Revista de Biología Marina y Oceanografía
Vol. 45, S1: 705-722, diciembre 2010
Article

El Niño induced changes of the coastal fish fauna off northern Chile and implications for ichthyogeography

Cambios de la fauna íctica del norte de Chile inducidos por El Niño y sus implicancias en la ictiogeografía

Walter Sielfeld[1], Jürgen Laudien[2], Mauricio Vargas[3] and Mario Villegas[1†]

[1]Universidad Arturo Prat, Av. Arturo Prat 2120, Iquique, Chile. walter.sielfeld@unap.cl
[2]Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161, 27515 Bremerhaven, Germany
[3]Servicio Nacional de Pesca, Pasaje Alessandri 470, Of. 110, Iquique, Chile

Abstract.- The coastal fringe off northern Chile (18º-23ºS) is inhabited by numerous neritic fish species of which 249 are commonly observed during normal and cold La Niña (LN) conditions. During El Niño (EN) the ichthyofauna of northern Chile changes significantly due to about 100 invading fish species normally inhabiting lower latitudes, named "septentrional invaders" and "tropic-equatorial fishes". This results in a composition including 15 fish families and 86 genera. Analyses showed that species affected by EN were not the same between the last three EN events revealing that only the epipelagic species *Anchoa naso, Albula vulpes*, *Atherinella nocturna* and *Scomberesox saurus stolatus* behaved consistently. Off northern Chile, EN 1982/83, 1986/87, 1991/92, 1997/98, 2002/2003 and the not clearly EN defined 2004/2005 period with their aligned thermal abnormalities of each particular event were directly related to the number of invading/affected species. Most of the alien species (>50%) were epipelagic, 25% were typical for sandy beaches and 14.6% for rocky shores. The shore fish community did not show major changes during and after EN events, as only a few invading species were recorded; just *Umbrina xantii* was found during all events considered. In order to understand the response of the fish community to ENSO events a biogeographical analyses of 721 fish species reported for neritic habitats (coastal epipelagic and benthic) distributed between 0°-57°S (Gulf of Guayaquil to Cape Horn) was made. Their distribution ranges for normal oceanic conditions were taken from the very numereous existing literature. It is concluded that the north/south migration of Panamic and Peruvian warm water fishes during EN/LN events along the north Chilean coast between 18º-23ºS, indicates that it represents a wide transition zone between the Peruvian and the Chilean ichthyogeographic provinces.

Key words: ENSO, neritic fishes, northern Chile, ichthyogeography

Resumen.- La franja costera de la zona norte de Chile (18º-23ºS) es habitada por numerosas especies de peces neríticos de las cuales 249 son comúnmente observadas durante condiciones normales y condiciones frías La Niña (LN). Durante El Niño (EN) la ictiofauna del norte de Chile experimenta cambios significativos a causa de la presencia de alrededor de 100 especies de peces invasores que durante periodos normales y/o fríos habitan en latitudes menores, siendo también nombrados "invasores septentrionales" y "peces trópico-ecuatoriales". Este conjunto incluye 15 familias y 86 géneros de peces. Los análisis mostraron que las especies afectadas por los EN no fueron las mismas durante los últimos tres eventos, revelando que solo las especies epipelágicas *Anchoa naso, Albula vulpes*, *Atherinella nocturna* y *Scomberesox saurus stolatus* fueron constantes. Frente al norte de Chile, durante los EN 1982/83, 1986/87, 1991/92, 1997/98, 2002/2003 y EN no claramente definido 2004/2005 y considerando las anomalías térmicas que caracterizaron a cada evento en particular, se encontró que la anomalía estuvo en relación directa con el número de especies invasoras/afectadas. Gran parte de las especies invasoras (>50%) fueron epipelágicas, 25% fueron típicas de playas de arena y 14,6% de ambientes rocosos. La comunidad de peces litorales no mostró cambios mayores durante y después de los eventos EN, registrándose pocas especies invasoras; solamente *Umbrina xantii* fue encontrada durante todos los eventos estudiados. Con el fin de entender la respuesta de la comunidad de peces a los eventos ENSO se realizó un análisis biogeográfico de 721 especies de peces reportados para hábitats neríticos (costero, epipelágico y bentónico) distribuidas entre 0°-57°S (Golfo de Guayaquil a Cabo de Hornos). La distribución latitudinal de cada especie bajo condiciones oceánicas normales se obtuvo de la numerosa literatura que existe al respecto. Se concluye que la migración norte/sur de peces de tipo panámico y peruano asociados a aguas cálidas a lo largo de la costa norte de Chile entre 18º-23ºS, representa una amplia zona de transición entre las provincias ictiogeográficas peruana y chilena.

Palabras clave: ENOS, peces neríticos, norte de Chile, ictiogeografía

[†]Deceased in March 2008.

INTRODUCTION

The coastal fringe off northern Chile and southern Peru is characterized by upwelling processes, caused by friction of the S and SW winds (Burkov *et al.* 1971, Fuenzalida 1990[1], 1992, Smith 1992, Figueroa 2002, Arntz *et al.* 2006). Upwelling is restricted to only a narrow coastal zone (*e.g.*, Schweigger 1960, Morales *et al.* 1996, Blanco *et al.* 2001, Hormazabal *et al.* 2001, Hormazabal & Shaffer 2002) fueling the ecosystem with high levels of new production (Ryther 1969, Cushing 1971, Barber & Smith 1981). Upwelling cells are practically permanent, showing clear seasonal variations (Fuenzalida 1990[1], 1992) and spatial-temporal correspondence with cold (La Niña, LN) and warm (El Niño, EN) periods (Alarcón 1975, Robles *et al*. 1976, Rutland 1982, Bernal *et al.* 1983). The area surrounding Peninsula de Mejillones (23º00'-23º30'S) have special importance as it represents the southern zoogeographical limit for several coastal warm water species (Castilla *et al.* 2002, Escribano *et al.* 2002).

Weakening of upwelling intensity and cyclic EN events of variable intensity (Quinn *et al.* 1978) affect species considerably (Arntz 1986, Martinez *et al*. 1985, Tomicic 1985, Vasquez & Alonso-Vega 2004, Arntz *et al.* 2006). Barber & Chavez (1983) found during 1982-83 EN that a reduction in primary productivity was caused by a depression of the nutricline though no reduction in the upwelling activity occurred. These events cause or allow a migration of organisms from their normal habitats to higher latitudes (Fitch 1951, Morrow 1957, Radovich 1961, Pequeño 1978, Vélez *et al*. 1984, Hoyos *et al*. 1985, Kong *et al*. 1985) reflected in records of several warm-water species registered only once off northern Chile (*e.g.*, Guichenot 1848, Delfín 1899, Mann, 1954, De Buen 1959 a, b, c, Bahamonde & Pequeño 1975, Pequeño 1989).

Bahamonde & Pequeño (1975) and Pequeño (1997) registered around 250 common fish species (caught more than once) off northern Chile (18º-23ºS). In the same region, additional 100 species were observed only during EN events (Kong *et al.* 1985, Sielfeld *et al.* 1995, Vargas *et al.* 1998, Vargas & Sielfeld 1999, 1999[2]). These periodical EN-induced faunistic latitudinal fluctuations off northern Chile (18º-20ºS) are directly related to the thermal regime. They lead to a wide and ranging transition zone between the Peruvian and Chilean zoogeographic province, as proposed by Balech (1954), López (1963), Lutjeharms (1990), Parin (1991), Pequeño & Lamilla (1995), Ojeda *et al.* (2000) and Pequeño (2000).

The aim of this review is to describe EN induced changes within the fish community registered off northern Chile (<23º40'S) between 1982 and 2005. This work represents the basis for the ongoing INCO-DEV project CENSOR and attempts to clarify whether changes of coastal fish assemblages are induced by the variability of the habitat structure (*i.e.*, kelp beds), food availability (qualitative/quantitative) and/or physical/chemical factors.

MATERIAL AND METHODS

The fish data used in this paper were compiled from the literature and own unpublished data. For ichthyogeographical purposes the latitudinal distribution between 0°S and 57°S (Gulf of Guayaquil to Cape Horn) of 719 neritic species normally captured at depths less than 200 m, including epipelagic, littoral and benthic species was considered. Previous studies of the benthic fish fauna of northern Chile showed that the depth level of 100-200 m separates a neritic and a demersal assemblage (Sielfeld & Vargas 1996, 1999), very coincident with the OMZ (Oxygen Minimum Zone) recently recognized by Fuenzalida *et al.* (2009) and associated with Equatorial Subsurface Water, transported from north to south along the continental slope by the Peru-Chile Undercurrent, as far south as 48°S (Silva & Neshyba 1979).

"Grey" literature on littoral warm water fishes found north of 23º40'S along the Chilean coast was reviewed. Landings of the ports of Arica (18º21´S), Pisagua (19º31´S), Iquique (20º12´S), Tocopilla (20º05´S), Mejillones (20º05´S) and Antofagasta (23º40´S) (Fig. 1) contributed most of the data. In addition, 20 years (1984-2004) records of the catch from several fishermen associations ("caletas de pescadores") located between Chipana beach (21º20'S) and Las Machas beach (18º10'S) were included. Furthermore, information on fishes inhabiting tide pools presented by Berrios & Vargas (2000, 2004) as well as records on sublitoral fishes associated to kelp beds (Sielfeld *et al.* 2002) were also included in the analyses.

Additionally, historic information and results from diverse museum collections and bibliographic sources (*e.g.*,

[1]Fuenzalida R. 1990. Proceso de surgencia en la región norte de Chile, latitudes 20°30'S-21º45'S. X Jornadas de Ciencias del Mar, Santiago, Resúmenes, p. 53.

[2]Vargas M & W Sielfeld.1999. Ictiofauna asociada al evento El Niño 1997-1998 frente a las costas de Tarapacá (I Región, Chile). XIX Jornadas de Ciencias del Mar, Iquique, Resumenes, p. 205.

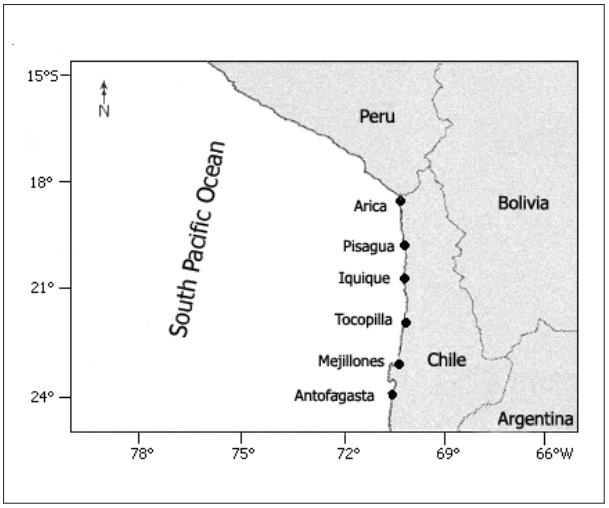


Figure 1. Main Northern Chilean ports between Arica and Antofagasta (18°21'S -23°40´S), for data collect and analysis to reveal El Niño induced changes on the coastal fish fauna / Principales puertos del norte de Chile entre Arica y Antofagasta (18º21'S y 23º40'S), considerados en el análisis y obtención de datos para conocer cambios inducidos por El Niño en la fauna de los peces costeros

Guichenot 1848, Delfin 1899, 1901, Oliver-Schneider 1943a, b, Fowler 1945, De Buen 1953, 1957, 1959a, b, c, Mann 1954, Zapata & Soto 1984[3], Kong *et al.* 1985, Kong & Valdés 1990, 1999), data from underwater fishing competitions, and monitoring of by-catch of the regional fisheries of Caleta de Pescadores "Guardiamarina Riquelme" between 1995 and 2003, were also considered.

In order to facilitate comparisons the listing of species (Table 1) follows Bahamonde & Pequeño (1975), Pequeño (1989, 1997) and Chirichigno & Vélez (1998).

Assemblages of species were determined using the hierarchical cluster analysis routine CLUSTER in the program PRIMER 6 (Clarke & Gorley 2006) bases on the Bray-Curtis similarity measure for abundance data and Sorensen's coefficient for presence/absence data. When using CLUSTER, the permutation test SIMPROF (at 5% level) was used to determine which clusters have significant internal structure. In the figure the later are joined by "fat" grey line.

Results

1. Historical overview

Occasional records of uncommon fish species

The review of the Chilean ichthyological literature revealed occasional records of fish species along the central Chilean coast apparently related with warm water events (Kong *et al.* 2002): the first uncommon species were *Katsuwonus pelamis* and *Mola mola* caught off Valparaiso (Guichenot 1848). The author does not provide further information; however, it is likely that the occurrence was related to a warm event. *Sphyrna peruana* (or *S. zygaena*) and *Mobula tarapacana* were mentioned by Philippi (1887) for northern Chile without additional data. The first species was recently (1997 and 2004) caught off Iquique and Antofagasta (details see Table 2). The second species has not been registered in the area since then. *Sarda chilensis* and *Scomber japonicus* off Valparaíso, *Istiophorus audax (=Istiophorus platypterus)* and *Leiurus peruanus (=Seriolella violacea)* off Iquique, *Hemanthias peruanus* with no indication of the catch locality, and *Mola euryptera (=Mola ramsayi)* at Chañaral are recorded by Delfín (1899) without catch date. Some of these species are regular visitors off northern Chilean waters, but the presence off central Chile is only likely during warm water events. The same holds true for *Makaira marlina* off Iquique cited by Bini (1952) as well as *Makaira mitsukuri (=Tetrapturus audax)* by Smith & Rivas (1955, *fide* Kong *et al.* 2002).

Historical records of fish related to EN events in the literature

The following historical fish records were related to EN events by the respective authors: *Mola mola* registered by Philippi (1892) at Chañaral in October 1889, related to EN 1889; *Pomadasys bipunctatus* by Steindachner (1898) off Iquique, related to EN 1896; *Pomatomus saltatrix* by Delfín (1899) off Valparaíso and related to EN 1899; *Rachycentron canadum* reported by Delfín (1903) off Iquique, related with EN 1911; *Thunnus thynnus* cited by De Buen (1953) for Curaumilla: Valparaíso during EN 1953; *Rhincodon typus, Sphyrna zygaena, Squatina armata, Mobula lucasana, Galeichthys peruvianus, Tylosaurus stolzmanni, Strongylura exilis, Hemiramphus saltator,*

[3] Zapata B & R Soto. 1984. Análisis preliminar de la ictiofauna de playas arenosas, desde Arica a Caleta Chipana, durante el período verano-otoño de l984. Terceras Jornadas Científicas Estudiantiles, 8-9 de noviembre 1984. Universidad Arturo Prat, Iquique.(Resumen)

Table 1. Warm-water fishes reported to be associated with warm events in the northern Chile between 1982 and 2004. (* indicates normal residents of the Peruvian province; other species are Panamic or oceanic origin) / Peces de aguas cálidas que se han reportado en asociación a eventos cálidos en el norte de Chile entre 1982 y 2004. (* indica residentes normales de la provincia Peruana; otras especies son de origen Panámico u oceánico)

Family	Species	Habitat	Southern limit of extended distribution	Year	Source
Dasyatidae	*Dasyatis violacea*	Epipelagic	Iquique	1987, 1988, 2001, 2002	Guzmán *et al.*1998; new data
	Dasyatis brevis	Epipelagic	Antofagasta	2000, 2001	Nelson Amado (pers. com.)
Rhinobatidae	*Rhinobatos planiceps*	Soft bottom	Chipana	1984	Guzmán *et al.* 1998
Squatinidae	*Squatina armata*	Soft bottom	Chipana	1992, 2002	Guzmán *et al.* 1998
Sphyrnidae	*Sphyrna zygaena*	Epipelagic	Antofagasta	1997/98/99, 2004/05	Kong *et al.* 1999, 2002; new data
			Iquique	1998, 2004/05	
			Chipana	1992	
			Arica	2004/05	
Muraenidae	*Gymnothorax equatorialis*	Rocky bottom	Antofagasta	1987/88	Kong *et al.* 2002; new data
			Iquique	1987	
	Gymnothorax aff. *castaneus*	Rocky bottom	Chipana	1995	New data
Ophichthidae	*Ophichthus tetratrema* (*)	Soft bottom	Arica	1999/2000	New data
	Ophichthus zophochir	Soft bottom	Arica	1996/1997	New data
Albulidae	*Albula culpes*	Epipelagic	Antofagasta	1983	Kong *et al.* 1985
Engraulidae	*Anchoa nasus*	Epipelagic	Arica	2000	Vargas & Peredo 2001b[5]
	Anchoa naso	Epipelagic	Chipana	1984, 1988, 1989	Guzmán *et al.* 1998, Sielfeld *et al.* 1999
			Iquique	1991, 1999	
Clupeidae	*Etrumeus teres*	Epipelagic	Iquique	1983, 1992, 1994	Kong *et al.* 1985, 2002, Guzmán *et al.* 1998
			Punta Arenas	1989	
			Arica	1989	
			Antofagasta	1998/99	
	Opisthonema libertate	Epipelagic	Iquique	1983	Kong *et al.* 1985, 1999, 2002, Guzmán *et al.* 1998
			Antofagasta	1984, 1998/99	
			Iquique	1998	
Synodontidae	*Synodus lacertinus*	Not defined	Iquique	1984	Kong *et al.* 1985, Guzmán *et al.* 1998
	Synodus scituliceps	Not defined	Antofagasta	1985, 1997	Kong *et al.* 2002
Atherinidae	*Atherinella nocturna*	Epipelagic	Arica, Pisagua, Iquique	1984, 1999	Kong *et al.* 1985, Guzmán *et al.* 1998, Sielfeld *et al.* 1999, new data
			Chipana	1984, 1990, 1991, 1997	
Fistularidae	*Fistularia commersoni*	Epipelagic	Iquique	1998	Guzmán *et al.* 1998
Exocoetidae	*Cypselurus heterurus*	Epipelagic	Antofagasta	1983	Kong *et al.* 1985, Guzmán *et al.* 1998
			Chipana	1983, 1994	
	Fodiator acutus	Epipelagic	Iquique	1992	Guzmán *et al.* 1998, Kong et al. 1999
			Chipana	1997/98	
			Antofagasta	1998/99	
	Hirundichthys rondeletti	Epipelagic	Pta. Madrid	1993	Guzman et al. 1998 ; new data
			Chucumata	1993	
			Chipana	1994	
Hemiramphidae	*Hemiramphus saltador*	Epipelagic	Antofagasta	1983/84	Kong *et al.* 1985
Belonidae	*Strongylura exilis*	Epipelagic	Caleta Errázuriz	1983	Kong *et al.* 1985, 1999, new data
			Antofagasta, Iquique	1984, 1997, 1998/99	
	Belone stolzmanni	Epipelagic	Iquique	1984, 1999	Guzmán *et al.* 1998, Sielfeld *et al.* 1999
			Chipana	1998	
Scomberesocidae	*Scomberesox saurus*	Epipelagic	Mejillones	1984	Kong *et al.* 1985, Guzmán *et al.* 1998, Sielfeld *et al.* 1999
			Iquique	1993, 1999	
Trachypteridae	*Trachypterus altivelis*	Epipelagic	Antofagasta	1983	Kong *et al.* 1985
			Iquique	1984	
	Zu cristatus	Epipelagic	Iquique	1987	Guzmán *et al.* 1998
			Punta Gruesa	1992	
Syngnathidae	*Hippocampus ingens* (*)	Not defined	Tocopilla	1983	Kong *et al.* 1985, 1999, 2002, new data
			Iquique	1998	
			Antofagasta	1998/99	
Scorpaenidae	*Prionotus stephanophrys*	Epipelagic	Antofagasta	1982, 1998/99	Kong *et al.* 1985, 2002, Guzmán *et al.*, 1998, new data
			Mejillones	1983	
			Iquique	1983, 1992	
	Prionotus quiescens	Epipelagic	Antofagasta,	1998/99	Kong *et al.* 1999, 2002
	Scorpaena hystrio (*)	Rocky bottom	Iquique	1996, 1999	Sielfeld & Vargas 2000

Table 1 continued / Continuación Tabla 1

Family	Species	Habitat	Southern limit of extended distribution	Year	Source
Priacanthidae	*Pristigenys serrula* (*)	Rocky bottom	Iquique Antofagasta	1993 1998/99	Kong *et al.* 1999, new data
Antennariidae	*Antennarius avalonis*	Rocky bottom	Iquique	2000	New data
Ariidae	*Galeichthys peruvianus* (*)	Soft bottom	Mejillones Antofagasta Iquique	1983 1995	Kong *et al.* 1985, Guzmán *et al.* 1998
	Arius seemanni	Soft bottom	Arica	2000	Vargas & Peredo 2001b[5]
Prolatilidae	*Caulolatilus princeps* (*)	Soft bottom	Iquique Pisagua	1992 2002	Guzmán *et al.* 1998, new data
Cliniidae	*Labrisomus xantii*	Rocky bottom	Caleta Buena	1999	New data
Coryphaenidae	*Coryphaena hippurus*	Epipelagic	Antofagasta	1983, 1998/99	Kong *et al.* 1985, 1999
Carangidae	*Caranx caninus*	Epipelagic	Iquique	1984, 1998	Guzmán *et al.* 1998, Vargas & Sielfeld 1999
	Caranx caballus	Epipelagic	Antofagasta	1983/84, 1998/99	Kong *et al.* 1985, 1999, 2002
	Pseudocaranx dentex	Epipelagic	Iquique	1998	New data
	Decapterus macrosoma	Epipelagic	Antofagasta Arica	1984, 1998/99 2000	Kong *et al.* 1985, 1999, 2002, Vargas & Peredo 2001b[5]
	Oligoplites refulgens	Epipelagic	Antofagasta	1998/99	Kong *et al.* 1999, 2002
	Trachinotus paitensis (*)	Epipelagic coastal	Mejillones Antofagasta Arica, Iquique Chipana	1983 1984 1990, 1992	Kong *et al.* 1985, Guzmán *et al.* 1998
	Naucrates ductor	Epipelagic	Pisagua Iquique	1984 1992, 1997, 1998	Guzmán *et al.* 1998, new data Vargas & Sielfeld, 1999
	Seriola peruana	Epipelagic	Antofagasta Iquique	1983, 1998/99 1992, 1997	Kong *et al.* 1985, Kong *et al.* 2002, new data
	Alectis ciliaris	Epipelagic	Iquique, Mejillones Antofagasta Iquique	1983, 1998/99 1984	Kong *et al.* 1985, 1999, 2002, Guzmán *et al.* 1998
	Selene peruviana	Epipelagic	Iquique, Mejillones Antofagasta Iquique	1983 1992	Kong *et al.* 1985, Guzmán *et al.* 1998
	Selene brevoorti	Epipelagic	Mejillones Antofagasta Iquique Antofagasta	1983 1984, 1998 1998/99	Kong *et al.* 1985, 1999, 2002, Guzmán *et al.* 1998
Nematistidae	*Nematistius pectoralis*	Epipelagic	Sur de Taltal	1992	Kong *et al.* 2002
Chaetodontidae	*Chaetodon humeralis*	Rocky bottom	Iquique Antofagasta	1984 1998/99	Kong *et al.* 1985, 1999, 2002
Echeneidae	*Rhombochirus osteochir*	Epipelagic	Frente río Loa	1998	Vargas & Sielfeld 1999[2]
Sparidae	*Calamus brachysomus*	Soft bottom	Frente río Loa Arica Antofagasta	1998 2000 1998/99	Vargas & Sielfeld 1999[2], Vargas & Peredo 2001b[5], Kong *et al.* 1999
Gerridae	*Eucinostomus argenteus*	Soft bottom	Caleta Errázuriz Iquique Antofagasta	1983 1985, 1999 1998/99	Kong *et al.* 1985 2002, Guzmán *et al.* 1998, Sielfeld *et al.* 1999
Bramidae	*Taractes rubescens*	Epipelagic	Iquique	1984	Kong *et al.* 1985
	Brama brama	Epipelagic	Mejillones Antofagasta	1984 1983	Kong *et al.* 1985
Sciaenidae	*Larimus pacificus* (*)	Soft bottom	Iquique	1983	Kong *et al.* 1985
	Paralonchurus dumerilii (*)	Soft bottom	Iquique	1983	Kong *et al.* 1985
	Paralonchurus peruanus (*)	Soft bottom	Arica	1985, 1993	Guzmán *et al.* 1998, new data
	Umbrina xantii	Soft bottom	Iquique Chipana Antofagasta	1983, 1999 1984, 1989 1998/99	Kong *et al.* 1985, 2002, Guzmán *et al.* 1998, Sielfeld *et al.* 1999
	Stellifer minor (*)	Soft bottom	Arica	1999, 2000	Vargas & Sielfeld 1999b[2], new data
	Stellifer erycimba (*)	Soft bottom	Iquique	1999	Sielfeld *et al.* 1999
	Sciaena starksii (*)	Soft bottom	Arica	2000	Vargas & Peredo 2001a[4]
	Menticirrhus undulatus	Soft bottom	Arica	2000	Vargas & Peredo 2001a[4]
Scaridae	*Nicholsina denticulatum*	Rocky bottom	Iquique	2000	new data
Kyphosidae	*Kyphosus analogus*	Rocky bottom	Antofagasta	1983	Kong *et al.* 1985
Mullidae	*Pseudupeneus grandisquamis*	Soft bottom	Iquique, Mejillones Antofagasta Iquique	1983 1983, 1984, 1998/99 1984, 1999	Kong *et al.* 1999, 2002, Guzmán *et al.* 1998, Sielfeld *et al.* 1999
	Mulloidichthys dentatus	Soft bottom	Arica	2000	Vargas & Peredo 2001b[5]

Table 1 continued / Continuación Tabla 1

Family	Species	Habitat	Southern limit of extended distribution	Year	Source
Labridae	*Bodianus eclancheri*	Rocky bottom	Iquique	1987	Vargas *et al.* 1998
	Halichoeres dispilus (*)	Rocky bottom	Arica Chucumata	1987 1987, 2000, 2001	Vargas *et al.* 1998, Sielfeld *et al.* 2002
Serranidae	*Epinephelus itajara*	Not defined	Antofagasta	1997/98	Kong *et al.* 1999; Rojas & Pequeño 2001
Polynemidae	*Polydactylus approximans*	Soft bottom	Iquique, Tocopilla, Mejillones Punta Arenas Antofagasta	1983 1992 1998/99	Kong *et al.* 1985, 1999, 2002, Guzmán *et al.* 1998
	Polydactylus opercularis	Soft bottom	Iquique, Mejillones	1983	Kong *et al.* 1985
Sphyraenidae	*Sphyraena ensis*	Epipelagic	Iquique, Mejillones, Antofagasta	1983, 1998/99	Kong *et al.* 1985, 1999, 2002
	Sphyraena idiasthes	Epipelagic	Iquique Antofagasta	1983, 1998 1984	Kong *et al.* 1985, Vargas & Sielfeld 1999
Scombridae	*Auxis thazard*	Epipelagic	Mejillones, Antofagasta	1983, 1998/99	Kong *et al.* 1998, 2002
	Auxis rochei	Epipelagic	Iquique Junin Punta Madrid Antofagasta	1989, 1993 1993 1992 1985, 1998/99	Guzmán *et al.* 1998, Kong *et al.* 1999, 2002
	Katsuwonus pelamis	Epipelagic	Antofagasta Caleta Lautaro	1984 1993	Kong *et al.* 1985, Guzmán *et al.* 1998
	Sarda chilensis (*)	Epipelagic	Antofagasta Iquique	1983 1992	Kong *et al.* 1985, Guzmán *et al.* 1998
	Scomberomorus sierra	Epipelagic	Antofagasta Chipana Arica	1983, 1997/98 1989 2000	Kong *et al.* 1985, 1999, Vargas & Peredo 2001b[3], Guzmán *et al.* 1998
Stromateidae	*Psenes sio*	Epipelagic	Iquique	1984, 1986	Kong *et al.* 1985, Guzmán *et al.* 1998
	Peprilus medius	Epipelagic	Chipana Antofagasta	1992 1997/98	Sielfeld *et al.* 1995, Kong *et al.* 1999, 2000
Centrolophidae	*Schedophilus medusophaghus*	Epipelagic	Frente río Loa	1992	Guzmán *et al.* 1998
	Centrolophus niger	Epipelagic	Punta Paquica	1992	Guzmán *et al.* 1998
Nomeidae	*Cubiceps carinatus*	Epipelagic	Patache	1989	Guzmán *et al.* 1998
	Cubiceps caeruleus	Epipelagic	Iquique, Mejillones, Antofagasta	1983	Kong *et al.* 1985
Tetragonuridae	*Tetragonurus cuvieri*	Epipelagic	Mejillones	1984	Kong *et al.* 1985
Bothidae	*Bothus constellatus*	Soft bottom	Caleta Buena	1998	Sielfeld *et al.* 2003
	Etropus ectenes	Soft bottom	Iquique	1999	Sielfeld *et al.* 2003
	Achirus klunzingeri	Soft bottom	Antofagasta	1984	Sielfeld *et al.* 2003
Symphuridae	*Symphurus elongatus*	Soft bottom	Arica	2000	Sielfeld *et al.* 2003
Balistidae	*Aluterus monocerus*	Rocky bottom	Mejillones Iquique	1983 1984	Kong 1985
	Balistes polylepis	Rocky bottom	Antofagasta Iquique	1983 1984, 2002, 2004	Kong *et al.* 1985, new data
	Pseudobalistes naufragium	Rocky bottom	Antofagasta	1983	Kong *et al.* 1985
Tetraodontidae	*Sphoeroides lobatus*	Rocky bottom	Caleta Errázuriz Iquique Antofagasta	1983 1989 1998/99	Kong *et al.* 1985, 1999, 2002 Guzmán *et al.* 1998
	Sphoeroides trichocephalus	Rocky bottom	Iquique Antofagasta	1989 1998/99	Guzmán *et al.* 1998, Kong *et al.* 2002
Diodontidae	*Chilomycterus affinis*	Epipelagic	Iquique Mejillones del Norte	1990 1998	Sielfeld & Vargas 2000
	Diodon hystrix	Epipelagic	Iquique	1984	Kong *et al.* 1985
Molidae	*Mola mola/ramsayi*	Epipelagic	Antofagasta Iquique	1983, 1985, 1998/99, 1984 1995	Kong *et al.* 1985, 2002, Guzmán *et al.* 1998
	Masturus lanceolatus	Epipelagic	Antofagasta Iquique	1985 1985	Kong *et al.* 2002, Guzmán *et al.* 1998

Fodiator acutus, Rachycentron canadum, Makaira audax, Neothunus macropterus, Mupus peruanus, Echeneis brachyptera and *Balistes polylepis* reported by De Buen (1957) in relation with EN 1957; *Mola ramsayi* mentioned by Oliver-Schneider (1930) for Coliumo, related to EN 1926/27; *Stellifer erycimba* and *Sphyraena ensis* registered by Ojeda (1978) for EN 1978; *Mola ramsayi* listed by Bahamonde (1963) off Isla Grande de Chiloé, *Pristigenys serrula* reported by Alberti (1963) off Antofagasta, *Cheilopogon heterurus, Prionotus stephanophrys, Sphyraena ensis* and *Scomberomorus sierra* reported by Kong *et al.* (1981), *Etropus ectenes, Achirus klunzingeri* and *Symphurus elongatus* by Sielfeld *et al.* (2003), *Alectis ciliaris, Selene peruviana* and *Pseudupeneus grandisquamis* mentioned by Martinez *et al.* (1983) and *Chilomycterus affinis* listed by Sielfeld & Vargas (2000), all for northern Chile, and *Arius seemanni, Sciaena starksii* and *Menticirrhus undulatus* landed at the harbour of Arica (Vargas & Peredo 2001a[4], b[5]).

Species lists of Chilean fishes

Several species lists of Chilean fishes (Fowler 1945, Bahamonde & Pequeño 1975, Pequeño 1989, 1997) include additional warm-water species, collected only once in Chilean waters and the occurrence was probably be related to warm events. Between these, the following are *Chromis intercrusma* reported by Hildebrand (1946) as "probable" species at the Juan Fernández Islands, and classified as "septentrional invader" by Mann (1954) reaching waters south of Coquimbo (central Chile). *Prionodes huascari (=Serranus huascari)* was recorded by Steindachner (1902) and again classified as "septentrional invader" by Mann (1954). This species may as well reach areas south of Coquimbo, *Hemianthias peruanus* reported by Jordan & Evermann (1898) for Tarapacá (northern Chile), unfortunately the authors don't provide the sampling locality, also not specified by Jordan & Eigenmann (1890) and Delfín (1901) for the same species. *Alfestes afer* (probably = *Alphestes immaculatus* registered by Hooker (1998) for Peru) was registered by Fowler (1945) for Chile, without locality and date. *Pinguilabrum punctatum (=Graus nigra)* listed by Chirichigno (1974) between Casma and Antofagasta (northern Chile), without mentioning sampling locality and date, is typical of the central coast of Chile and very rare north of 14ºS (Vargas & Pequeño 2004). The same holds true for *Diplectrum conceptione* for which the author indicated a geographical range from Ecuador to Talcahuano (central Chile). *Bodianus diplotaenia* was registered by Schmeltz (1869, 1874 *fide* Fowler 1945) for Chile without stating the collection locality. *Peprilus medius* was found by Sielfeld *et al.* (1995) off Iquique, and *Bodianus eclancheri* and *Halichoeres dispilus* were reported by Vargas *et al.* (1998) off Iquique the first, and off Arica and Iquique, the second (northern Chile).

2. Records of fishes related to warm water events

General considerations

A relationship of alien fishes to EN events was first established by Mann (1954). He found two categories and proposed the term "stenotherm fishes of warm waters" for species regularly inhabiting subtropical waters around the Chilean oceanic islands and "septentrional invaders of the Peru Current" for fishes restricted to the Peruvian coast during cold events and expanding their distribution during the warm phase of the ENSO.

Species list

Since EN 1982-83, a systematic record of fish species from tropical waters begun, Kong *et al.* (1985) and Kong & Bolados (1987) reported 51 species for northern Chile. Guzmán *et al.* (1998) expanded the list for northern Chile since 1987. Samples were archived in the zoological collection of the Universidad Arturo Prat, Iquique.

Furthermore, information on warm-water fish species caught during EN events off northern Chile between 1982 and 2002 have been presented by Kong *et al.* (1985), Sielfeld *et al.* (1995) and Vargas *et al.* (1998) and summarized in Table 2. This list includes 96 species (5 chondrycthians and 91 teleosteans) corresponding to 49 families. For eight of these species the present review is the first record for the Chilean coast (*Gymnothorax* aff. *equatorialis, Ophictus tetratrema, O. zophochir, Labrisomus xantii, Caranx georgianus, Nicholsina denticulata, Hirundichthys rondeletii, Antennarius avalonis*) (Table 2). Species normally distributed during summer of non-EN years north of Antofagasta (<23ºS, Fig. 1) like *Sardinops sagax* and *Scomber japonicus*, but which extend their distribution to the south during EN events (Kong *et al.* 1985) have been

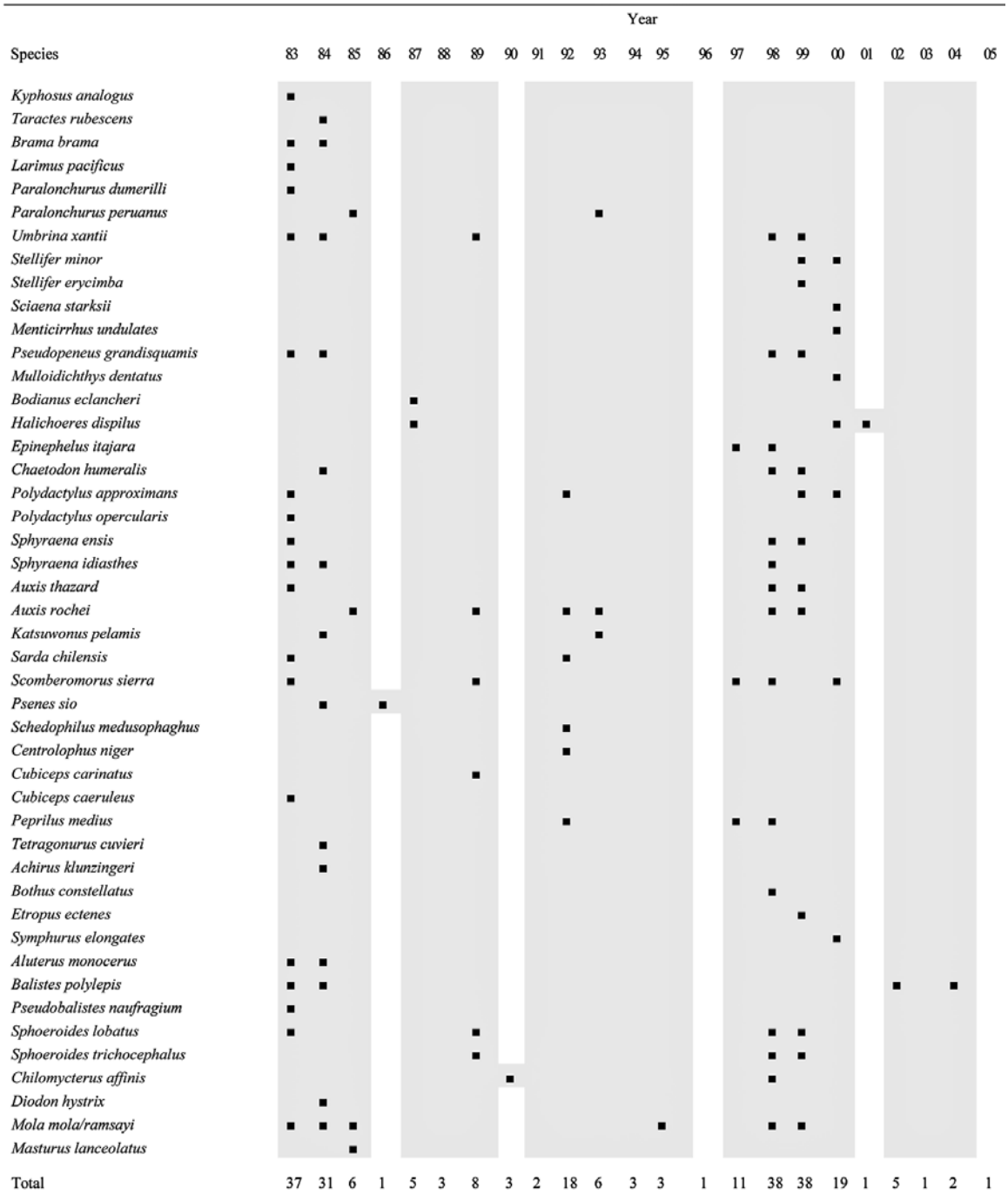
[4]Vargas M & R Peredo. 2001a. Primer registro en Chile de *Sciaena starksi* y *Menticirrhus undulatus* (Pisces, Sciaenidae) y su interes para la pesca artesanal de la I Región. XXI Congreso de Ciencias del Mar, Viña del Mar, Resúmenes, p. 106.

[5]Vargas M & R. Peredo. 2001b. Nuevos registros de peces en las costas de Arica (I Región, Chile) durante el período 2000 – 2001, y su relación con eventos El Niño. XXI Congreso de Ciencias del Mar, Viña del Mar, Resúmenes, p. 106.

Table 2. Fish species associated with warm-water events (grey) and recorded between 1982 and 2004 off northern Chile (Shadding and frame indicate the different warm events and after-event subsisting warm water species) / Especies de peces asociados a eventos cálidos (gris) y registrados entre 1982 y 2004 frente al norte de Chile (el sombreado y marco indica los diferentes eventos cálidos y la subsistencia de las especies de aguas cálidas post-evento

	Year																					
Species	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05
Dasyatis violacea					■	■													■	■			
Dasyatis brevis																		■	■				
Rhinobatos planiceps		■																					
Squatina armata										■										■			
Sphyrna zygaena										■					■	■	■			■	■	■	■
Gymnothorax aff. *equatorialis*					■	■																	
Gymnothorax castaneus													■										
Ophichthus tetratrema																	■	■					
Ophichthus zophochir															■								
Opisthonema libertate	■	■														■	■						
Anchoa nasus																		■					
Anchoa naso		■				■	■		■								■						
Albula vulpes	■																						
Etrumeus teres	■						■			■		■					■						
Atherinella nocturna		■						■	■						■		■						
Belone stolzmanni		■														■	■						
Fistularia commersoni																■							
Strongylura exilus	■	■													■	■	■						
Scomberesox saurus		■									■						■						
Cypselurus heterurus	■											■											
Fodiator acutus										■					■	■	■						
Synodus lacertinus		■																					
Synodus scituliceps			■												■								
Hemiramphus saltator	■	■																					
Hirundichthys rondeletti											■	■											
Trachypterus altivelis	■	■																					
Zu cristatus					■					■													
Hippocampus ingens	■															■	■						
Prionotus stephanophrys	■									■						■	■						
Prionotus quiescens																■	■						
Scorpaena hystrio														■			■						
Pristigenys serrula											■					■	■						
Antennarius avalonis																		■					
Galeichthys peruvianus	■												■										
Arius seemanni																		■					
Rhombochirus osteochir																■							
Nicholsina denticulatum																		■					
Nematistius pectoralis										■													
Labrisomus xantii																	■						
Caulolatilus princes										■										■			
Coryphaena hippurus	■															■	■						
Caranx caninus		■														■							
Caranx caballus	■	■														■	■						
Caranx georgianus																■							
Decapterus microsoma		■														■	■	■					
Oligoplites refulgens																■	■						
Trachinotus paitensis	■	■						■		■													
Naucrates doctor		■								■					■	■							
Seriola peruana	■									■					■	■	■						
Alectis ciliaris	■	■														■	■						
Selene peruviana	■									■													
Selene brevoorti	■	■														■	■						
Calamus brachysomus																■	■	■					
Eucinostomus argenteus	■		■													■	■						

Table 2 continued / Continuación Tabla 2



excluded from Table 2. They may be considered as EN visitors for central Chile, but normal for northern Chile.

Habitat preference of warm-water species

Fishes occurring during EN events mainly mobile epipelagic species (55 species: 55%; Table 3) probably migrating with the water masses. Littoral species (25) include fishes typically inhabiting sandy beaches and soft bottom habitats mainly represented by the family Sciaenidae, are the second dominant group (Vargas 1993), while 16 species associated with rocky shores were registered (Sielfeld *et al.* 2002.) (Table 3). This tend is valid for all warm events analysed, where epipelagic and soft bottom migrating fishes always were the most frequent (Table 3).

North-south gradient in species number of invading fishes

Table 4 lists the number of southwards invading Panamic and Peruvian fish species and families found at different locations (see also Fig. 1) along the northern Chilean coast during warm water events. A clear north-south gradient is obvious (Fig. 2) supporting the transition character of the study area between the Chilean and Peruvian zooprovinces (*sensu* Balech 1954), already emphasized by Sielfeld & Vargas (1996) for engybenthic fish assemblages (*sensu* Mead 1970) for fishes living not demersal, but up to 20 metres above the bottom.

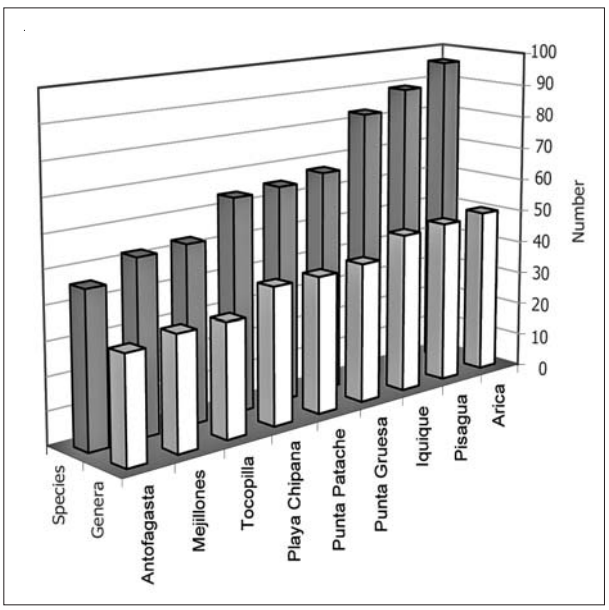


Figure 2. North south gradient in the number of warm-water fishes recorded along the northern Chilean coast / Gradiente norte sur en el número de peces de aguas cálidas registrados a lo largo de la costa chilena del norte

Table 3. Fishes associated to EN events in northern Chile and its habitat preference / Peces asociados a eventos EN en el norte de Chile y sus preferencias de habitat

	Habitat type									
	Epipelagic		Soft bottom		Rocky shore		Not defined		TOTAL	
EN events	N	%	N	%	N	%	N	%	N	%
82/85	38	66.6	12	21.1	6	10.5	1	1.8	57	100
87/89	9	56.3	1	6.3	5	31.3	1	6.3	16	100
91/95	22	73.3	5	16.7	3	10.0	0	0.0	30	100
97/98	34	54.8	16	25.8	9	14.5	3	4.8	62	100
02/04	2	40.0	2	40.0	1	20.0	0	0.0	5	100
All events	55	55.0	25	25.0	16	16.0	4	4.0	100	100

Relation with thermal anomaly degree

Table 5 shows that the intensity of the thermal anomaly is related to the number of invading warm-water fish species off northern Chile. Species involved vary between events. Only the following epipelagic species *Anchoa naso, Albula vulpes*, *Atherinella nocturna* and *Scomberesox saurus* were found consistently during the last three EN events. Nearshore fish communities were affected by EN to a much lesser degree, resulting from only a few invading species, and with only *Umbrina xantii* found during all events considered.

3. Septentrional invaders and particular EN events

The invasion of fish species during EN events has been reported in the literature. Table 6 summarizes this information including original data from 1997/98, 2002/03 and 2004/05.

The effect of EN 1982/83 included 57 invading warm-water species (northern most sampling site) of which 67% (38) were still detected as far south as Antofagasta (23º40'S) (Table 6). 67% (38 species) were epipelagic, 21% soft-bottom coastal fishes, and 10.5% (6 species) rocky-shore fishes (Table 3). The epipelagic species which reached Antofagasta were carangids (8 species, except *Naucrates ductor* just reaching Iquique), coryphaenids (1 species), scombroids (5 species), sphyraenids (2 species), a nomeioids (1 species) and tetragonurids (1 species). Littoral fishes were principally sandy shore inhabitants (4 sciaenids), 2 balistids and 1 chaetodontid, both rocky shore inhabitants. EN invading sciaenids extended their distribution as far south as Chipana (21º20´S).

Table 4. Record of the number and percentage of fish species and families having extended their distribution to northern Chilean waters during EN events between 1983 and 2003. For locations see also Fig.1 / Registro del número y el porcentaje de especies de peces que extendieron su distribución al norte de Chile durante eventos EN entre 1983 y 2003. Para localidades ver tambien Fig. 1

Location		Fish species		Fish families	
Localities	Latitude	N	%	N	%
Arica	18º21´S	100	100	52	100.0
Pisagua	19º31´S	90	90	50	96.2
Iquique	20º12´S	89	89	48	92.3
Punta Gruesa	20º20´S	69	69	43	82.7
Punta Patache	20º50´S	68	68	42	80.8
Playa Chipana	21º20´S	66	66	42	80.8
Tocopilla	22º05´S	57	57	38	73.1
Mejillones	23º05´S	56	56	37	71.2
Antofagasta	23º40´S	53	53	35	67.3
Total	18º21´-23º40´S	100	100	52	100.0

EN 87/88 triggered the southward migration of 16 warm-water fishes, with 56% epipelagic species and 31% rocky-shore fishes (Table 3). Most of these species were only distributed as far south as Iquique (20º12'S), 44% until Chipana (21º20'S) and only 6% south of Tocopilla (22º05'S) (Table 6). Pelagic-oceanic species detected were *Zu cristatus, Dasyatis violacea, Auxis rochei, Scomberomorus sierra* and *Cubiceps carinatus.* Pelagic-coastal species (*Anchoa naso, Etrumeus teres* and *Atherinella nocturna*) only reached as far south as Chipana. Rocky-shore fishes registered were *Bodianus eclancheri* and *Halichoeres dispilus*, detected as far south as Iquique and Punta Gruesa (20º20'S). In sandy-shore habitats only *Umbrina xantii* was identified as occasional visitor off Chipana.

During EN 91/93, 29 warm-water fishes were detected (Table 3). 76% were epipelagic, 17% soft bottom inhabitants and only one species typical for rocky shores (Table 3). EN 97/99 induced strong changes in the ichthyofaunal composition, affecting particularly the epipelagic assemblage. Typical warm-water epipelagic, oceanic species occurred as far south as Antofagasta (23º40'S) (Table 2; *Dasyatis brevis, Sphyrna zygaena, Strongylura exilis, Fodiator acutus, Sphyraena ensis, Peprilus medius, Mola mola/ramsayi*, scombrids: *Auxis rochei/thazard* and *Scomberomorus sierra*, carangids: genera *Caranx, Decapterus, Oligoplites, Naucrates, Alectis, Selene*). Several species were only detected as far south as Iquique (20º12'S) and Chipana (21º20'S) (*Naucrates ductor, Dasyatis violacea, Belone stolzmanni, Fistularia petimba,*

Table 5. Positive thermal anomalies of EN events and recorded warm-water species off northern Chile (Chile/Peru: Fuenzalida 1992, Fuenzalida *et al.* 1999, Garcés-Vargas *et al.* 2005; 5ºN-5ºS/120ºW-170ºW: Mc Phaden 2003) / Anomalías termicas positivas de los eventos EN a las especies de aguas cálidas registradas frente al norte de Chile (Chile/Perú: Fuenzalida 1992, Fuenzalida *et al.* 1999, Garcés-Vargas *et al.* 2005; 5ºN-5ºS/120ºW-170ºW: Mc Phaden 2003)

ENSO Events	82/83	87/88	91/92	97/98	02/04
T° anomaly off Chile/Peru	+ 5.5°C	+ 2.5°C	+ 4.0°C	+ 5.0°C	+ 2.0°C
T° anomaly in the tropical Pacific	+ 2.5°C	+ 1.0°C	+ 1.5°C		
Warm-water fishes off northern Chile	57	16	30	62	5

Scomberesox saurus and *Sphyraena idiastes*). Typical Peruvian coastal pelagic species were also detected at the bays of Arica (*Anchoa nasus*), Iquique (*A. naso*), Chipana (*Atherinella noctura*) and Antofagasta (*Etrumeus teres* and *Opistonema libertate*) (Table 2). The soft-bottom littoral community included *Ophicthus zophochir, O. tetratrema, Sciaena starksii, Stellifer minor, Symphurus elongatus, Mulloidichthys dentatus* and *Arius seemanni* at Arica Bay, *Bothus constellatus* at Caleta Buena, *Etropus ectenes* and *Stellifer erycimba* at Iquique, and *Umbrina xantii, Eucinostomus argenteus, Pristidactylus approximans, Pseudupeneus grandisquamis* and *Sphoeroides lobatus/trichocephalus* as far south as Antofagasta (Table 2). At the rocky shore, *Labrisomus xantii* was detected in Caleta Buena; *Scorpaena hystrio, Antennarius avalonis, Nicholsina denticulatum* and *Halichoeres dispilus* as far south as Iquique, and *Pristigenys serrula, Chaetodon humeralis* and *Hippocampus ingens* off Antofagasta (Table 2).

The weak EN 02/03 triggered the southward migration of only a few species, mainly the pelagic *Sphyrna zygaena* as far as Antofagasta and *Dasyatis violacea* as far as Iquique, *Caulolatilus princeps* down to Pisagua, *Balistes polylepis* as far as Iquique and *Squatina armata* was found off Chipana (Table 2).

4. Biogeographical implications

The latitudinal distribution of neritic fishes between 0°S and 57°S (Gulf of Guayaquil to Cape Horn) (Fig. 3) during normal conditions indicate south of the Ecuatorial Front, the existence of three main assemblages (separation under 40% of similarity): 5°-13°S (Paita to Pisco), 13-41°S (Pisco to Puerto Montt) and 41-57°S (Puerto Montt to Cape Horn). The coastal fish assemblages distributed north of the Equatorial Front during normal conditions belong to the Panamic Province that reaches north to the Gulf of California and south to Cabo Blanco (north Peru). Hooker

Table 6. Number of invading warm-water fishes associated with EN events off northern Chile between 1983 and 2004 / Número de peces invasores de aguas cálidas asociados a eventos EN frente al norte de Chile entre 1983 y 2004

	Periods				
Localities	83-85	87-89	91-95	97-00	02-04
Arica	57	16	30	62	5
Pisagua	56	16	29	53	5
Iquique	55	16	29	51	4
Punta Gruesa	46	10	14	37	2
Patache	46	8	13	36	2
Chipana	46	7	13	36	2
Tocopilla	42	1	5	33	1
Mejillones	41	1	4	33	1
Antofagasta	38	1	4	33	1

(2009) discussed the presence of tropical fishes in northern Peru and Hooker (1998) showed the presence of several of these species as far south as Pucusana Bay (12º28'S) during EN 1997/98.

This distribution pattern is consistent with further biogeographic classification proposed by Balech (1954), López (1963), Lutjeharms (1990), Parin (1991) and Pequeño & Lamilla (1993) who have suggested a Peruvian, Chilean and Magellan Zooprovince for the southeast Pacific. Pequeño (2000) proposed a different classification, but also related with the before ones, considering a Capricornic Province that includes an Atacaman District and a Central Chilean District, and the Fjord Province including a Chiloé District, and the Fuegian District.

Ojeda *et al.* (2000) suggested the existence of only two instead of three fish groups with different association: the tropical and subtropical species, corresponding to the Peruvian Province, and subantarctic species, corresponding to the Magallan Zooprovince. The zone between 30°S and 42°S (central Chile) corresponds to a transition zone inhabited by subantarctic, subtropical, panoceanic and some endemic species as quoted by Mead (1970). This concept is also supported by the main biogeographical features observed by Castilla *et al.* (1993) and Fernández *et al.* (2000) separating the Chile-Peru Province, located between Paita and Valparaíso and the Magellan Province between Chiloé and Cape Horn.

In the present classification (see Fig. 3) the 13-41°S cluster represents a Chile-Peru Province, including a 13-34°S subcluster (13-21°S and 21-34°S with 0.80 similarity). The 34-41°S zone represents the south part of the province and can not be regarded as a transition zone into the Magellan Province (41-57°S) because of their low similarity level (20%).

The differences between Ojeda *et al.* (2000) and the present results may be explained because of numerous Panamic and south Peruvian warm-water species, were not considered by the first author.

Discussion

The warm EN and the cold LN phases of the southern Pacific Oceans sea surface temperature induce a latitudinal displacement of the fauna, for which two categories of migrating species were proposed: The "stenoterm fishes of warm waters" comprehend fishes that regularly inhabit subtropical waters associated to the Chilean oceanic islands, while "septentrional invaders of the Peru Current" are migrants to southern latitudes (Mann 1954), of panamic origin, invading the Peruvian and Chilean coast, and Peruvian species that migrate to northern Chile during EN events.

The southern distribution limit of these warm-water fishes during EN is related with the intensity of the positive temperature anomaly of the events analysed. In many cases, and especially in the case of coastal species (sciaenids, ariids, labrids, ophichthids, bothids), Península de Mejillones represents a natural barrier for the southerly migration of several species, proposed by Escribano *et al.* (2002) and Castilla *et al.* (2002).

Epipelagic fishes (scombrids, carangids, centrolophids, exocoetids) seem to react more rapidly to EN conditions (see Tables 2 and 3) compared to the more resilient littoral fishes. Oceanic fishes probably migrate off-shore from southern Peru along the temperature gradient of subtropical waters described by Schweigger (1960) and Blanco *et al.* (2001), west of the coastal upwelling cells off northern Chile. In contrast the southerly migration of rocky-shore fishes is slow because they are not that mobile and in many cases with territorial behaviour like clinids and blennids. The specimens caught after EN conditions are normally fully developed and can be detected for a much longer period revealing a time lack compared to oceanographic conditions. For example *Halichoeres dispilus, Ophicthus tetratrema, Antennarius avalonis, Nicholsina denticulatus* and *Arius semanni* (Table 1) were captured in 2000/2001 during LN conditions, 3 years after EN 97/98. They probably are not able to reproduce successfully due to unfavourable environmental conditions.

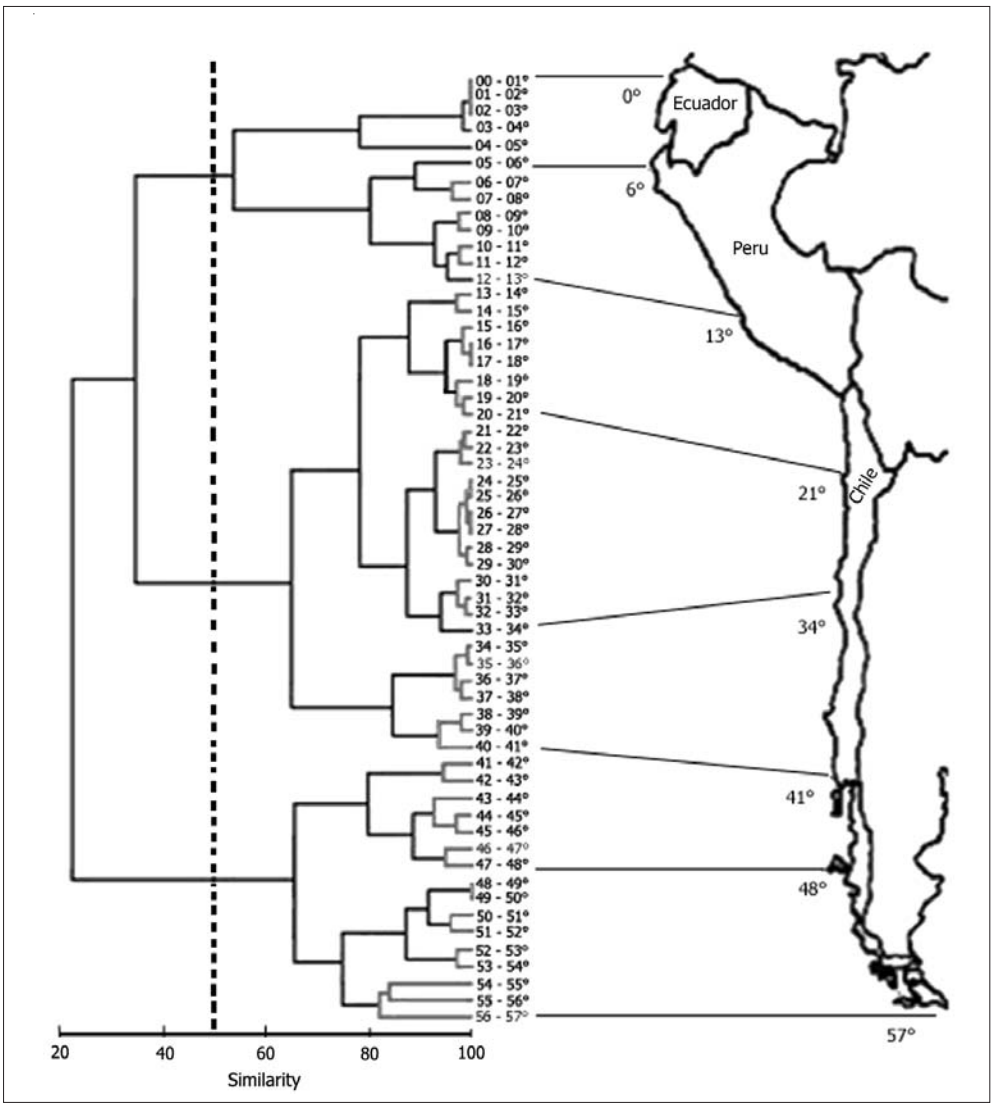


Figure 3. Sorensen similarity dendrogramm of neritic fish assemblages using the hierarchical cluster analysis routine CLUSTER in the program PRIMER 6 and SIMPROF permutation test (at 1% level) to determine significant internal structure of the clusters / Dendrograma de similitud de Sorensen de los ensambles de los peces neríticos utilizando la rutina de analisis jerárquico de agrupaciones CLUSTER del programa PRIMER 6 y el test de permutación SIMPROF (al nivel del 1%) para la determinación de estructuras internas significativas de las agrupaciones

From a ichthyogeographical point of view, inside the 13-41°S cluster (Pisco/Puerto Montt) (Fig. 3) the southward oscillations of the normal 20-21° zoogeographic border (Pisco-Chipana cluster) south to 24°S (south of Antofagasta) during strong ENSO (1982/83 and 1997/98) (Fig. 4), is very consistent with the oceanographic changes associated to ENSO (Fig. 5). Otherwise if a northward oscillations of the 21-34°S cluster during strong La Niña may be expected, than the the area investigated during this study (18°-21°S) may be regarded as a transition zone between the central Chilean and the Peruvian faunistic zones, with north/south oscillations following to the respective thermal anomalies and oceanographic patterns linked to EN events.

Acknowledgments

In memory of Ismael Kong we express our recognition for his enormous contributions to knowledge of biology and systematic of the fishes of northern Chile. His work is an unquestionably legacy for the coming generations of ichthyologists of the future. We also remember our friend Mario Villegas, colleague of many meetings, scientific discussions and field trips, who deceased in March 2008, during the development of the EU Project CENSOR. Finally our thanks to the EU Project CENSOR (Climate Variability and El Niño Southern Oscillation: Implications for Natural Resources and Managament, contract 511071) and the Programa Bicentenario de Ciencia y Tecnología CONICYT-CENSOR-RUE02, which funded this study.

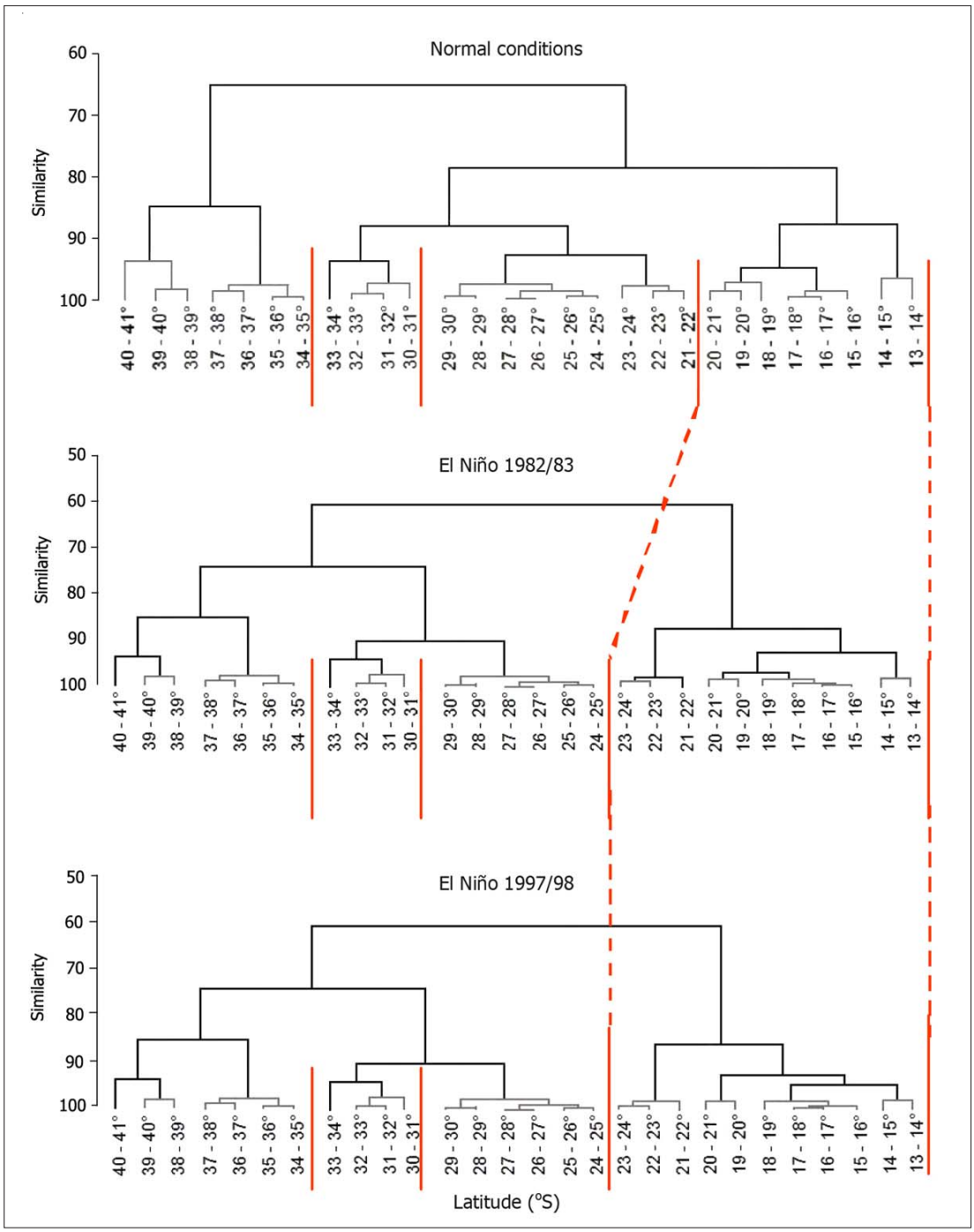


Figure 4. Sorensen similarity dendrogramm of neritic fish assemblages during normal conditions, El Niño 1982/83 and 1997/98 using the hierarchical cluster analysis routine CLUSTER in the program PRIMER 6 and SIMPROF permutation test (at 1% level) to determine significant internal structure of the clusters / Dendrograma de similitud de Sorensen de las agrupaciones de los peces neríticos durante condiciones normales, El Niño 1982/83 y 1997/98 utilizando la rutina de analisis jerárquico de agrupaciones CLUSTER del programa PRIMER 6 y el test de permutación SIMPROF (al nivel del 1%) para la determinación de estructuras internas significativas de las agrupaciones

Figure 5. Schematic representation of the principal water masses of the southeast Pacific during 1) normal conditions 2) cold La Niña conditions and 3) warm El Niño conditions. (*fide* Keyl *et al.* 2008[6]) / Representación esquemática de las principales masas de agua del Pacífico suroriental durante 1) condiciones normales, 2) condiciones frías La Niña y 3) condiciones cálidas El Niño. (*fide* Keyl *et al.* 2008[6])

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Recibido el 20 de julio de 2009 y aceptado el 29 de mayo de 2010