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Jean-Claude Dauvin, Jean-Claude Sorbe. Oceanic dispersal and seamount colonization by the Neritic Mysid Anchialina Agilis (G.O. Sars, 1877) in the North-eastern Atlantics. Journal of Marine Biology and Oceanography, 2021, 10 (1), pp.1000223. hal-03163525

HAL Id: hal-03163525

https://normandie-univ.hal.science/hal-03163525

Submitted on 11 Mar 2021

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Journal of Marine Biology & Oceanography

Research Article

A SCITECHNOL JOURNAL

Oceanic Dispersal and Seamount Colonization by the Neritic Mysid *Anchialina Agilis* (G.O. Sars, 1877) in the North-eastern Atlantics

Jean-Claude Dauvin[1*], Jean-Claude Sorbe[2]

Abstract

The neritic mysid *Anchialina agilis* (G.O. Sars, 1877) had been recorded off the Portugal coast and on the Lusitanian and Azores Atlantic seamounts. This mysid shows daytime migration; it was near the sea-bottom during the day and migrated towards the surface waters during the night. Current advection from the coast to offshore is probably the origin of the large dispersal of the species from the Iberian and north-African coast to the seamounts. On seamounts at water depths compatible with the existence of a benthic population, permanent populations composed of juveniles, immature specimens, and incubatory females and matures males were established in a seamount retention system. The existence of a regular flux of coastal individuals from the north-eastern Atlantic continental shelf and the reproduction within seamount-established populations appears sufficient to maintain offshore populations of this species.

Keywords

Atlantic; Seamounts; Mysid; Current transport; Daily migration

Introduction

The study of marine biogeography provides important information about the dispersal capabilities and indication of the role of marine islands and seamounts in species expansion [1-6]. Numerous seamounts are present in the North Atlantic Ocean between Europe and North America and several questions arise about the origin of the seamount fauna and their establishment in such isolated environments [1, 7-10]. Many studies have considered seamounts as stepping stones for the transoceanic species dispersal [11], and questions remain about the composition of seamount fauna and its relationship to those of the surrounding abyssal plain, continental shelf, and other seamounts and mid-oceanic islands. Several authors have suggested that seamount species were originally widespread oceanic species, which were subsequently transported by ocean currents and recruited to form seamount populations in suitable environments [12]. Moreover, there was a continuing debate on species endemism and the functioning of such isolated ecosystems [3,4,9,12].

In their review, Clark et al. [12] showed that oceanic seamounts host diverse and abundant benthic communities whose composition was broadly similar to neighboring continental slopes; they highlighted the important role of dispersal capabilities of species in seamount connectivity. Rowden et al. [9] presented evidence that seamounts offer stepping-stones for dispersal, representing oases of abundance and biomass as well as hotspots of species richness, but without high levels of endemism. Seamounts appeared to be centers of biological productivity, which could sustain important oceanic offshore ecosystems with an aggregation of higher trophic levels such as fish. At the same time, Schlacher et al. [3] indicated high levels of biodiversity and endemism, playing important roles in marine biogeography, with hotspots of biological carbon processing that favor substantial fisheries. Moreover, they pointed that recent studies demonstrating that seamounts had comparable benthic diversity and endemism compared to continental margins. Similarly, Shank [4] estimated that seamount endemism was challenged by inconsistencies in sampling approaches, and the evidence did not support genetic connectivity between seamounts and the neighboring continental slopes.

Many authors showed that the faunal diversity of these systems depended on the water depth seamount summit, as well as the habitats, the availability of substrates, and retention circulation around the seamount [4,12]

Planktonic larvae represent the main dispersal stage of many benthic organisms, but adults can also spread over long distances for the colonization of other sites. According to many authors, marine benthic invertebrates use different dispersal mechanisms, which lead to a wide geographical distribution [9]. Individuals may remain suspended on the water surface where they are likely to become attached to algae, while floating increases the dispersal by rafting. Recently, Wildish and Chang [13] demonstrated that driftwood was the only rafting platform able to support the dispersal of talitrid amphipods from west to east across the North Atlantic. However, ocean surface currents are the most important factor interfering with the colonization of different islands or seamounts. Therefore, the surface water circulation between the Atlantic coast of Europe and the north-eastern coast of Africa and the Azores Archipelago is dominated by Portugal and Canary currents, which thus represent the main source of transport of larvae and adult organisms towards the Azores and Atlantic seamounts [14].

They are numerous Lusitanian seamounts at various distances from the Iberian margin and others located in the area south of the Azores. Lusitanian seamounts have a small area (100 Km^2) with a 200 km separation distance and are located more than 1,000 km from the African coasts [15]. The South Azores seamounts are characterized by a sloped area of about 500 km^2 to 1,000 km^2, with the farthest seamount being located 1,200 km from the Azores [16].

French oceanographic cruises (Seamount 1 exploring the Lusitanian seamounts and Seamount 2 exploring the Azores seamounts) have led to the discovery and description of several invertebrates new to science [17-22]. Therefore, it remains to elucidate

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Received: December 20, 2020 **Accepted:** December 31, 2020 **Published:** January 10, 2021

SciTechnol International Publisher of Science, Technology and Medicine

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the colonization of these seamounts in such isolated habitats by benthic species, especially those without pelagic larval stages [14]. For the studied polychaetes from the Iberian and South Azores seamounts, two seamount groups had been distinguished [14,23,24]. The first group corresponded to coastal seamounts and the second to offshore seamounts. However, there appeared to be no relationship between these seamount environments and the type of larval development (planktotrophic or direct, with or without pelagic larval dispersion).

Several papers on the biology and ecology of Atlantic Seamounts [25] and more recent researches focused on the northeastern Atlantic highlighted the interest of the scientific community for these isolated marine habitats. Martin and Nellen (2004) [26] described the composition and distribution of zooplankton from the Great Meteor Seamount. Cartes et al. [27] studied the distribution and biogeographic trends of decapod assemblages from Galicia Bank (NE Atlantic) at depths between 700 m and 1,800 m. Zooplankton distribution patterns have been described on two seamounts in the subtropical and tropical NE Atlantic (the Lusitanian seamount Ampere) and the Senghor seamount near the Cape Verde Islands [28, 29].

Among holobenthic species without a pelagic dispersal phase, the benthic peracarid fauna of the Atlantic seamounts remains poorly known. Hesthagen (1970) [30] studied the near-bottom benthic fauna of the Josephine and Meteor seamounts with a Beyer epibenthic sledge and presented some information about the abundance of amphipods, isopods, and mysids on the upper tabular part of both seamounts. This author estimated a mean mysid abundance of 16.1 ind. 100 m^{-3} on Josephine and 75.8 ind. 100 m^{-3} on Meteor.

The neritic mysid *Anchialina agilis* is known to be transported offshore by coastal and oceanic currents; it has been observed in deep waters of the northern part of the Mediterranean Sea [31]. This mysid is well-known in the north-eastern Atlantic Ocean and the Mediterranean Sea; it has been recorded in the Bay of Biscay [32], the Portuguese continental shelf [33], the Atlantic part of the Ibero-Moroccan domain, and off the coast of Morocco [34]. *A. agilis* shows daily vertical movements allowing its dispersal away from the shelf and offshore transport by surface currents to islands and oceanic seamounts. A population has been recorded in Gran Canaria [35]. As with other neritic mysids, it lives on or near the sea bottom during the daytime and migrates very rapidly to the water surface during the hours of darkness [36-40].

The present study gives new information on the geographical distribution of *A. agilis* in the north-eastern Atlantic, in areas including offshore Portugal and Atlantic seamounts, and investigates the long-distance dispersal of this species by surface ocean currents about its daily migratory behavior.

Sites and Sampling

The material was collected during several cruises in the north-eastern Atlantic:

1. On the west Iberian continental margin during the 'Aveiro 94' cruise in July-August 1994 and the 'Seamount 1' cruise in September-October 1987. During the Aveiro 94 cruise, plankton sampling was carried out in surface neritic waters (0-0.7 m below the ocean surface) using an FAO net with an opening area of 0.79 m^2 and a 0.5 mm mesh size. Supplementary near-bottom hauls were performed with a suprabenthic sledge equipped with TSK (Tsurimi-Seiki-Kosakusho) flow meters to estimate the volume filtered by the 0.5 mm nets [37] at six stations of a bathymetric transect from 22 to 299 m (Table 1). During the 'Seamount 1', plankton sampling was performed with a cylindroconical net (IOSN: Indian Ocean Standard Net) equipped by TSK flow meters, with an opening area of 1 m^2 and 0.335 mm mesh size: horizontal tows at 50 m below the surface or oblique tows in the 0-100 m water layer (Table 1). A beam trawl (CP) towed on the sea bed was equipped with a small plankton net (0.5 mm mesh size); the samples obtained by this technique were only qualitative.

2. During the 'Seamount 2' cruise, qualitative oblique plankton sampling was performed in surface waters with two WP2 (Working Party 2) nets (0.2 and 0.3 mm mesh size). A new version of the Macer-Giroq suprabenthic sledge equipped with TSK flow meters and WP2 zooplankton net (0.5 mm mesh size) was used from the summit of the seamounts to a maximum depth of 2,235 m on the abyssal plain (Table 1) [41]. Surface plankton sampling was carried out above the summit/upper slope of the seamounts and at mid-distance between the seamounts on the abyssal plain, mainly during the night-time. Some supplementary samples were collected near Gran Canarias Island (Table 1).

During the 'Seamount 1' cruise, seven Lusitanian seamounts were explored successively: Gorringe, Josephine, Lion, Unicorn, Seine, Ampere, and Galicia (Figure 1).

During the 'Seamount 2' cruise, five seamounts south of the Azores Islands were explored: Meteor, Hyeres, Irving, Plato, and Atlantis (Figure 1).

A total of 126 samples were collected corresponding to 108 planktonic samples and 18 suprabenthic hauls, fixed on board with 10% formaldehyde, then specimens collected were sorted and preserved in 70% alcohol. (Table 1).

Among the fauna recorded, all the *Anchialina agilis* specimens were counted and their abundances per 100 m^3 were estimated using filtered volumes of seawater. Then all the specimens separated into six categories according to sex and maturity condition (37):

1) Juveniles (J) specimens without any secondary sexual characters.

2) Immature males (M_i) with development of penes between the eighth thoracopods and appearance of pleopods on the abdomen.

3) Mature males (M_m), with the appearance of a thick brush of setae on the distal part of the antennular peduncle.

4) Immature females (F_i) with oostegites developing between the last pairs of thoracopods.

5) Incubating females (F_{ic}), with well-developed marsupium with eggs or embryos.

6) Post-incubating females (F_{pi}) with developed oostegites and empty marsupium.

In each sample, the individuals of each category were counted to establish the percentage of these six categories (Tables 2, 3, and 4). The carapace length (CL in mm) of all individuals collected was measured from the tip of the rostrum to the posterior dorsal margin of the carapace with a micrometer under a binocular microscope

Results

Iberian margin

Anchialina agilis was collected near the sea-bottom and the surface

Table 1: Main characteristics of the surficial planktonic and near-bottom samples during the offshore Aveiro Portugal, seamount 1 and seamount 2 cruises in the north-eastern Atlantic Ocean.

Campaign	N°	S	Date	H	Latitude	Longitude	Depth	Vol	Ni	D
Portugal-Iberian margin										
	Pks295	Sf	07/30/94	00:46	40°38.94	09°15.75	148	204	917	449
	Ts297	187	07/30/94	09:12	40°37.84	09°19.88	187	133	3	2.2
	Ts298	185	07/30/94	10:20	40°37.97	09°19.79	185	76	1	1.3
	Ts299	299	07/30/94	11:13	40°39.05	09°20.36	299	54	0	0
	Ts300	125	07/30/94	12:56	40°38.70	09°11.98	125	22	796	3,618
	Ts302	91	07/30/94	14:02	40°38.43	09°06.54	91	18	648	3,600
	Ts320	22	08/01/94	16:08	40°37.76	08°48.34	22	60	0	0
Seamount 1										
Iberian slope	PK01	50	09/21/87	20:40	36°53.60	09°05.70	365	130	5	4
Shelf/Gorringe	PK02	50	09/22/97	02:23	36°44.90	10°08.70	3,723	136	1	0.7
Gorringe	CP20	313	09/24/87	14:40	36°30.70	11°30.10	313	-	35	-
Gorringe	PK22	50	09/24/87	20:25	36°31.80	11°30.50	230	377	939	249
Gorringe	PK23	100	09/24/87	21:34	36°33.00	11°30.70	215	318	351	110
Iberian shelf	PK31	100	09/27/87	14:24	38°28.40	09°34.70	170	675	0	0
Gorringe/Josephine	PK36	100	10/04/87	02:03	36°36.40	12°59.30	3,480	416	0	0
Josephine	CP40	218	10/04/87	13:44	36°38.60	14°15.90	218	-	1	-
Josephine	PK44	100	10/04/87	21:33	36°42.00	14°14.90	215	367	2,348	640
Josephine	PK54	50	10/07/87	04:22	36°41.10	14°15.00	200	317	2,627	829
Josephine/Lion	PK62	100	10/08/87	02:58	35°59.80	15°00.20	1,763	442	0	0
Lion	PK65	100	10/08/87	20:45	35°14.90	15°36.60	645	563	1	0.2
Unicorn	PK66	100	10/09/87	04:32	34°44.50	14°26.90	875	526	0	0
Unicorn/Seine	PK67	100	10/09/87	08:33	34°14.60	14°29.90	4,325	323	0	0
Seine	PK74	100	10/09/87	20:48	33°44.60	14°24.80	165	450	100	22
Seine	CP79	251	10/10/87	11:48	33°49.00	14°22.60	251	-	1	-
Seine	CP83	310	10/10/87	19:10	33°48.00	14°23.90	310	-	1	-
Seine	PK85	50	10/10/87	22:58	33°48.70	14°21.80	205	672	74	11
Seine/Ampère	PK86	100	10/11/87	04:04	34°20.00	13°46.80	3,930	704	0	0
Ampère	PK96	100	10/11/87	22:48	35°04.50	12°55.50	215	538	0	0
Ampère/Gorringe	PK103	100	10/13/87	01:24	35°40.30	12°32.60	4,820	419	0	0
Iberian shelf	PK104	100	10/17/87	12:29	41°25.80	09°11.30	173	333	0	0
Galice	PK114	100	10/19/87	20:25	42°42.60	11°47.80	165	516	0	0
Seamount 2										
Gran Canaria	PK123	Sf	01/05/93	13:09	28°05.78	15°53.08	320	120	4	3.3
Gran Canaria	PK127a	Sf	01/05/93	18:54	28°07.11	15°52.76	360	117	0	0
Gran Canaria	PK127b	Sf	01/05/93	19:25	28°07.45	15°52.30	345	108	0	0
Gran Canaria	PK131	Sf	01/06/93	15:01	28°08.96	15°52.56	660	127	0	0
Gran Canaria	PK134a	Sf	01/06/93	22:03	28°02.77	15°54.03	330	112	0	0
Gran Canaria	PK134b	Sf	01/06/93	22:40	28°03.57	15°54.18	330	135	0	0
Gran Canaria	PK137a	Sf	01/09/93	21:19	30°02.18	28°29.39	305	113	0	0
Gran Canaria	PK137b	Sf	01/09/93	22:00	30°02.93	28°28.50	305	123	0	0
Gran Canaria	PK141a	Sf	01/10/93	11:34	29°59.97	28°28.41	298	106	0	0
Gran Canaria	PK141a	Sf	01/10/93	12:05	30°00.65	28°27.77	310	119	0	0
Gran Canaria	PK150a	Sf	01/11/93	14:19	30°13.50	28°23.75	1,110	136	0	0
Gran Canaria	PK150b	Sf	01/11/93	15:02	30°13.36	28°22.29	1,620	114	0	0
Gran Canaria	PK153a	Sf	01/11/93	22:20	30°05.25	28°22.28	590	123	0	0
Gran Canaria	PK153b	Sf	01/11/93	22:49	30°05.00	28°21.69	590	112	0	0
Gran Canaria	PK154a	Sf	01/12/93	08:14	29°56.44	28°27.95	300	121	0	0
Gran Canaria	PK154b	Sf	01/12/93	09:06	29°55.29	28°27.68	300	135	0	0
Meteor	TS155	302	01/12/93	10:47	29°56.60	28°27.16	302	131	1	0.8
Meteor	PK160a	Sf	01/13/93	08:12	29°40.68	28°26.34	290	104	0	0
Meteor	PK160b	Sf	01/13/93	09:00	29°39.61	28°25.94	300	119	0	0

Meteor	PK160c	Sf	01/13/93	09:57	29°38.06	28°25.20	505	114	0	0
Meteor	PK160d	Sf	01/13/93	11:13	29°41.07	28°26.03	290	104	0	0
Meteor	TS163	290	01/13/93	16:06	29°40.19	28°25.96	290	191	21	11
Meteor	PK168a	Sf	01/14/93	10:58	30°05.76	28°38.88	320	113	0	0
Meteor	PK168b	Sf	01/14/93	11:47	30°04.57	28°38.38	315	98	0	0
Meteor	PK175a	Sf	01/15/93	08:17	29°59.14	28°38.58	320	107	0	0
Meteor	PK175b	Sf	01/15/93	09:00	29°58.19	28°38.65	325	117	0	0
Meteor	PK175d	Sf	01/15/93	10:15	29°56.22	28°38.20	310	123	0	0
Meteor	PK181a	Sf	01/16/93	11:02	31°23.71	28°52.82	650	108	0	0
Meteor	PK181b	Sf	01/16/93	11:45	31°21.96	28°52.08	530	118	0	0
Hyeres	PK187a	Sf	01/17/93	09:26	31°24.40	28°50.80	975	123	0	0
Hyeres	PK187b	Sf	01/17/93	10:26	31°24.05	28°50.30	1,010	103	0	0
Hyeres	PK194a	Sf	01/18/93	08:08	31°16.22	28°30.10	1,780	108	0	0
Hyeres	PK194b	Sf	01/18/93	09:05	31°17.98	28°29.85	1,805	111	0	0
Hyeres	PK201a	Sf	01/19/93	08:11	31°20.23	28°53.69	715	117	0	0
Hyeres	PK201b	Sf	01/19/93	09:07	31°21.72	28°52.76	515	107	0	0
Irving	PK211a	Sf	01/26/93	22:08	31°59.79	28°01.27	258	106	44	43
Irving	PK211b	Sf	01/26/93	22:52	32°00.29	28°03.16	258	117	98	84
Irving	TS212	260	01/27/93	08:39	32°01.28	27°58.98	260	132	2	1.5
Irving	TS213	260	01/27/93	09:59	32°00.42	27°59.25	260	118	23	19
Irving	PK220a	Sf	01/28/93	22:19	32°02.57	27°55.76	775	102	0	0
Irving	PK220a	Sf	01/29/93	23:04	32°03.73	27°56.12	830	114	0	0
Irving	PK228a	Sf	01/29/93	00:19	32°07.59	28°08.28	817	97	2	2
Irving	PK228a	Sf	01/29/93	01:01	32°08.53	28°09.43	990	103	2	2
Irving	TS234	1,870	01/30/93	10:16	32°00.49	27°41.63	1,870	113	0	0
Irving	PK239a	Sf	01/31/93	02:45	32°45.21	28°07.16	3,265	128	0	0
Irving	PK239a	Sf	01/31/93	03:31	32°46.66	28°07.31	3,410	114	0	0
Plato	PK245a	Sf	01/31/93	23:48	33°11.78	29°05.21	980	121	0	0
Plato	PK245b	Sf	01/31/93	00:33	33°12.10	29°36.07	1,193	118	0	0
Plato	PK252a	Sf	02/01/93	22:11	33°16.64	29°33.24	1,295	93	0	0
Plato	PK252b	Sf	02/01/93	22:54	33°17.22	29°33.48	2,020	114	0	0
Plato	PK253a	Sf	02/02/93	02:54	33°42.79	29°55.07	3,115	109	0	0
Plato	PK253a	Sf	02/02/93	02:54	33°42.79	29°55.07	3,115	109	0	0
Plato	PK253b	Sf	02/02/93	03:36	33°41.63	29°56.07	3,108	121	0	0
Atlantis	PK266a	Sf	02/03/93	22:42	34°28.73	30°36.27	558	88	0	0
Atlantis	PK266b	Sf	02/03/93	23:23	34°27.73	30°35.20	590	94	0	0
Atlantis	TS267	2,235	02/04/93	10:09	34°22.48	30°22.48	2,235	115	0	0
Atlantis	TS269	330	02/04/93	18:35	34°05.54	30°15.00	330	126	0	0
Atlantis	TS270	330	02/04/93	20:35	34°04.82	30°14.94	330	84	0	0

N: sampling number; S: maximum sampling depth from the sea water surface; H: HTC/GMT; Vol: sampling volume in m^3; Ni: number of *Anchialina agilis* individuals; D:density per 100 m^3. Sf: surface. PK: plankton net; Ts; Sorbe suprabenthic sledge; TS: Macer-Giroq suprabenthic sledge.

(Table 1). The near-bottom samples showed that the population was mainly located on the mid-part of the continental shelf (3,600 ind. 100 m^{-3} at 91 m and 3,618 ind.100 m^{-3} at 125 m), while it was absent in the coastal fringe (Ts320, 22 m) as well as on the upper slope (Ts299, 299 m) (Table 1). The near-bottom samples included specimens of the six demographic categories (Table 2). Immature males, immature females, and juveniles dominated the population, while few numbers of mature males and mature females were present (Table 2).

A. agilis was never sampled during the daytime in surface waters (PK31, PK104) (Table 1). However, part of the near-bottom population migrated up to the surface during the night-time, as shown by the nocturnal concentration of this species in the hyponeuston on July 1994 representing about 13-14% of the near-bottom abundance (PKs 295: 449 ind.100 m^{-3} in the water layer 0.70 cm below the ocean surface) (Table 1). All the demographic categories were presented in this surface plankton sample, including immature males and immature females (Table 2). Juveniles were present in smaller proportions than in the near-bottom population (Table 2). Brooding females were present in the hyponeuston during the night-time (Table 2).

This nocturnal hyponeustonic population might be swept away from the continental shelf by surface currents, as suggested by the low abundance of individuals in surface waters above the upper part of the continental slope (PK01, 365 m depth: 4 ind. m^{-3}), and above the abyssal plain between the Iberian margin and Gorringe (PK02, 3,723 m depth: 1 ind. m^{-3}, observed in September 1987 during the Seamount 1 cruise). Such offshore-transported specimens were mainly represented by juveniles (CL from 0.75 and 0.99 mm), but an immature (CL=1.27 mm) and a mature male (CL=2.93 mm) were also collected (Table 2).

Lusitanian seamounts

During the Seamount 1 cruise, five surface plankton samples

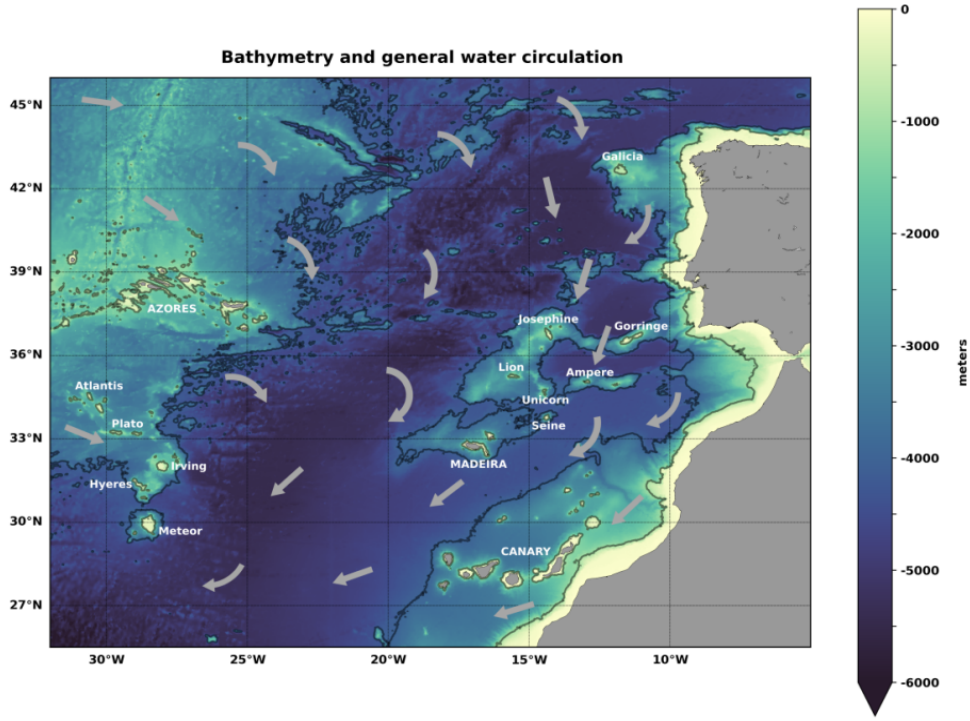


Figure 1: Bathymetric map showing location of the studied north-eastern Atlantic seamounts. The arrows indicate the major features of water circulation near the surface, redrawn by M. Boutet from Gillet and Dauvin (2000) and Surugiu et al. (2008) [14].

Table 2: Size range (CL in mm) of *Anchialina agilis* in nocturnal hyponeuston (Pks 295) and near-bottom samples (Ts 300-302) from the continental off Aveiro (July 1994).

Demographic Components							n
	J	F_i	F_{ic}	F_{pi}	M_i	M_m	
Hyponeuston Population							
Range	1.04-1.34	1.28-2.30	1.95-2.65	1.96-2.57	1.16-1.96	1.78-2.06	
Mean Size	1.15	1.82	2.32	2.27	1.63	1.95	917
Standard Deviation	0.08	0.23	0.14	0.12	0.17	0.18	
Proportion in %	1.6	34.2	9.3	9.1	43.6	2.2	
Near-bottom Population							
Range	0.80-1.30	1.00-2.18	2.20-2.67	2.04-2.87	0.86-2.08	1.82-2.75	
Mean Size	1.02	1.47	2.34	2.32	1.33	2.09	1,444
Standard Deviation	0.11	0.26	0.17	0.18	0.23	0.19	
Proportion in %	20.8	26.7	2.6	0.6	45.5	3.8	
N: number of individuals; J: juveniles; F_i: immature females; F_{ic}: incubating female; F_{pi}: post incubating females, M_i: immature males, M_m: mature males							

were collected during the night-time (PK36, PK62, PK67, PK86, and PK103), and no *A. agilis* specimen was found.

Conversely, *A. agilis* was collected on the Lusitanian seamounts, both in the near-bottom environment as well as in the surface waters, except for Ampere, Unicorn, and Galicia. The near-bottom data from diurnal hauls between 218 and 313 m depth were scared and only qualitative (Gorringe, CP20: 35 individuals; Josephine, CP40, one individual; Seine, CP79, one individual and CP83, one individual), indicating the presence of a probably more abundant population on the upper part of the seamount slope. In surface waters (oblique tows), the highest nocturnal abundances were recorded on Josephine (PK44, 640 ind.100 m^{-3} and PK54, 829 ind.100 m^{-3}) and at Gorringe (PK22, 249 ind.100 m^{-3}; PK23, 110 ind.100 m^{-3}). The abundance for the other seamounts was lower (Seine, PK74, 22 ind.100 m^{-3}; Lion, PK65 <1 ind.100 m^{-3}) (Table 1).

In the near-bottom environment (CP20, CP40, CP79, and CP 83), the population was mainly composed of juveniles and was characterized by the absence of brooding females and matures males (Table 3). In the surface waters above the seamounts, the plankton population was mainly dominated by juveniles at PK22 (Gorringe), PK44, and PK54 (Josephine), and PK 74 (Seine). By contrast, a different demographic structure was observed in PK23 (Gorringe) and PK85 (Seine) with a higher proportion of immature and mature individuals. Nevertheless, all the demographic components appeared

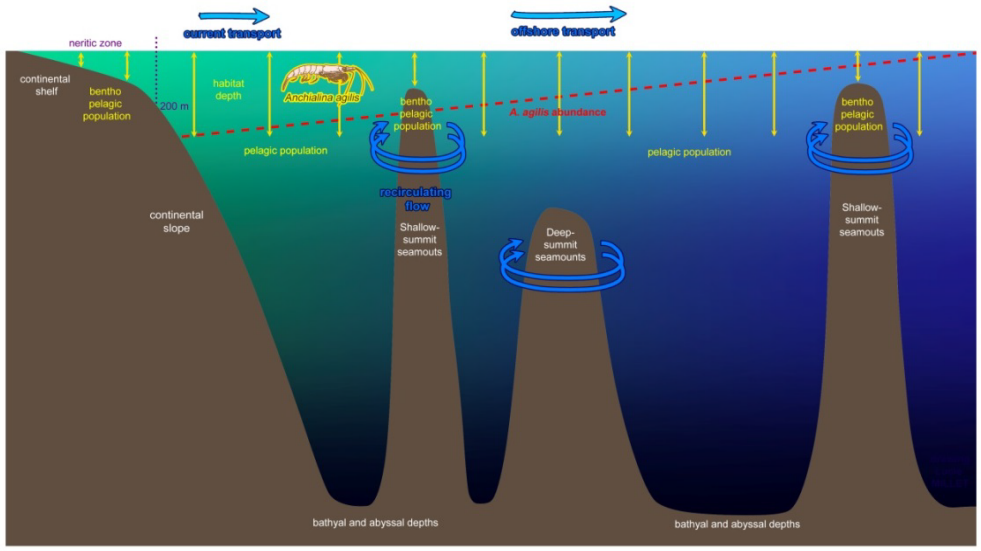


Figure 2: Schematic colonization of Lusitanian and Azores seamounts by the neritic mysid *Anchialina agilis* (redraw by L. Millet from Mallek-Zouhiri, 1999 and Shank, 2010) [4].

Table 3: Size range (CL in mm) of *Anchialina agilis* in surficial planktonic and near-bottom samples (Ts 300-302) from the Lusitanian seamount sampled during the seamount 1 cruise in September-October 1987.

Demographic components							n
	J	F_i	F_{ic}	F_{pi}	M_i	M_m	
Planktonic population							
Range	0.75-1.54	1.39-2.93	2.30-3.09	2.10-3.17	1.03-2.18	1.98-3.29	6,440
Mean Size	1.07	2.12	2.66	2.56	1.75	2.46	
Standard Deviation	0.16	0.34	0.2	0.24	0.23	0.26	
Proportion in %	88.8	2	0.5	1.5	3.7	3.5	100
Near-bottom population							
Range	0.87-1.39	1.39-1.59	-	2.50-2.57	1.35-2.06	-	38
Mean Size			-			-	
Standard Deviation			-			-	
Proportion in %	73.7	13.2	-	5.2	7.9	-	100

Table 4: Size range (CL in mm) of *Anchialina agilis* in surficial and near-bottom samples from the Azores seamounts sampled during the seamount 2 cruise in January-February 1993.

Demographic components							n
	J	F_i	F_{ic}	F_{pi}	M_i	M_m	
Planktonic population							
Range	0.65-1.05	1.70-2.36	-	2.13-2.84	0.98-2.23	1.70-3.29	193
Mean Size	0.94	1.99	-	2.61	1.38	2.69	
Standard Deviation	0.11	1.23	-	0.27	0.27	0.37	
Proportion in %	13.5	4.7	-	3.1	71	7.7	100
Near-bottom population							
Range	0.60-1.12	1.52-2.08	2.68	2.12-2.68	1.04-1.64	2.20-2.44	54
Mean Size	0.86	1.85	-	2.39	1.45	2.32	
Standard Deviation	0.19	0.25	-	0.16	0.24	0.17	
Proportion in %	31.5	7.4	1.8	25.9	29.7	3.7	100

able to reach the surface waters during the night-time, including brooding females and mature males as represented by the overall proportion (Table 3).

South Azores seamounts

During the Seamount 2 cruise, 23 planktonic samples were collected at the mid-ocean ridge seamounts of the south Azores. Ten of these samples were collected during the night-time, and *A. agilis* was present in three of them: one at Gran Canaria (PK123) and two at Irving seamount (PK211 and PK228). The highest abundance was recorded at Irving (84 ind. 100 m^{-3} at PK211, 258 m depth).

In the near-bottom layer explored during the Seamount 2 cruise, eight diurnal samples were taken. *A. agilis* was recorded in two hauls at Meteor (TS155, < 1 ind.100 m^{-3} and TS163, 11 ind.100 m^{-3}) and two at Irving (TS212, 1.5 ind. 100 m^{-3} and TS213, 19 ind. 100 m^{-3}).

Immature males dominated in the surface population, while the other demographic components were present at lower percentages (Table 4). This population was characterized by the absence of brooding females. In the near-bottom population, juveniles, immature males and post-incubating females were present with similar percentage abundances. Conversely, to the surface population, the near-bottom population was characterized by the presence of brooding females (Table 4). The immature males reached the surface waters in quantitatively significant amounts, but the other demographic components of the population migrated to the surface in small percentages

Discussion

Seamounts had been considered as stepping stones [4,12]. In the case of Pacific seamounts, Parker and Tunnicliffe (1994) [2] had established that currents between these environments and neighbouring coastal systems were an important dispersal factor for the larvae and concluded that seamounts tended to be dominated by species inhabiting the nearest shelf areas.

The Lusitanian and South Azores seamounts represent topographic features of the Atlantic Ocean between the Azores and Iberian and African margins. They are mainly colonized by European and African continental shelf species transported by surface currents of the eastern Atlantic [14,21,25]. A large anticyclonic gyre circulation characterizes the North Atlantic surface Ocean. Along the European coasts, Portugal and the Canarias currents move in a south-easterly direction to the north of Madeira Island and south of the Azores Islands [42] (Figure 1).

Anchialina agilis in the North-eastern Atlantic

All the *Anchialina* specimens collected belong to *A. agilis*; its geographical distribution in the north-eastern Atlantic ranges from north of the Orkneys [43] to the Gulf of Guinea [44]. It is also reported in the western Mediterranean Sea [36, 38, 39].

Anchialina agilis is one of the commonest mysids in surface waters off the Moroccan coast during the night-time, but it is poorly represented in the water column during the day-time [34]. Occurring throughout the night-time, its vertical migration to the surface is particularly intense in front of Cape Ghir in spring. Some of these planktonic individuals might be swept away from the continental shelf towards oceanic waters.

A population of *A. agilis* was recorded off Gran Canaria in the suprabenthic bottom layer, occurring in five *Cymodocea nodosa* shallow sea-grass meadows, showing a maximum abundance in May 2011 with 334 ind. 100 m^{-3} [35]. Papiol et al. (2019) had analyzed the near-bottom zooplankton over three seamounts of the eastern Canary Islands (Amanay, El Banquete, and Concepción). Juveniles of *Anchialina* (probably *A. agilis*) were recorded from 27 to 566 m, with maximum abundances (663 ind.100 m^{-3}) in shallow waters (32-87 m).

In the south-eastern Bay of Biscay, *A. agilis* had been regularly sampled in the sub-surface water layer during the night-time (Sorbe, 1984 [37]; plankton samples above station 3 at 91 m depth), with other species of mysids showing lower abundances. However, *A. agilis* was never observed in the surface plankton sampling carried out monthly in 1990-92 on the upper continental slope [45] or either in the water column of the Cap Ferret canyon above 1,800 m water depth [31].

The near-bottom abundances during monthly sampling from January 1981 to June 1982, on a transect of four stations from 31 to 179 m offshore Arcachon (south Bay of Biscay) showed a maximum abundance of 4,733 ind.100 m^{-3} at station 5 at 126 m in May 1982 [37]. At two other stations (station 3 at 91 m depth and station 7 at 179 m depth), abundances higher than 1,000 ind.100 m-3 were regularly recorded, but *A. agilis* was absent at the shallowest stations (1 at 31 m depth) all year round.

Moreover, the species was sampled with a suprabenthic sledge in the upper part of the Cap Breton canyon (south-eastern Bay of Biscay) between 642 and 797 m [46] with a mean abundance of 367 ± 504 ind.100 m^2. Frustos and Sorbe (2014) [47] reported *A. agilis* on the southern margin of the Cap Breton Canyon at the two shallowest stations (175-182 m) with abundances of up to 58 ind.100 m^2, but the species was absent from their six deeper stations at 300 m. The species was also absent from a deeper transect of 13 stations sampled in 1989 from 350 to 1,100 m depth south of the Cap-Ferret Canyon offshore Arcachon Bay in the southern Bay of Biscay [45].

A. agilis had also been recorded in the benthic fauna of slope pockmarks from the Kostarrenkala area (Cap Breton Canyon, Bay of Biscay) in samples from 400 to 500 m depth [32]

A. agilis is a very common species in the English Channel and shows very high abundances in the western part of the Channel; moreover, its abundances near the sea-bottom are high during the day and very low during the night. *A. agilis* shows seasonal changes with a maximum in September [48]. The maximum abundance was recorded at 75 m depth offshore Plymouth (UK), with 1,523 ind.100 m^{-3} in October 1994, and at a station offshore Roscoff (Brittany, France) on coarse sand at 75 m depth with 1,874 ind. 100 m^{-3} in September 1989 [40].

The presence of *A. agilis* was noted by Fraser (1970) [49] and Mauchline (1986) [50] on the top of the Rockall Bank (about 118 nautical miles from the shelf edge). Mauchline (1986) [50] suggested that these isolated resident populations might be supplemented by recruitment through advection from the shelf population to the east.

Anchialina agilis on Atlantic Seamounts

A near-bottom population was sampled at the Gorringe, Josephine, and Seine seamounts (218-313 m depth), but the species was absent on Galicia, Lion, Unicorn, and Ampere seamounts. *A. agilis* was not found at Galicia, Lion or Unicorn, probably because the tops of these seamounts were not at suitable depths for this mysid (respectively 675, 625 and 875 m depth below the surface). The apparent absence of *A.*

agilis at Ampere was more surprising since this seamount is located at mid-distance between the Gorringe and Seine seamounts, which have their summits between 40 to 56 m below the ocean surface.

A. agilis was found only in two Azores seamounts: Irving and Meteor but not at Gran Canaria, Hyeres, Plato, or Atlantis. These seamounts are characterized by greater water depths than the Lusitanian seamounts (summit of the seamounts from 250-270 m depth at Meteor and Irving to 660 m at Gran Canaria). Irving and Meteor are located 952 and 1,007 nautical miles respectively from the Cape Saint Vincent and 670 and 709 nautical miles from the Seine seamount. *A. agilis* was collected in the plankton on these two seamounts during the night-time and in near-bottom samples during the day-time.

The mean sizes of all demographic components (except for the juveniles) of the Iberian margin population were lower than on the Lusitanian seamounts, excepted for the juveniles in the near-bottom water layers, which showed similar sizes on the two sites (Tables 2 and 3). Besides, the minimum size of *A. agilis* individuals from the Iberian margin was lower than on the Lusitanian seamounts. Hence, individuals from the Iberian margin appeared to attain maturity more rapidly than those collected on seamounts. This was probably because Iberian margin habitats were more suitable for the early attainment of maturity, whereas seamount individuals tended to reach a larger maximum size. The same pattern was observed in the planktonic and near-bottom environments.

There were similar percentage abundances of juveniles, immature females, incubating females, and mature males between the Lusitanian and south Azores seamounts (Tables 2, 3, and 4). Nevertheless, post-incubating females and immature males were more abundant in the south Azores' seamount samples.

All demographic components of the fauna from the south Azores seamounts appeared smaller than those from the Lusitanian seamounts, with a difference regarding immature females whose minimum size was greater in the near-bottom environment (Tables 2, 3, and 4).

A. agilis was abundant in surface waters during the night-time and near the sea-bottom during the day-time (Table 1). The abundances per 100 m^3 decreased from the Iberian margin to the Azores seamounts. The maximum abundance was nearly 3,600 individuals near the sea bottom and 450 individuals in surface waters on the Iberian margin, 829 individuals on Josephine seamount at the surface, 84 individuals on Irving at the surface. A total of 19 individuals was sampled with suprabenthic sledges during the day-time on Irving and 11 individuals on Meteor.

The maximum abundances along the Iberian margin was of the same order of magnitude as those found in the western part of the English Channel (>1,500 ind.100 m^{-3}) and the southern Bay of Biscay>1,000 ind.100 m^{-3} with a spring peak at 4,733 ind. 100 m^{-3}. The Josephine seamount yielded lower abundances of around 830 ind.100 m^{-3}, which was higher than values estimated by Herrera et al. (2014) [33]: 334 ind.100 m^{-3}. The abundances observed on Meteor and Irving were lower <100 ind.100 m^{-3} (Table 1).

Offshore advection of *Anchialina agilis* from the coast

A. agilis was very common in the nocturnal hyponeuston sampled in the submarine canyons on the continental shelf and slope of the north-western Mediterranean [38]. These authors showed offshore dispersal along the axis of the canyons resulting from passive transport due to the local currents and hydrodynamics of near-shore canyons. Macquart Ribera (1995) [39] studied the nocturnal migratory activity of *A. agilis* in vertical migrations from inshore to slope waters off the Marseilles area. Males showed intense migratory activity leading to a hyponeustonic distribution in mid-shelf and slope waters a few hours after dusk. Females and juveniles showed continuous pelagic phases and uniform distribution from dusk to dawn.

Hypotheses to explain the establishment of *Anchialina agilis* populations on Atlantic seamounts

Our observations showed that *A. agilis* continued to swim actively between deep oceanic layers and surface waters from day to night; these diurnal migrations probably did not exceed a depth range of 250-300 m. This active movement, plus the passive transport from shallow waters of the continental shelf to offshore, could explain the mode of colonization of north-eastern Atlantic seamounts (Figure 2). *A. agilis* shows a wider southward latitudinal distribution than other neritic mysids from the eastern Atlantic probably due to its diurnal migration and the passive transport of a hyponeuston population by the Canary current. *A. agilis* swims upward in the water column to reach surface waters during the night-time, and then returns to deeper layers during the day-time. In cases where there is a suitable sea-bottom depth, a population can become established on the seamount. *A. agiis* dispersion depends on the proximity of seamounts to each other as well as the distance to the Iberian and African margins. This is shown by the strong decrease in the abundance of the hyponeustonic population from the Iberian margin to the south Azores seamounts (Table 1). When the depth of a seamount summit is compatible with the depth-range of the diurnal vertical migration (up to 200-300 m), *A. agilis* can establish a bottom population such as on the Lusitanian seamounts (Josephine, Gorringe and Seine, summits between 220 and 310 m below the sea surface) and Azores seamounts (Irving and Meteor, with summits at 250 and 270 m depth, respectively). No sea-bottom populations had been observed in deeper seamount summits (Table 1).

The presence of established populations is validated by the representation of all categories of individuals from juveniles to mature males and females in planktonic and suprabenthic samples collected from the seamounts (Tables 2, 3, and 4).

Similarly to the surface planktonic abundances, the near-bottom populations of *A. agilis* showed a decrease in abundance from inshore to offshore from the Iberian margins (3,600 ind.100 m^{-3}) to the Azores (10-20 ind.100 m^{-3}). The reproductive population established on the Azores seamounts was established at 1,000 km-1,200 km from the coast, as against only 200 km for the Lusitanian seamounts. The settlement of juveniles would be ensured by a continuous input of individuals transported by the Canary surface current from the European and African margins, in addition to the existence of a relay population established on Grand Canaria Island [35]. Figure 2 summarizes our hypothesis for the colonization of north-eastern Atlantic seamounts by the neritic mysid *A. agilis*.

Conclusion

Such a pattern of colonization was observed for the mysid *Gnathophausia longispina* G.O. Sars, 1883 by Wilson and Boehlert (1993) [51] on the Hancock seamount (North Hawaiian Ridge, Pacific Ocean). These authors suggested that the population was well established on this isolated site, where all the population categories

were observed; they added that a resident population rather than migrant individuals could ensure the settlement.

Finally, our observations supported the hypothesis of an 'oasis' effect' [7], with active migration undertaken by individuals to maintain their proximity to the seabed on seamounts. This effect would provide habitats associated with biophysical mechanisms such as diurnal vertical migration leading to the trapping of established migrant individuals.

Acknowledgment

The authors thank Drs Philippe Bouchet and Serge Gofas (MNHN, Paris) who supervised the 'Seamount 1' and 'Seamount 2' campaigns. Thanks to Michael Carpenter for his help and comments on the English text, to Souad Mallek-Zouhiri for her assistance in the suprabenthic identification of taxa collected during the Seamount 2 campaign, and Lucie Millet and Martial Boutet for the figures.

The drafting of this paper began during the late 1990s, but the results have remained unpublished for the last three decades. Jean-Claude Sorbe, one of the two authors of this paper, passed away in December 2019. It remains for me to finish writing up our paper. It is my memory tribute to Jean-Claude, who was both a colleague and a friend; it was always a pleasure to work with him and exchange views. He spoke passionately about his crustaceans; the science community will miss him.

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