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The biogeography of *Artemia*: an updated review

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Abstract

An updated list of more than 350 *Artemia* sites is provided. It includes geographical coordinates of the sites and available data on the mode of reproduction of the locally occurring brine shrimp.

The geographical distribution of *Artemia* is related to different types of climate. The classification of climate according to Thornthwaite provides a good correlation with the geographical occurrence of *Artemia*, as a result of which the world distribution pattern of *Artemia* can be predicted. Moreover, areas with possible *Artemia* sites and areas suited for transplantation and/or inoculation with *Artemia* can be identified on the basis of water balance data. This is illustrated for three case studies (Peru, the Philippines and Sri Lanka).

The relation between the biogeographical distribution of *Artemia* and its speciation in different sibling species as well as its reproduction mode is discussed.

Introduction

It is generally known that the brine shrimp *Artemia* is widely distributed on the five continents in many salt lakes, coastal lagoons, and solar saltworks. In 1915 Abonyi already published a list of 80 *Artemia* sites located in 21 different countries. Later on, some less extensive distribution lists were reported by Artom (1922) (18 sites), Stella (1933) (28 sites), and Barigozzi (1946) (29 sites). The most recent review of the distribution of *Artemia* (Persoone and Sorgeloos, 1980) included a list of 243 sites distributed over 48 countries.

In recent years interest in *Artemia* has increased steadily and as a result the occurrence of *Artemia* has been studied and recorded in a growing number of countries.

The present paper provides an updated list of *Artemia* sites resulting from a thorough literature study (Vanhaecke, 1983) and numerous personal communications received at the Artemia Reference Center. The distribution lists have been completed with the geographical coordinates of the sites and the available data on the mode of reproduction and the sibling species.

The present distribution list of *Artemia* sites was further used to determine a logical trend in the distribution pattern of *Artemia* sites. This in order to allow the identification of areas where *Artemia* might occur, or areas that might be suitable for brine shrimp transplantation or inoculation. With this aim correlations were evaluated between the geographical distribution of *Artemia* and different classifications of climate.

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Finally the biogeography of *Artemia* is discussed in relation to the differentiation between sibling species and in relation to the reproduction mode of *Artemia.*

The world distribution of *Artemia* sites

The listings of *Artemia* sites in the Tables I through VIII only include those biotopes in which the population reappears each year, and do not cover temporal *Artemia* populations mostly introduced through inoculation in seasonal salt operations (*e.g.* Panama, Costa Rica, Burma, Thailand, Philippines, Viet Nam, Indonesia). In view of favorable climatic conditions and/or specific management allowing for year-round storage of brine, some of these inoculated strains might, however, become established as natural strains and should be added to the listings in due time, *e.g.* Cam Ranh Bay, Viet Nam (Vu Do Quynh and Nguyen Ngoc Lam, 1987) and Aguadulce, Panama (Pang, pers. commun.).

The world distribution of *Artemia* is presented in Fig. 1. Although about 360 *Artemia* sites could be traced back, the present distribution list remains provisional. It is interesting to note that within a time period of not more than 6 years 117 new *Artemia* biotopes have been recorded. This observation not only indicates that an increasing number of investigations have been carried out recently, but also confirms our hypothesis that more extensive survey work should lead to the discover of many more *Artemia* biotopes in different parts of the world. On the other hand, as history has already proved, brine shrimp populations and biotopes might disappear not only as a consequence of human intervention but also from natural causes such as temporal climate changes, *e.g.* Lymington, UK; Capodistria, Yugoslavia).

The common feature of all *Artemia* biotopes is their high salinity. Salinity is without any doubt the predominant abiotic factor determining the presence of *Artemia* and consequently limiting its geographical distribution. This was clearly illustrated by Hammer (1978) who studied the salinity and presence of *Artemia* in 60 salt lakes in the Saskatchewan region. Whereas salinity ranged from 2.4 up to 370 ‰, *Artemia* was only found in those five lakes with salinities over 94 ‰. An analogous distribution of *Artemia* in relation to salinity has been reported by McCarraher (1970) for Nebraska lakes. The impact of other parameters such as temperature, light intensity, primary food production, *etc.* on the *Artemia* distribution is limited to the quantitative population development of brine shrimp or may cause only a temporary absence of *Artemia.*

Although high salinity is imperative to allow brine shrimp to persist, not all salt lakes or highly saline biotopes are populated with *Artemia, e.g.* for the continental USA McCarraher (1972) listed over 30 highly saline lakes (> 100 ‰) not inhabited by *Artemia,* in West Victoria (Australia) *Artemia* is absent in 15 natural salt lakes (> 100 ‰) (Williams, 1981). Apparently, none of the distribution vectors wind, birds nor man allowed *Artemia* to colonize these biotopes. In the particular case of Australia, however, it is not unlikely that the endemic genus *Parartemia* which is better adapted to the specific conditions of Australian salt lakes minimizes the chance of an introduced *Artemia*-population to develop (Geddes, 1980ab, 1981).

Although *Artemia* is widely distributed throughout the world, these observations clearly illustrate that it is not ubiquitous nor can it even be considered a cosmopolitan organism, as it is not present in every suitable biotope.

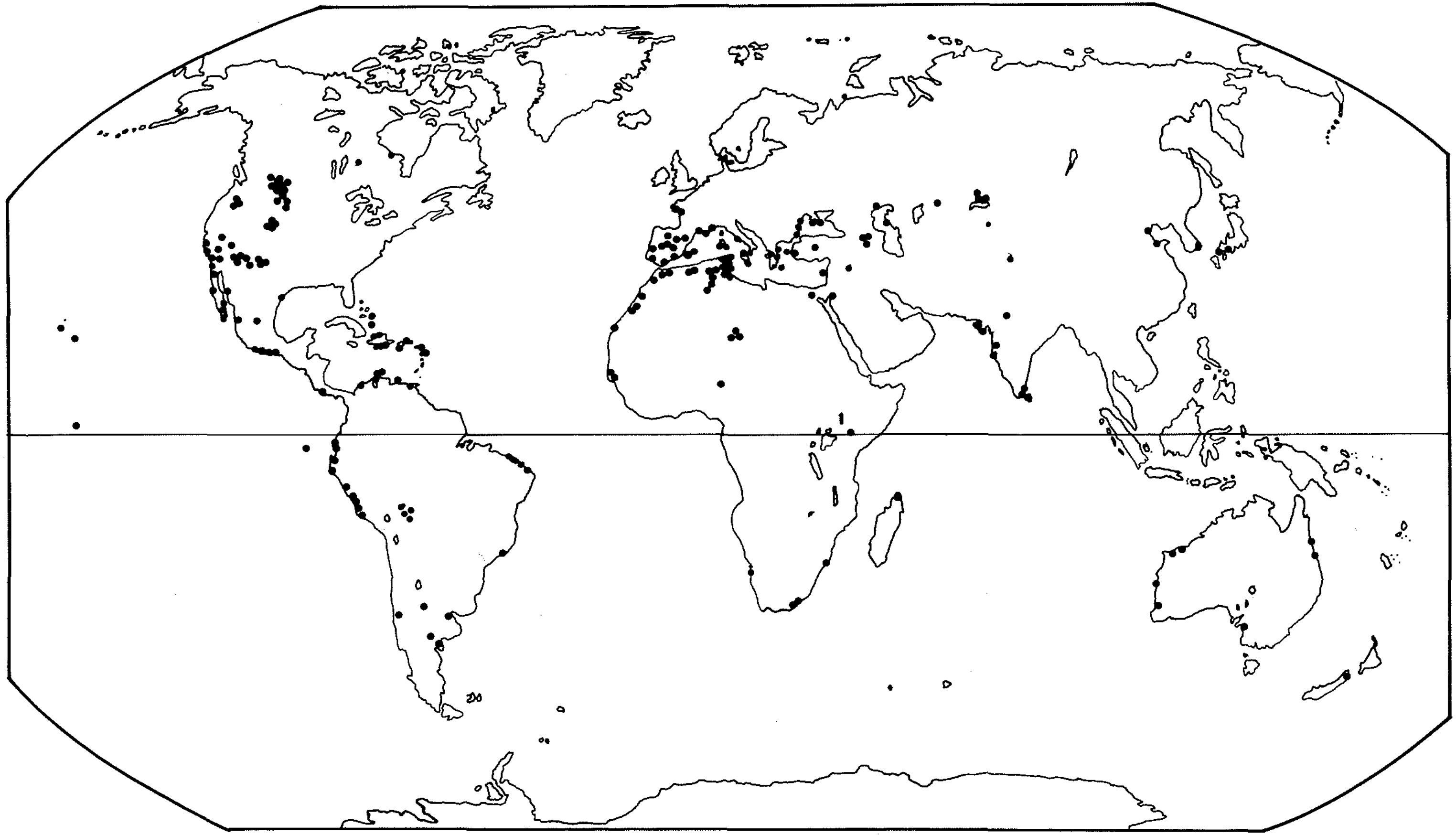

FIG. 1. The world distribution of *Artemia*.

TABLE I

Artemia sites in Africa

Country	Locality	Geographical coordinates	Reproduction mode[1]	Sibling species[2]	References[3]
Algeria	Chegga Oase	34°29'N-05°53'E	–	–	131
	Chott Djeloud	34°03'N-06°20'E	–	–	131
	Chott Ouargla	31°57'N-05°20'E	–	–	12,24
	Dayet Morselli	35°30'N-00°46'W	–	–	24
	Gharabas Lake	35°35'N-00°25'W	–	–	131
	Sebket Djendli	35°43'N-06°32'E	–	–	131
	Sebket Ez Zemouk	35°53'N-06°33'E	–	–	131
	Sebket Oran	35°32'N-00°48'W	–	–	131
	Tougourt	33°06'N-06°07'E	–	–	73
Egypt	Ismailia	30°36'N-22°15'E	–	–	179
	Wadi Natron*	30°10'N-30°27'E	B(180)	–	122
	Solar Lake	29°10'N-34°50'E			24,37,38
Kenya	Elmenteita	00°27'S-36°15'E			121
Libya	Mandara	26°40'N-13°20'E	B(180)	–	20,73
	Ramba-Az-Zallaf (Fezzan)	27° N-13° E			83
	Quem el Ma	26°41'N-13°22'E	–	–	20,73
	Trouna	26°50'N-13°30'E	–	–	20
	Gabr Acun (Fezzan)	27° N-13° E	–	–	20,73,81
Madagascar	Salins de Diego Suarez	12°19'S-49°17'E	–	–	133,150
Marocco	Larache	35°12'N-02°20'W	P	pa	63
	Moulaya estuary	35°07'N-02°20'W			131
	Qued Ammafatma	28°18'N-12°00'W			73
	Qued Chebeica	28°25'N-11°50'W			73
	Sebket Bon Areg	35°10'N-02°50'W			131
	Sebket Zima	32°05'N-08°40'W			131
Mozambique	Lagua Quissico	24°41'S-34°46'E			40
Namibia	Vineta Swakopmund*	22°40'S-14°34'E	P(180)	pa	181
Niger	Teguidda In Tessoun	17°26'N-06°39'E			122
Senegal	Dakar	14°34'N-17°29'W			122
	Lake Kayar	14°55'N-17°11'W			122
	Lake Retba	14°50'B-17°20'W			73
South Africa	Coega Salt Flats	33°46'S-25°40'E			159
	Swartkops	33°52'S-25°36'E			159
Tunisia	Bekalta*	36°48'N-10°20'E	B	t	101
	Chott Ariana*	36°54'N-10°18'E	B	t	44,101
	Chott El Djerid	33°42'N-08°26'E			131
	Megrine*	36°47'N-10°14'E	B	t	101
	Sebket Kowezia*	36°26'N-09°46'E			131
	Sebket mta Moknine*	35°39'N-10°53'E	B	t	101
	Sebket Sidi el Hani*	35°31'N-10°27'E			131
	Sfax*	35°45'N-10°43'E	B	t	101

[1] (B) : bisexual ; (P) parthenogenetic. Legend to reference numbers in parentheses is given in Table VIII.
[2] (f) *Artemia franciscana* ; (m) *A. monica* ; (pa) : *A. parthenogenetica* ; (pe) *A. persimilis* ; (t) *A. tunisiana* ; (u) *A. urmania.* Legend to reference numbers in parenthesis is given in Table VIII.
[3] See list in Table VIII.
* Cyst sample present in the cyst bank of the Artemia Reference Center.

TABLE II

Artemia sites in Australia and New Zealand (legend to abbreviations in Table I)

Country	Locality	Geographical coordinates	Reproduction mode	Sibling species	References
New Zealand	Lake Grassmere*	41°38'S-174°05'E	B		94
Queensland	Bowen	20°00'S-184°16'E			56,80
	Port Alma*	23°22'S-150°32'E	B		56,44,80
South Australia	Dry Creek, Adelaide	34°55'S-138°20'E			26,48,56,80
Western Australia	Dampier	20°35'S-116°51'E			56
	Lake Mc Leod	23°59'S-113°40'E			56
	Port Hedland*	20°25'S-118°35'E	P(114)		56
	Rottnest Island	32°00'S-115°27'E	P(114)		56,44,80,86
	Shark Bay*	25°15'S-113°20'E	P(B)(103)		56,80

TABLE III

Artemia sites in North America (legend to abbreviations in Table I)

Country	Locality	Geographical coordinates	Reproduction mode	Sibling species	References
Canada	Akerlund Lake	52°18'N-109°15'W			124
	Alsask Lake	51°20'N-109°52'W			124
	Aroma Lake	51°18'N-108°33'W			4,124
	Berry Lake	52°07'N-105°30'W			124
	Boat Lake	50°17'N-109°59'W			124
	Burn Lake	49°49'N-105°27'W			124
	Ceylon Lake	49°27'N-104°36'W			124
	Chain Lake	50°30'N-108°43'W			124
	Chaplin Lake*	50°25'N-106°38'W	B(104,105)	f(102,103)	4,124
	Churchill	58°45'N- 94°00'W			182
	Coral Lake	49°51'N-102°21'W			124
	Drybore Lake	49°43'N-105°30'W			124
	Enis Lake	52°10'N-108°19'W			124
	Frederick Lake	49°59'N-105°38'W			124
	Fusilier Lake	51°50'N-109°44'W			124

TABLE III. Continued

Country	Locality	Geographical coordinates	Reproduction mode	Sibling species	References
Canada	Grandora Lake	52°06'N-107°00'W			124
	Gull Lake	50°06'N-108°27'W			124
	Hatton Lake	50°02'W-109°50'W			124
	Horizon Lake	49°32'N-105°17'W			124
	Ingerbright Nath	50°22'N-109°19'W			124
	Landis Lake	52°13'N-108°27'W			124
	La Perouse	55°14'N- 98°00'W			182
	Little Manitou Lake	51°48'N-105°30'W	B	f(105)	4,24,44,46,90,124
	Lydden Lake	52°09'N-108°13'W			124
	Mawer Lake	50°46'N-106°22'W			124
	Meacham Lake	52°07'N-105°47'W			124
	Muskiki Lake	52°20'N-105°45'W			124
	Neola Lake	52°02'N-107°49'W			124
	Oban Lake	52°09'N-108°09'W			124
	Richmond Lake	52°01'N-108°01'W			124
	Shoe Lake	49°55'N-105°27'W			124
	Snakehole Lake	50°30'N-108°30'W			124
	Sybouts Lake-East	49°02'N-104°24'W			124
	Sybouts Lake-West	49°02'N-104°27'W			124
	Verlo West	50°19'N-108°37'W			124
	Vincent Lake	50°13'N-108°57'W			124
	Wheatstone Lake	49°49'N-105°24'W			124
	Whiteshore Lake	52°08'N-108°17'W			124
USA-Arizona	Kiatuthlana Red Pond	34°50'N-109°26'W	B(114)	f(102,105)	11,12,13,24,44
	Kiatuthlana Green Pond	34°50'N-109°26'W	B(114)	f(102,105)	11,12,13,24,44
-California	Carpinteria Slough	34°24'N-119°30'W			43
	Chula Vista	32°36'N-117°05'W			112
	Mono Lake*	38°00'N-119°00'W	B(44)	m(105,120)	6,12,22,24,58,66
	Moss Landing, Monterey Bay	36°42'N-121°49'W			44,87
	Owens Lake	36°25'N-117°56'W			24
	San Diego	32°50'N-117°10'W			44
	San Francisco Bay*	37°28'N-122°30'W	B(44,180)	f(102,105)	21,44,76,90
	San Pablo Bay*	38°00'N-122°16'W	B(104)	f(105)	77,123
	Vallejo West Pond	38°12'N-122°15'W			21,44

USA-Hawaii	Christmas Islands*	01°50'N-157°20'W			97,98
	Hanapepe	21°54'N-159°30'W			23
	Laysan Atoll	25°30'N-167°00'W			23
-Nebraska	Alkali Lake	43°32'N-100°38'W			24
	Ashenburger Lake	42° N-102° W			24
	Cook Lake	42° N-102° W			12,24,49
	East Valley Lake	42° N-102° W			24
	Grubny Lake	42° N-102° W			24
	Homestead Lake	42° N-102° W			24
	Jesse Lake*	42°06'N-102°39'W	B	f(102)	11,12,49
	Johnson Lake	42° N-102° W			12,24
	Lilly Lake	42° N-102° W			11,12,49
	Reno Lake	42° N-102° W			24
	Richardson Lake	42° N-102° W			12,24,49
	Ryan Lake	42° N-102° W			12
	Sheridan County Lakes	42° N-102° W			12
-Nevada	Fallon	39°31'N-118°52'W			58,95
-North Dakota	Miller Lake	–			24
	Stink (Williams) Lake	–			24
-New Mexico	Laguna del Perro*	34°32'N-106°01'W			126
	Loving Salt Lake	32°17'N-104°04'W	B(114)		129
	Quemado*	34°17'N-108°28'W	B	f(105)	44
	Zuni Salt Lake	34°27'N-108°46'W	B(114)	f(102)	5,11,12
-Oregon	Lake Abert*	42°35'N-120°15'W	B(130)		125
-Texas	Cedar Playa	32°49'N-102°07'W			75
	McKenzies Playa	32°41'N-102°10'W	B(180)		75
	Mound Playa	33°10'N-101°56'W			75
	Playa Thahoka*	33°12'N-101°34'W	B(180)		24,75
	Raymondville*	26°10'N- 97°48'W	B(180)		124
	Rich Playa	33°13'N-102°03'W			75
	Snow drop Playa	32°59'N-101°40'W			75
-Utah	Great Salt Lake*	41°00'N-112°30'W	B(44,104,106)	f(102,105)	11,12,18,19,24, 30,31,32,42,90
-Washington	Hot Lake	48°58'N-119°29'W			3,7
	Omak Plateau	48°25'N-119°24'W			7,11
	Soap Lake	47°33'N-119°25'W	B(114)		44

TABLE IV

Artemia sites in Central America (legend to abbreviations in Table I)

Country	Locality	Geographical coordinates	Reproduction mode	Sibling species	References
Bahamas	Great Inagua*	21°00'N- 75°20'W	B		44
	Long Island*	23°20'N- 75°07'W	B(180)		124
	San Salvador	24°00'N- 74°35'W			128
British Virgin Islands	Anegada	18°45'N- 64°24'W			160
Caribbean Islands	Antigua	17° 0'N-61°45'W			144
	St. Kitts	17°20'N- 62°45'W			144
	St. Martin	18°04'N- 63°06'W			160
Costa Rica	Gulfo Nicoya	10°00'N- 84°49'W			146
Dominican Republic	Isla Cabra	19°53'N- 71°40'W	B		115
	Las Calderas		B		115
	Monte Cristi	19°52'N- 71°39'W	B		115
	Puerto Alejandro		B		115
	Punta Salinas*	18°20'N- 71°04'W	B(180)		130
Haiti	Grandes salines	18° N- 72° W	B	f	180
Mexico	Bahia de Cueta*	24°05'N-107°00'W	B(180)		29
	Carretas, Pereyra	15°30'N- 93°13'W			107
	Chanchuto Panzacola				107
	Chiapas	15°56'N- 93°30'W			29
	Guerrero Negro	28°06'N-114°03'W			29
	Isla del Carmen	26°00'N-111°40'W			107
	Laguna der Mar Muerto	16° N- 94° W			107
	La Joya, Buenavista	27°27'N-106°15'W			107
	Las Salinas	22°40'N-101°42'W			140
	Los Palos, Solo Dios				107
	Pichilingue Island	24°17'N-110°20'W	B(114)		29,44
	Salina cruz	16°10'N- 95°10'W			29
	San Jose Island	25°00'N-110°50'W	B(114)		151
	San Quintin	30°28'N-115°58'W			44
	Yavaros	26°43'N-109°33'W	B	f(102,104)	29
Netherlands Antilles	Aruba	12°30'N- 70°00'W			15
	Bonaire Duinmeer*	12°04'N- 68°13'W	B	f(102,104)	33
	Gotomeer	12°14'N- 68°23'W			15,33
	Pekelmeer	12°04'N- 68°16'W			15,33,84
	Martinus	12°09'N- 68°17'W			14,15
	Slagbaai	12°16'N- 68°25'W			14,15
	Curaçao Fuik	12°03'N- 68°51'W			14,15
	Rifwater	12°08'N- 68°57'W			14,15
Puerto Rico	Bahia Salinas*	17°57'N- 67°12'W	B(180)	f(102)	170
	Bogueron*	18°01'N- 67°10'W			170
	Cabo Rojo*	17°56'N- 67°08'W	B(114)		85
	La Parguera	17°59'N- 67°03'W			52
	Ponce	18°00'N- 66°38'W			170
	Tallaboa	18°00'N- 66°42'W			44

TABLE V

Artemia sites in South America (legend to abbreviations in Table I)

Country	Locality	Geographical coordinates	Reproduction mode	Sibling species	References
Argentina	Bahia Blanca	38°43'S-62°15'W			120
	Buenos Aires*	34°30'S-58°20'W	B	pe(102,104)	
	Hidalgo	37°10'S-63°32'W			44,65,88,89
	Mar Chiquita	30°39'S-62°30'W			172
Bolivia	Lake Canapa		B		173
	Lake Chulluncani	16°22'S-67°30'W			173
	Lake Hedonia				173
	Lake Poopo	18°23'S-66°58'W	B		173
Brazil	Aracati	4°32'S-37°45'W			108
	Cabo Frio*	22°51'S-42°03'W	B	f(102)	16
	Fortaleza	3°45'S-38°35'W			108
	Icapui	4°42'S-37°21'W			154
	Macau*	5°00'S-36°40'W	B	f(102,104)	68
	Mundau	3°15'S-39°24'W			108
Chili	Atacama Lake	23°30'N-68°10'W			184
	Pichelimu	34°22'S-79°09'W			70
Colombia	Galerazamba*	10°25'S-74°40'W	B	f(102)	128
	Manaure*	12°09'S-71°55'W	B	f(102,104)	128
Ecuador	Galapagos	0° S-89° W			44
	Pacoa*	2°00'S-80°50'W	B(180)		156
	Salinas	2°20'S-80°58'W			156
Peru	Caucato	13°40'S-76°05'W			148
	Chicama	7°42'S-79°27'W			148
	Chilca*	12°35'S-76°41'W	B(180)		157,148
	Estuario de Virrila*	5°50'S-80°50'W	B(180)		148
	Guadalupe	7°17'S-79°28'W			148
	Pampa de Salinas	11°14'S-77°35'W			148
	Pampa Playa Chica	11°14'S-77°35'W			148
	Puerto Huarmey	10°03'S-78°08'W			148
	Tumbes*	3°37'S-80°27'W	B(180)		148
Venezuela	Boca Chica	10°57'N-64°26'W			60,166
	Coya Sal	10°56'N-68°15'W			166
	Coche	10°41'N-63°58'W			166
	Coro Coastline	11°30'N-69°45'W			152
	La Orchila	11°49'N-66°00'W			166
	Las Aves	12°00'N-67°17'W			166
	Los Roques	11°50'N-66°38'W			164,166
	Port Araya*	10°39'N-64°17'W	B(102,104)		165
	Tucacas*	10°48'N-68°19'W	B(180)		166

TABLE VI

Artemia sites in Asia (legend to abbreviations in Table I)

Country	Locality	Geographical coordinates	Reproduction mode	Sibling species	References
China	Aibi Lake*				175
	Tientsin*	39°10'N-117°00'E	P	pa(102)	127,145
	Tsingtao*	36°00'N-120°25'E			127,147
	Urumuchi Lake	43°43'N- 87°38'E			175
India	Bhayander, Bombay*	18°55'N- 72°50'E	P(180)		34,61,62
	Didwana	27°17'N- 74°25'E			135
	Jamnagar	22°30'N- 70°08'E			28,62
	Karsewar Island	8°50'N- 78°10'E			1
	Kutch*	23°20'N- 71°00'E	P	pa(44)	28,137
	Mithapur*	23°00'N- 70°10'E	P(180)		28,62,139
	Pattanamaruthur	8°55'N- 78°08'E			59
	Spic Nagar	8°50'N- 78°08'E			59
	Thirispuram	8°50'N- 78°08'E			59
	Tuticorin	8°50'N- 78°08'E	P	pa(102)	26,27,57,59,62
	Vadala, Bombay	18°55'N- 72°50'E			26,27
	Vedaranyam	10°01'N- 79°50'E			110
	Veppalodai	8°59'N- 78°08'E			59
	Vivar, Bombay	18°55'N- 72°50'E			136
Iraq	Abu-Graib, Baghdad	33°20'N- 44°30'E	P(114)		141
	Basra	30°25'N- 47°51'E			2
	Dayala	33°30'N- 44°30'E			2
	Mahmoodia	33° N- 44° E			2
Iran	Ormia*	37°20'N- 45°40'E	B	u(44)	12,24,45
	Schor-Gol	37°03'N- 45°32'E			12,24,45
	Shurabil	48°17'N- 38°15'E			109
	Athlit	32°42'N- 34°56'E			96
Israel	Eilat North*	29°32'N- 34°56'E	P	pa(44)	142
	Eilat South	29°28'N- 34°56'E			142
Japan	Chang Dao	34° N-132° E			55
	Tamano	34°35'N-133°59'E			51
	Yamaguchi	34°10'N-131°32'E	P(114)		44,51
Kuwait		29° N- 47° E			149
Korea	Pusan	35°05'N-129°02'E			176
Sri Lanka	Bundala	6°12'N- 81°15'E			180
	Hambantota*	6°07'N- 81°07'E			180
	Palavi	7°58'N- 79°51'E			180
	Putallam	8°02'N- 79°50'E	P(180)	pa(180)	153
Taiwan	Peinan Salina				177
Turkey	Aivalik				134
	Izmir (Camalti)*	38°25'N- 27°08'E	P	pa(102)	35
	Tuz Golii	38°45'N- 33°30'E			10

TABLE VII

Artemia sites in Europe (legend to abbreviations in Table I)

Country	Locality	Geographical coordinates	Reproduction mode	Sibling species	References
Bulgaria	Burgas*	42°33'N-27°29'E	P	pa(102)	8,47
	Pomorye	42°26'N-27°41'E			8,47
Cyprus	Akrotiri lake	34°34'N-32°58'E			17
	Larnaca lake*	34°56'N-33°35'E	B(111)	t(102,104)	17
France	Aigues Mortes*	43°34'N- 4°11'E	P(180)		132
	Carnac-Trinité sur Mer	47°36'N- 3°05'W			82
	Guérande-le Croisic*	47°20'N- 2°26'W	P(180)		82
	La Palme	42°59'N- 3°00'E			154
	Lavalduc*	43°24'N- 4°56'E	P	pa(102,104)	132
	Mesquer-Assérac	47°26'N- 2°29'W			82
	Porte La Nouvelle	42°57'N- 3°02'E			112
	Salin de Berre*	43°24'N- 5°05'E	P(180)	pa(102)	155
	Salin de Fos	43°26'N- 4°56'E			155
	Salin de Giraud*	43°24'N- 4°44'E	P	pa(102)	154
	Salins d'Hyères	43°07'N- 6°12'E			155
	Salin des Pesquiers	43°07'N- 6°12'O			155
	Sète*	43°25'N- 3°42'E		pa(144,102)	78,79
Greece	Embolon	40°38'N-22°58'E	P		117
	Kalloni	39°16'N-26°16'E	P		117
	Katerini	40°15'N-22°30'E	P		161
	Kitros	40°22'N-22°34'E	P		117
	Mesolongi*	38°21'N-21°26'E	P		161
	Milos	36°44'N-24°25'E	P		116,161
	Porto		P		117
Italy	Cagliari, Sardinia	39°13'N- 9°08'E			118
	Carloforte Sardinia	39°08'N- 8°17'E			118
	Cervia	44°16'N-12°21'E			180
	Commachio*	44°41'N-12°10'E	P	pa(63)	78,79
	Margherita di Savoia*	41°25'N-16°05'E	P	pa(102)	167
	San Antioco, Sardinia	39°02'N- 8°30'E			118
	Santa Gilla, Sardinia	39°14'N- 9°06'E	P(114)		78,79
	Siracuse, Sicily	37°04'N-15°18'E			143
	Tarquinia	42°29'N-11°45'E			118
	Trapani, Sicily	38°01'N-12°30'E			168
Portugal	Alcochete	38°45'N- 8°57'W	P	pa(102)	63
	Tejo estuary	38°50'N- 9°00'W			168
	Sado estuary	38°25'N- 8°43'W			168
	Ria de Aveiro	40°37'N- 8°38'W			168
	Ria de Farc	37°02'N- 7°55'W			168
Rumania	Lake Techirghiol*	43°04'N-28°34'E	P(114)		9,36,39
Spain	Armalla*	40°54'N- 1°59'W			63
	Ayamonte	37°13'N- 7°24'W	P		63
	Cabo de Gata*	36°48'N- 2°14'W	P	pa	63
	Buyaraloz	41°29'N- 0°10'W			63,71
	Cadiz*-San Felix	36°30'N- 6°20'W	B		41,63,67,71
	-San Fernando	36°22'N- 6°17'W	B		41,63,67,71
	Calpe*	38°39'N- 0°03'E	P	pa(102)	63
	Campos del Puerto, Mallorca	39°26'N- 3°01'E			63,71
	Delta de Ebro*	36°25'N- 6°18'W	P	pa	63
	Gerri de la Sal	42°20'N- 1°04'E	P	pa	63,71
	Imon	41°10'N- 2°45'W			63

TABLE VII. Continued

Country	Locality	Geographical coordinates	Reproduction mode	Sibling species	References
Spain	Isla Cristina	37°13'N- 7°19'W	P	pa	63
	Janubio, Lanzarote	28°56'N-13°50'W	P	pa	63
	Laguna de Quero	39°34'N- 3°17'W			63
	Las Palmas	28°10'N-15°28'W			96
	Lepe	37°15'N- 7°12'W			63
	Lerin	42°29'N-10°59'W			63
	Medacineli	41°12'N- 2°30'W			63
	Molina del Segura	38°03'N- 1°11'W			63
	Peralta de la Sal	42°00'N- 0°24'E			63
	Poza de la Sal	42°40'N- 3°30'W			63,71
	Rienda	41°06'N- 2°34'W			63
	Roquetas	40°50'N- 0°30'E			63
	Saelices	39°55'N- 2°49'W			63
	Salinera Catalena	37°37'N- 0°51'W			63
	Salinera Espanola, Formentera	38°40'N- 1°26'E	B(114)		63
	Salinera Espanola, Ibiza	38°55'N- 1°35'E	B		63,71
	Salinera Punta Galera	37°42'N- 0°54'W			63
	San Juan del Puerto	37°20'N- 6°50'W			63
	Sanlucar de Barrameda*	36°43'N- 6°23'W	PB		63
	San Pedro del Pinatar	37°50'N- 0°50'W	B	t	63
	Santa Pola-Bonmati*	38°13'N- 0°35'W	PB	pa(102)	63
	-Bras de Port	38°13'N- 0°35'W	P	pa	63
	-Salinera Espanola	38°13'N- 0°35'W	B		63
	Siguenza	41°04'N- 2°38'W			63
	Villena	38°39'N- 0°52'W			63
USSR	Bolshoe Otar Mojnakshoe	45° N-33° E			53
	Bolshoe Yarovoe*	53°00'N-78°30'E	P(180)		143
	Burlinskoe ozero	53°12'N-78°30'E			24,178,183
	Szharylgach	45°35'N-32°56'E			53,54
	Ghenicheskoe Lake	46°15'N-35°00'E			74
	Karachi Lake	41°16'N-72°00'E			92
	Kazakhstan*	49°00'N-50°00'E			69
	Kuchukskoe	52°40'N-79°40'E			24
	Kujalnic estuarium	46°43'N-30°40'E	P(180)		9,119
	Kyzyl-Jar Lake (Primorsk)	40°14'N-49°33'E			92
	Mangyshlak penisula*	43°40'N-52°30'E			149
	Moekba*				178
	Odessa*	46°30'N-30°45'E	P(111)	pa(44)	69
	Ontario Lake				92,93
	Petukhovshoe	52°10'N-78°40'E			24
	Popovskoe Lake	45° N-33° E			54
	Sakshoe	45°10'N-33°30'E			24,53,72
	Sasyk Lake*	45°15'N-33°25'E			50,53,72,92
	Sasykol Lake	53°40'N-61°40'E			64
	Seitenj*				178
	Tambukan				24
	Tinaki Lake*		P(180)		169
	Tobechicskoe Lake	45°10'N-36°05'E			53,162
	Turkomama				171
	Yalovoye*				169
Yugoslavia	Portoroz*	45°39'N-13°36'E	P	pa	113
	Strunjan	45°32'N-13°36'E	P	pa	113
	Ulcinj	41°55'N-19°12'E	P	pa	113

TABLE VIII

List of references given in Tables I through VII

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The geographical distribution of *Artemia* in relation to climate

Since habitat salinity is function of local water supply (*i.e.* precipitation, ground water seepage and surface water runoff) and of local evaporation rates, it is obvious that climate will have an important effect on the geographical distribution pattern of *Artemia* biotopes. In this regard, we have studied the distribution of *Artemia* sites in relation to the classification of the different types of climate. We have used the classification system of Thornthwaite (1948), and Thornthwaite and Mather (1955, 1957) which is based on the calculation of the water balance of the soil taking into account monthly data on precipitation and potential evaporation. The system of Thornthwaite makes use of the parameter "precipitation efficiency" which is determined by the index I_m.

$$I_m = I_p - I_a$$

$$\text{with } I_p = \frac{100\,S}{n} \text{ and } I_a = \frac{100\,d}{n}$$

whereby S = yearly surplus
d = yearly deficit
n = yearly need of water.

According to the numerical value of I_m, six climate types can be distinguished A = perhumid, B_4 - B_1 = humid, C_2 = humid-subhumid, C_1 = dry subhumid, D = semiarid, E = arid (Thornthwaite and Mather, 1955). This system furthermore allows characterization of the seasonal aspect of humidity or aridity. In analogy to the classification based upon the „precipitation efficiency" the so-called "adapted potential evapotranspiration" can be calculated to consider the "temperature efficiency" classification. This provides five climate types : A'_1 = megathermal, B'_4 - B'_1 = mesothermal, C'_2 - C'_1 = microthermal, D' = tundra, E' = frost. Seasonal characters of temperature efficiency can also be determined.

We have determined the type of climate corresponding to each *Artemia* site by using the monthly and yearly data on potential evapotranspiration, precipitation, water deficit, and surplus (Thornthwaite Associates 1962, 1963abc, 1964abc, 1965) or by use of climatic maps (Burgos and Vidal, 1951 ; Carter, 1954 ; Carter and Mather, 1966).

The distribution of the *Artemia* biotopes over the different types of climate (Table IX) reveals that the geographical distribution of brine shrimp is limited by climatological conditions, *i.e.* no

TABLE IX

The classification of *Artemia* sites (in %) in relation to the climate types according to Thornthwaite

Precipitation efficiency	Temperature efficiency						
	A'	$B'_{3\text{-}4}$	$B'_{1\text{-}2}$	$C'_{1\text{-}2}$	D'	E'	Total
E	15	6	2	0	0	0	23
D	9	12	12	1	0	0	34
C_1	5	6	17	12	0	0	40
C_2	1	0	2	0	0	0	3
B_4-B_1	0	0	0	0	0	0	0
A	0	0	0	0	0	0	0
Total	30	24	33	13	0	0	100

Artemia is found in perhumid (A) or humid (B_4 - B_1) climate types, and 97 % of the biotopes are located in areas where yearly evaporation exceeds yearly precipitation (negative I_m index : C_1, D, E).

The predominant effect of aridity on the distribution pattern of *Artemia* is further stressed when considering the seasonal aspect. Indeed, more than 97 % of the *Artemia* sites are located in areas where not just on a yearly basis, but also during the different seasons of the year, no or a very small water surplus can be noted. This is only a logical consequence of the limitation of *Artemia* presence to those biotopes where the salinity remains sufficiently high on a year-round basis. The 3 % of biotopes found in the humid sub-humid, C_2 climate type are all operational saltworks (three in France, four in India, one in Argentina, and one in Japan). Human interventions to keep high salinity levels do allow *Artemia* to survive in these biotopes, *e.g.* drainage or pumping of the freshwater stratification layer (Jones *et al.*, 1981), storage of brine in deep reservoirs (Richard, pers. commun.).

Aside from humidity the "efficiency of temperature" seems also to affect the distribution pattern of *Artemia.* No *Artemia* are found in the cold tundra and frost climate types (D' and E') as the prevailing low temperatures preclude *Artemia* development. Potential evaporation will also be very limited in these regions. Nonetheless a few salt lakes have been reported in Antarctica (Burton, 1981).

The proportional distribution of *Artemia* biotopes in the different climatic types (Table IX) is not correct. The number of *Artemia* sites in the arid (E) climates is probably underestimated since prospecting in those deserted and hardly accessible areas has been limited so far.

In view of the good correlation between the climate types, in particular aridity, and the geographical distribution of *Artemia,* we have outlined the potential distribution pattern of brine shrimp on a global level (Fig. 2). It is obvious, however, that this map only provides a general view of the potential distribution of *Artemia.* Climate types may vary significantly even within relatively short distances. Furthermore specific local conditions may result in isolated micro climates eventually (un)suitable for *Artemia.* Comparison of the potential distribution pattern with the actual known locations of *Artemia* sites reveals that on almost every continent extended areas exist which may contain many more *Artemia* biotopes. Africa in particular seems to be promising in this regard, *i.e.* Mauretania, Egypt, Somalia, Ethiopia, Sudan, etc. In Asia more in-depth searches may lead to the discovery of *Artemia* sites in Iraq, Iran, Afghanistan, Pakistan, and Turkey. It is expected that in the USSR as well as along the coasts of Mexico, Peru, Chile, and Argentina many more salt lakes or lagoons are inhabited by *Artemia* or might be suitable for *Artemia* but have not been colonized yet by lack of dispersion, e.g. the many saltworks in northeast Brazil are now populated with *Artemia* since the human intervention in Màcau in 1977, followed by dispersion by wind and local waterbirds over an area of more than 1 000 km.

The positive correlation between aridity and the presence of *Artemia* is not only obvious at the world level but even at the scale of small islands characterized by different climate types. In Sri Lanka, for instance, a preliminary investigation led to the discovery of one *Artemia* biotope in Puttalam (Ferdinando, pers. commun). From the climate map of Sri Lanka (Fig. 3, after Carter, 1954) it appeared that only the northwest (near Puttalam) and the southern tip of the island might permit the occurrence of *Artemia.* A recent survey resulted in three other *Artemia* sites precisely located in the few suitable climatic zones.

The study of the climate constitutes a fundamental guideline not only for the search of existing *Artemia* biotopes, but also for the planning and site selection for inoculation and/or transplan-

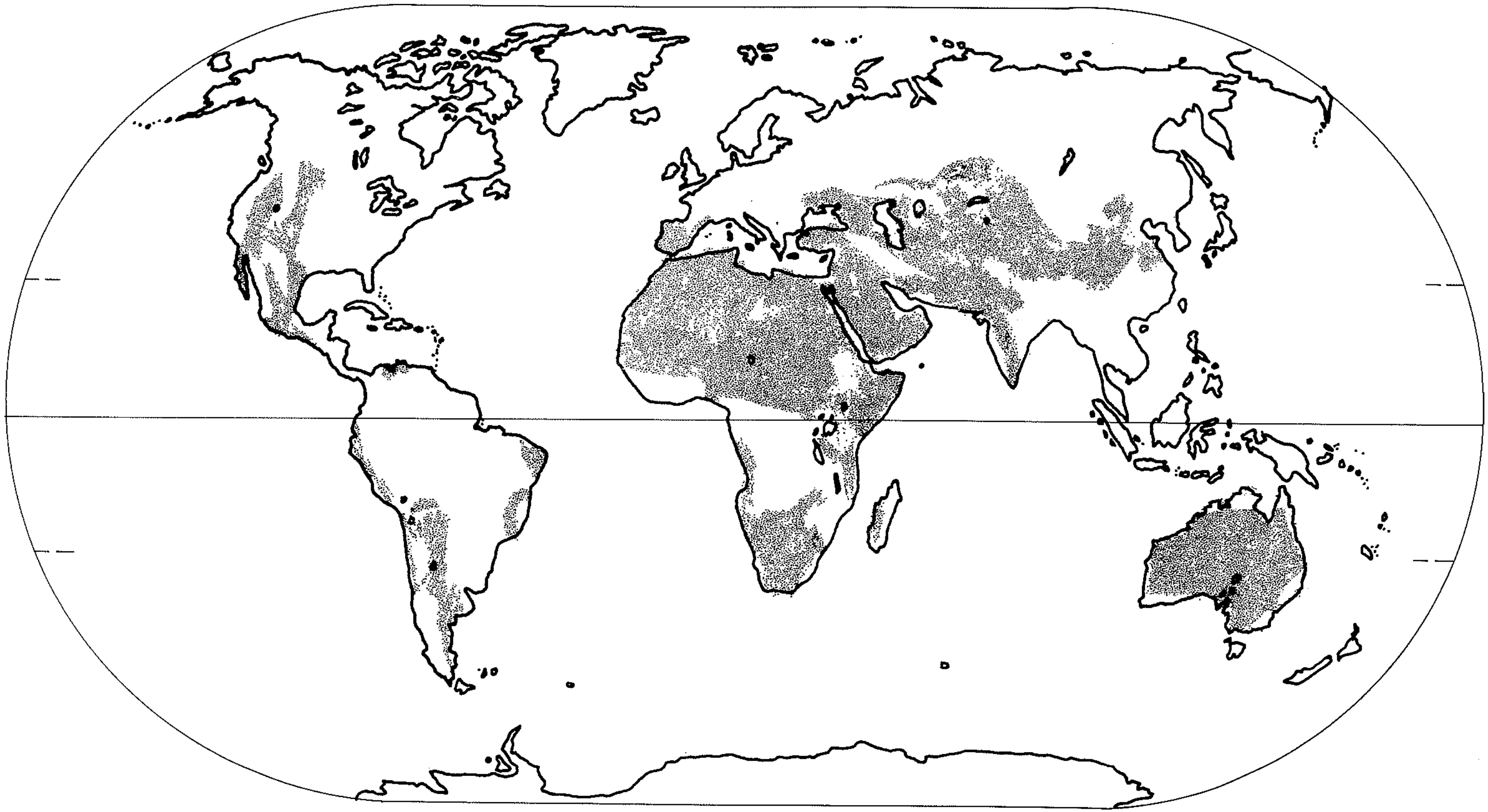

FIG. 2. The potential distribution pattern of *Artemia* at the world level.

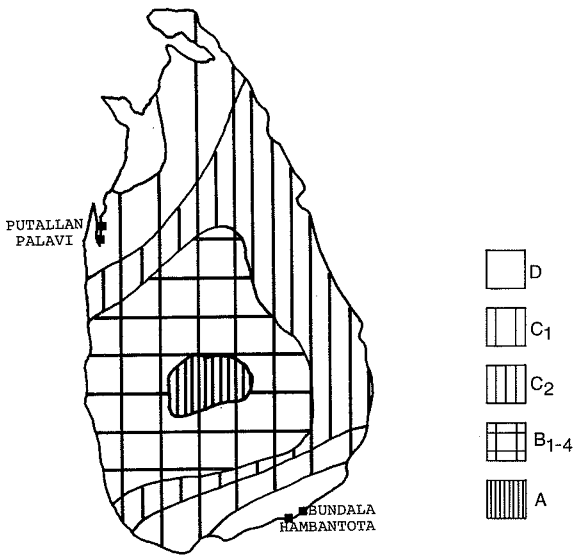

FIG. 3. The humidity types of Sri Lanka.

tation of *Artemia*. Yearly and seasonal evaporation-precipitation ratios will indicate if a given area may be suited for *Artemia* production, and whether one single inoculation (then better called transplantation) may be sufficient to create a persistent *Artemia* population or whether inoculations have to be repeated on a yearly basis to achieve seasonal *Artemia* production. The D and E types of Thornthwaite are most suitable for transplantations. Dry subhumid areas (C_1) are nevertheless promising provided, however, that no yearly period of water surplus occurs. As a result potential areas for *Artemia* transplantation correspond to the regions in Fig. 2 where *Artemia* biotopes may be found.

Artemia production is still possible, however, in areas not characterized by a C_1, D, or E climate.

Generalizing maps such as Fig. 2 need to be used with great caution. Besides aridity, seasonal distribution of precipitation and evaporation are also important. This means that in some cases more detailed climatological conditions and water balance data have to be used (Thornthwaite Associates 1962, 1963abc, 1964abc, 1965). This is illustrated for two case studies: the Philippines and Peru. The Philippines are characterized by a tropical humid climate. On a yearly basis precipitation always exceeds evaporation. As a result no natural biotopes can be located and transplantation of *Artemia* will fail to be successful. However, Fig. 4 reveals that in several areas evaporation exceeds precipitation for a consecutive number of months. The duration of this dry season varies considerably from site to site. It is evident that longer dry seasons offer better possibilities for *Artemia* biomass and cyst production. Furthermore, stratified low-salinity waters may eventually be drained during periods of rainfall resulting in opportunities to extend *Artemia* (biomass) production far into (or even throughout) the rainy season (Wongrat for Thailand, pers. commun.; Jumalon for the Philippines, pers. commun.). From the climatological point of

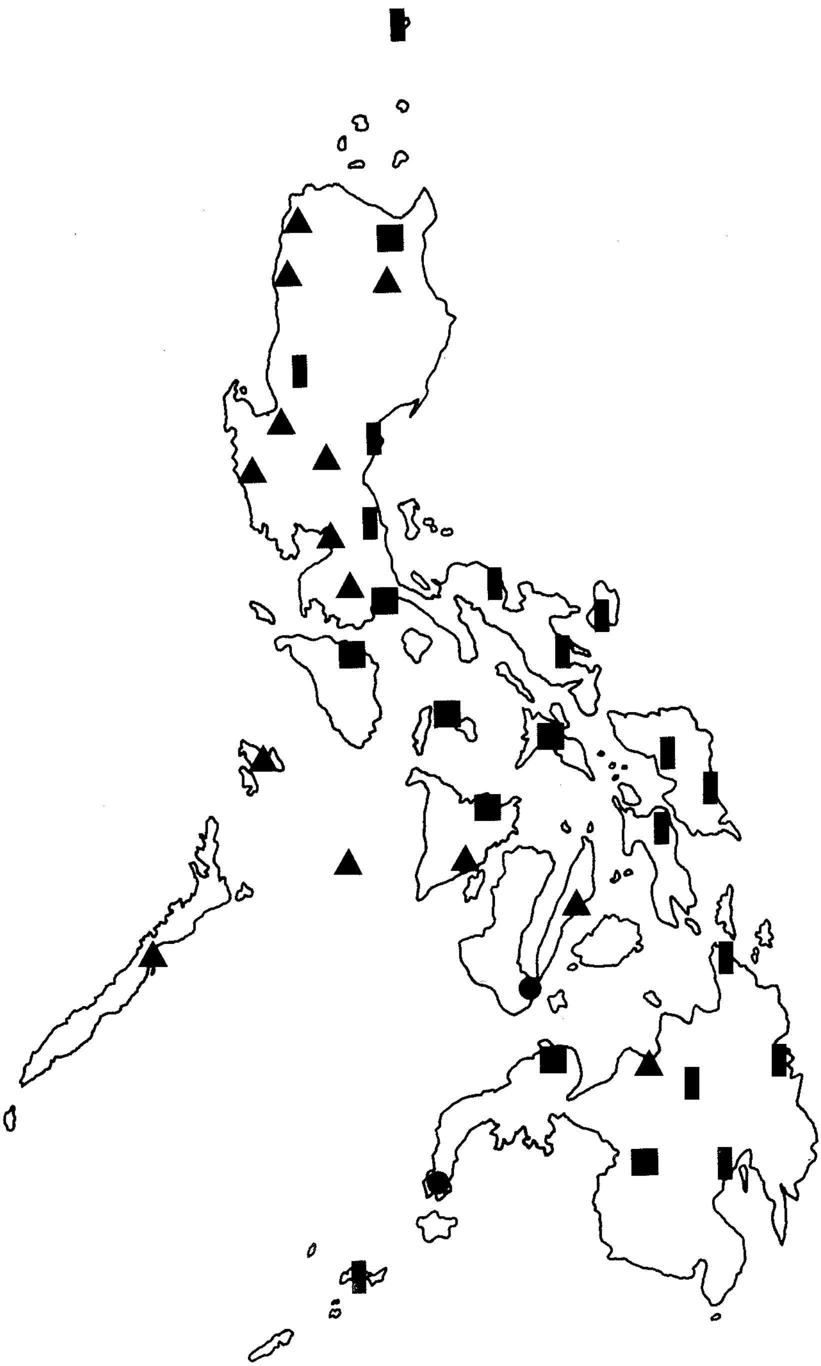

FIG. 4. Seasonal distribution of precipitation in the Philippines. (●) >6 months dry season; (■) 2-3 months dry season; (▲) 4-5 months dry season; (▮) no dry season.

view the areas in SW-Mindanao and SE-Negros are best suited. Several other regions, *i.e.* W.-Luzon, Mindoro, and Panay, are also suited for inoculation purposes, taking into account that high water temperatures (mostly over 25 °C) guarantee a short generation time (De los Santos *et al.*, 1980). The eastern coasts of the Philippines, which lack a distinct dry season, should not be taken into consideration for *Artemia* inoculation.

The situation in Peru is totally different (see Fig. 5). The coastal area is characterized by an arid climate ; as a consequence this zone seems to be suited for *Artemia* transplantation. In the interior, on the contrary, a subhumid or humid climate prevails and transplantation or even inoculation is unlikely to be successful. In the few interior sites where a dry season occurs, *Artemia* production possibilities are very limited since mean monthly temperatures maximally reach 15 °C, a temperature at which the generation time of *Artemia* is more than 2 months (Lenz, 1980). Next to water balance, temperature is indeed an important parameter to be taken into account for site selection for *Artemia* production. In this regard the Peruvian coast north of Lima (20-30 °C year-round) is more interesting than the zone south of Lima (20-30 °C for 6 to 9 months a year).

Speciation and reproductive mode of *Artemia* in relation to its biogeography

Several authors have searched for a correlation between the different "types" or sibling species of *Artemia* and their geographical distribution pattern. Stella (1933) failed to find a relation between the *Artemia* "biotypes" and the geographical location of their biotopes. Barigozzi (1946, 1957) could not correlate the different "forms" of *Artemia* to specific geographical areas. Bowen *et al.* (1978) reported that "... a search for geographical patterns and latitudinal lines of alleles also yielded negative results". The latter authors could not find a relation between the electromorphs of the different *Artemia* populations and the salinity (variations often larger within a biotope than between biotopes ; Vanhaecke, 1983) or ionic composition of their biotopes.

More recent studies reveal a certain pattern in the distribution of different *Artemia* sibling species. As pointed out by Browne and MacDonald (1982) it is striking that reproduction is exclusively sexual in the Americas. With the exception of the geographically isolated *Artemia persimilis* sibling species in Argentina, all *Artemia* in the New World belong to the *Artemia franciscana* sibling species. On the other hand, all Asian brine shrimp are parthenogenetic (*Artemia parthenogenetica*) with the exception of one *Artemia urmiana* population in Iran. In Europe, Africa, and Australia apparently both parthenogenetic and bisexual forms occur. However, the few bisexual populations in Europe and Africa (only limited data available) belong to the *Artemia tunisiana* sibling species.

Based on genetic studies, Abreu-Grobois and Beardmore (1980, 1982) postulated that the ancestral bisexual form originated in the Mediterranean and the Middle East. Furthermore, on the basis of genetic distances they concluded that the following evolutionary steps may have occurred : first separation between the bisexual form of the Old and the New World, after which the parthenogenetic form arose from the European bisexual form, finally *Artemia persimilis* arose from *Artemia franciscana.* The distribution of *Artemia franciscana* in the New World may largely be explained through dispersion by birds. *Artemia* biotopes are known to be feeding grounds for many birds, in particular flamingos (Rooth, 1976). Furthermore important migration routes in the Americas, *i.e.* the Pacific route from the Middle West of the USA along the Mexican coast,

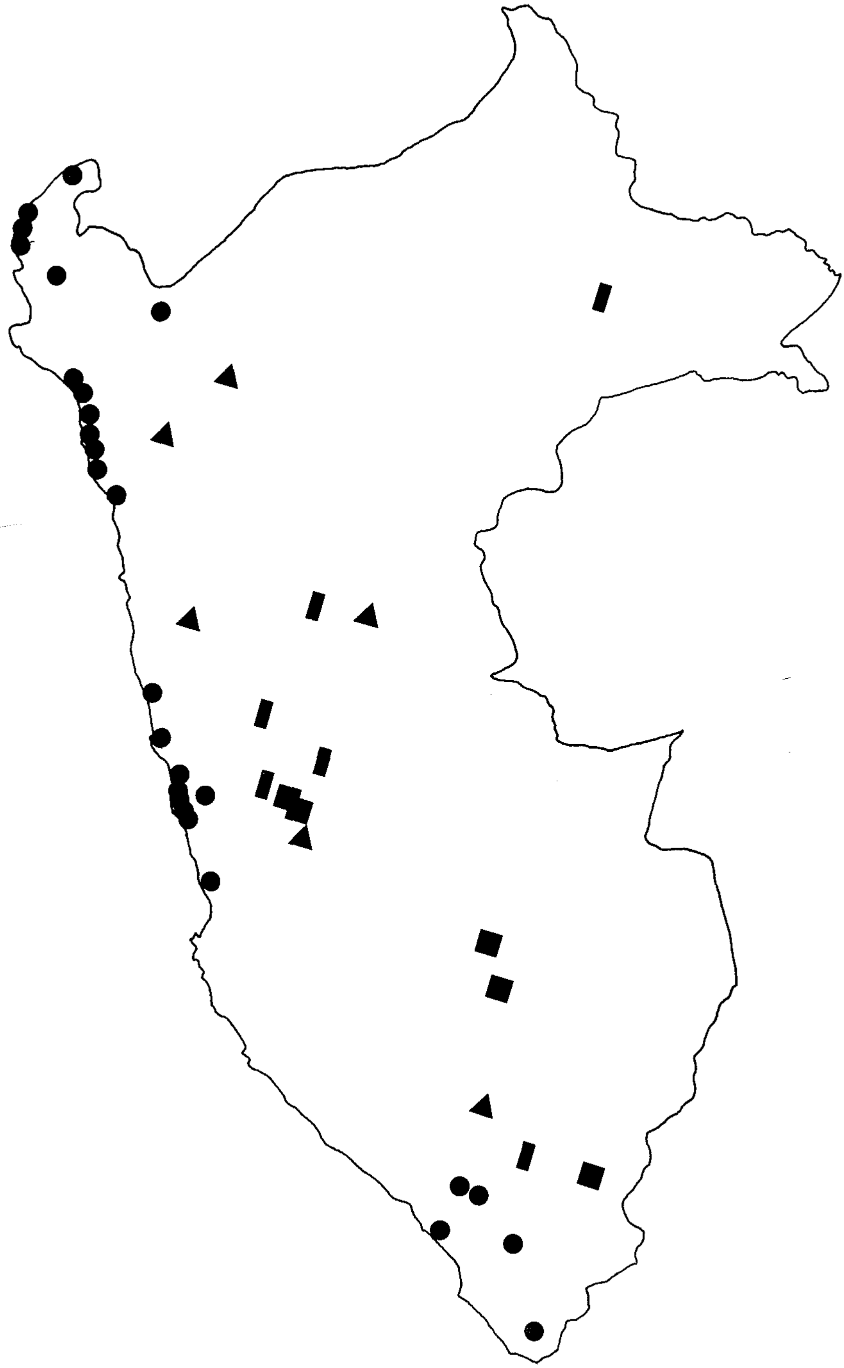

FIG. 5. Seasonal distribution of precipitation in Peru. (●) no water surplus ; (■) 3 months dry season ; (▲) 5-6 months dry season ; (▮) no dry season.

as well as the route form the West Indies through Venezuela and Colombia (Dorst, 1962 ; Rooth, 1976) cover many existing *Artemia* biotopes. Taking into account that cysts remain viable for 1 to 3 days upon ingestion by birds (Löffler, 1964 ; Proctor *et al.*, 1967 ; MacDonald, 1980) and that migrating birds can reach a speed of 50-100 km/h (Dorst, 1962), it is obvious that they can play an important role in dispersing *Artemia* over large distances. Birds are also thought to be responsible for the north-south transfer of *Artemia* in Europa and Africa and for the *Artemia* distribution in India (Royan *et al.*, 1970 ; Achari, 1971). In Australia, both *Artemia parthenogenetica* and *Artemia franciscana* were introduced by man (Clark and Bowen, 1976 ; Geddes 1980ab ; Jones *et al.*, 1981).

Contrary to the hypothesis of Browne and MacDonald (1982) it appears from our data that there is no correlation between the mode of reproduction and the appearance of *Artemia* in either inland salt lakes or coastal salt operations. Not only *Artemia franciscana* but also European and African bisexual brine shrimp are found in both types of biotopes. Furthermore neither climate nor latitude seem to have a major influence on the distribution pattern of the different sibling species. This can be explained by the fact that among populations from the same sibling species substantial genetic differentiation occurs (Abreu-Grobois and Beardmore 1980, 1982). This is expressed in terms of different tolerance towards abiotic conditions such as temperature and salinity (Vanhaecke *et al.*, 1984). In the case of *Artemia parthenogenetica* polyploidy may account for higher heterozygosity and genetic variability (Abreu Grobois and Beardmore, 1980, 1982). It is interesting to note that in Europe no bisexual populations are found north of 39° latitude (see also Browne and MacDonald, 1982). This is rather surprising since European *Artemia* populations studied so far seem to be the least tolerant to high temperatures (Vanhaecke *et al.*, 1984).

Finally, it should be stressed that uncontrolled introduction of *Artemia* in different biotopes may not only disturb the geographic distribution pattern but also lead to a decrease of natural variability. In this regard transplantation trials need to be planned very carefully and whenever possible with locally available *Artemia*.

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