG (Atlantic Water Anticyclonic Gyre), originating in the Atlantic jet. During Almofront, the eastern Alboran gyre has be found to be collapsed (Folkard et al., 1994); the inflow of Atlantic water is then constrained to the southern position. According to Prieur et al. (1993), salinity inside the gyre is a little higher then in the jet core, confirming that water in the gyre are more aged than in the jet. As the gyre lasts several weeks it could serve as a device for maintaining the larvae near favourable settling sites along the Moroccan coast and preventing transport to the open sea.

Vertical distribution of echinoderm larvae

In the Mediterranean site the shallow distribution of larvae and poslarvae can be explained by the presence of a interface between Atlantic and Mediterranean water, chosen as the depth of the isohaline 37.5 (~28.0 kg m^3 at 72 m)

observed in the CTD profiles (Prieur *et al.*, 1993). It is likely that larvae that are weak swimmers and that do not migrate vertically are incapable of traversing such discontinuities. At the site 6, the presence of holothuroids larvae in the upper layer of 75 m and *Ophiopluteus compressus* in deeper and most dense and salty water, coincides with the presence of two different hydrodynamical structures. However a closer spatial sampling grid in this area would have been necessary to relate differences in the pattern of larval distribution with a subsurface divergence of the flow.

In sites under influence of Atlantic water, echinoderm larvae were abundant in superficial layers and postlarvae were found in deeper layers up to 600 m depth in the right side (site 1) of the jet. According to Prieur *et al.* (1993) the isopycnal downwelling from the left (site 5) to the right (site 1) side of the frontal jet indicated a frontal convection. Moreover the existence of a deep chlorophyll maximum at about 110 m at site 1 (Videau *et al.*, 1994; Claustre *et al.*, 1994), suggests as well downward isopycnal transport of biomass. Comparable phenomena were observed in Ligurian Sea by Gorsky *et al.* (1991) for biomass and by Pedrotti (1990) for echinoderm larvae. Due to the vertical mixing of the water column during winter, echinoderm larvae were actively transported by the frontal circulation from the surface layer along the inclined isopycnals to a depth of 400 m (Pedrotti, 1990). According to Seguin *et al.* (1994), it is likely that in Alboran Sea secondary production is also exported through the frontal secondary circulation; the presence of juvenile stages of copepods in the divergence zone and more mature stages at sites 1 and 2 indicates that ecological succession corresponds with the patterns of circulation. In the Alboran Sea, it is likely that echinoderm larvae were advected downward along isopycnals towards the south of the jet frontal system due to the existence of a secondary circulation across the frontal zone (Zakardian, 1994). At site 1, the high concentration of individuals up to 175 m could be explained by this hydrodynamical context. Such a transport would also increase larval concentration at site 2 were maximal larval and post-larval abundance were observed. As physical parameters of the water masses show no significant variations below 200 m between sites (Prieur *et al.*, 1993), the presence of postlarvae in deeper layers up to 600 m in site 1 could be explained in part by the accumulation of larvae under the Atlantic/Mediterranean interface as observed by Gorski *et al.* (1994) concerning the distribution of suspended particles.

Biological mechanisms involved in larval distribution

In general, invertebrate larvae use strategies as vertical and ontogenetic migration associated with physical processes (selective tidal stream transport, wind action, internal waves) to limit dispersal and promote larval retention near adult populations (Shanks, 1985; Shanks and Wright, 1987; Epifano, 1988; Hill, 1994; Rowe and Epifano, 1994; Thiébaut *et al.*, 1994). With regard to the echinoderms found in the present study, little is known concerning their ability to behaviourally regulate their vertical positions. Results from laboratory experiments and from *in situ* samples showed that echinoderm larvae have a very slow swimming speed (Mileikovsky, 1973; Chia *et al.*, 1984; Pedrotti, 1990), no ontogenetic and a weak vertical migration (a few meters) and a low sinking rate (Banse, 1964; 1986; Pennington and Emlet, 1986; Pedrotti, 1990). Larvae seem to orient themselves more by gravity than by light (Mladenov and Chia, 1983; Young and Chia, 1984). According to Banse, (1986) the depth of larvae are governed by hydrographic processes rather than active orientation. In Alboran Sea, the ophiuroids larvae studied are capable of undergoing metamorphosis in mid-water and adults have a large bathymetric distribution, thus, if passive deposition occurs when metamorphosis takes place, larvae have more chances for recruitment. The major problem would then concern neritic echinoids which need a suitable shallow benthic environment to undergo metamorphosis and settling. If postlarvae sink passively to reach the bottom, the presence of a cross frontal isopycnal downwelling and an anticyclonique gyre in its southward position, near to the coast, may contribute to a local successful recruitment. Because of the behaviour of echinoderm larvae it is likely that vertical distribution, transport and retention processes are strongly dependent on the mesoscale hydrodynamical structures in the Alboran Sea.

Acknowledgments

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