Revista Chilena de Historia Natural
73:585-603, 2000

Disjoint geographical distribution of intertidal and nearshore benthic invertebrates in the Southern Hemisphere

Distribuciones geográficas disyuntas de invertebrados bentónicos intermareales y del submareal somero en el Hemisferio Sur

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ABSTRACT

Biogeographical explanations for the extant and paleo disjoint geographical distribution in the southern hemisphere of five species of nearshore marine benthic invertebrates: *Gaimardia trapesina*, *Ostrea chilensis*, *Pyura stolonifera* taxonomic complex, *Aulacomya ater* and *Concholepas concholepas*, showing distinctive reproductive strategies and early life history characteristics are reviewed and analyzed. Through the use of published and new information we contrasted the following hypotheses: a) vicariance-historical process, b) epiplanktonic larval dispersal, c) juvenile/adult dispersal through rafting and d) planned or accidental anthropogenic dispersal mechanisms. The juvenile/adult transoceanic dispersal hypothesis by rafting was the only one impossible to be rejected for the species analyzed. The implication and future direction for research in this area are discussed.

Key words: paleobiogeography, vicariance, larval dispersal, rafting, anthropogenic dispersal, bivalves, gastropods, tunicates, invertebrates, nearshore, southern hemisphere.

RESUMEN

Se revisa y analiza las posibles explicaciones para la distribución geográfica disyunta, presente y pasada, en el hemisferio sur de cinco especies de invertebrados bentónicos marinos litorales: *Gaimardia trapesina*, *Ostrea chilensis*, el complejo taxonómico *Pyura stolonifera*, *Aulacomya ater* y *Concholepas concholepas,* con estrategias reproductivas y características de historia de vida distintas. Se discute y pone a prueba, usando información original o publicada, las siguientes hipótesis: a) procesos históricos de vicarianza, b) dispersión de larvas epi-planctónicas, c) dispersión de juveniles o adultos por transporte pasivo y d) dispersión antropogénica planificada o accidental. La hipótesis de dispersión transoceánica de juveniles o adultos fue la única imposible de rechazar para las especies analizadas. Se discute las direcciones futuras de investigación en esta área.

Palabras clave: biogeografía, paleobiogeografía, vicarianza, dispersión larvaria, transporte, dispersión antropogénica, bivalvos, gastrópodos, tunicados, invertebrados, litoral, hemisferio sur.

INTRODUCTION

A taxon´s geographical distribution is the result from a combination of historic, regional and local processes, ecological interactions and accidental or planned introductions (Knox 1980, Ruiz et al. 1997, Lindberg 1991, Castilla et al. in press). The deep ocean that separates South America from South Africa, New Zealand and Australia represents a major barrier for the dispersal of sessile or slow mobile nearshore marine benthic invertebrates (NSBI= those found in rocky intertidal and/or shallow subtidal inshore environments of less than ca. 100 m of depth). The hypotheses for the southern hemispheric geographical distribution of benthic nearshore invertebrates fall into 4 main categories: (H1) the vicariance-historical hypothesis, contenting that the disjoint geographical distributions of NSBI may be the result of ancient continuous distributions following the break-up of Gondwanaland (late Mesozoic) and posterior, but concurrent, paleoceanographic changes (Knox 1980, Zinsmeister 1982, Kott 1985); (H2) the oceanic epiplanktonic larval dispersal hypothesis, contenting that larval dispersal had occurred via the southern hemisphere oceanic circulation of water masses generated by Coriolis forces, and the west-wind-drift and moving oceanic water masses predominantly westward (Fell 1962, Orensanz 1990, Ó Foighil et al. 1999); (H3) the oceanic dispersal of juveniles or adults hypothesis, contending that the dispersal of individuals occurred via rafting; e.g., the transport of sessile or sedentary juvenile or adult stages of an organism on a drifting object or transporting agents, such as kelps, logs, seagrasses or pumice (Scheltema 1977, Jokiel 1984, 1989, Highsmith 1985, Jackson 1986, Ó Foighil 1989, Worcester1994); and (H4) the planned or accidental anthropogenic dispersal hypothesis, such of those occurring via aquaculture, ship fouling (Monniot & Monniot 1994) or ballast seawater (Carlton & Geller 1993).

Five elements, independent or combined, have been used in the hypotheses testing of NSBI disjoint paleo and/or extant biogeographic distribution of this part of the world: (1) evidence of plate tectonic and paleoceanographic changes occurred over time in the southern hemisphere; (2) paleobiological reconstruction; (3) phylogenetic relationship of the taxa investigated; (4) the knowledge on the life history of the species involved, particularly the extension of larval stages; and (5) the genetic structure (particularly molecular genetics) of local populations, which may provide independent evidence for genetic boundaries, temporal frameworks for species divergence, phylogenetic reconstruction and information on geography of allelic variants within species (Palumbi 1996).

In this paper we analyzed the biogeographical quest presented by a selected group of southern hemisphere NSBI invertebrate species that show transoceanic geographical distributions and distinctive reproductive strategies and early life history characteristics, and argue about dispersal/transport mechanisms. As it has been suggested by several authors, it is expected a positive relationships between the length of planktonic larval time and geographic distribution; thus, a species with short, or no planktonic stage, is supposed to have a small geographic range, while a long planktonic phase may promote a wider distribution range (Mileikovsky 1971, Scheltema 1978, 1986a, Crisp 1978, Jablonski 1986; but see Johannesson 1988).

We selected the following species: (1) *Gaimardia trapesina* (Lamarck, 1819), a small bivalve showing internal fertilization and brooding strategy; (2) the Chilean oyster O*strea chilensis* (Philippi, 1845), showing external fertilization and retention of the larvae inside the mantle cavity of the adult; (3) ascidians of the *Pyura stolonifera* (Heller, 1878) taxonomic complex (see Kott 1997, 1998), showing external fertilization and a larvae with a short free-swimming planktonic period (few hours); (4) the ribbed mussel *Aulacomya ater* (Molina, 1872), showing external fertilization and larvae with long free-swimming planktonic period (several weeks), and (5) the gastropod muricid "loco" *Concholepas concholepas* (Bruguière, 1789), showing internal fertilization (copulation) and a larvae with a long free-swimming planktonic period (several months). For each of them we discuss the most plausible hypotheses to explain their extant and paleo geographical distribution.

MATERIAL AND METHODS

The geographical distribution of the species analyzed and suggestions for the routes and mechanisms of dispersal are based on published information. For the brooding bivalve, *G. trapesina*, we used information from Ojeda & Santelices (1984), Zinsmeister (1984), Castilla (1985) and the work of Helmuth et al. (1994) for evidences on long distance dispersal kelp-rafting. For the Chilean oyster, *O. chilensis*, we followed papers referring to characteristics of the larvae (Chanley & Dinamani 1980, DiSalvo et al. 1983), genetic work (Buroker et al. 1983, Ó Foighil et al. 1999), and particularly the work of Foighil et al. (1999) that uses paleobiological, phylogenetic analyses and archaeological information to address the contenting hypotheses. For the southern hemisphere *P. stolonifera* taxonomic complex we followed Kott's (1997, 1998) interpretation. Additionally, we discussed their larval life history (Clarke et al. 1999), phylogenetic analysis of DNA sequences and derived PAU trees for the South African, Australian and Chilean populations (Castilla et al. unpublished data). Summaries for the specific methods used (i.e. tunicate DNA sequencing) are included within the species analysis. For the ribbed mussel, *A. ater*, we followed Osorio & Bahamonde (1968), Cancino & Becerra (1978), Ojeda & Santelices (1984), Zinsmeister (1984), Castilla (1985), Suchanek (1986), Erkon Schuring & Griffiths (1990) and Crame (1999). For the muricid C. *concholepas* we incorporated recent published information about their paleogeographical distribution (DeVries 1995, Vermeij 1998). For extant populations of *C. concholepas* we discuss the characteristics of its reproduction and planktonic larvae (DiSalvo 1988, DiSalvo & Carriker 1994), growth, ecology, genetic differentiation of populations in central and northern Chile and archaeological findings (Castilla & Jérez 1986, Jerardino et al. 1992, Guiñez et al. 1992, Castilla 1999).

RESULTS AND DISCUSSION

Gaimardia trapesina (Lamarck, 1819): a brooder species with no free-living larval stage

Present disjoint biogeographical distribution: *G. trapesina* exhibits a wide geographic distribution (Fig. 1) throughout the Scotia Arc, including Cape Horn, Falkland Islands, South Georgia, South Sandwich Islands, Crozet Island, Marion Island and the Kerguelen Islands (Fell 1962, Dell 1964, Ralph & Maxwell 1977, Blankey & Grindley 1985, Thiriot-Quievreux et al. 1988, Helmuth et at. 1994, Linse 1999). The species broods its young and has no free-living larval stage (Thiriot-Quievreux et al. 1988). Therefore, according to the larval dispersal hypothesis it is no expected to find *Gaimardia* populations with so wide and disjoint distribution: i.e. the Falkland Islands which are located approximately 1,300 km east-northwest of the Antarctic island South Georgia, and the later approximately 2,000 km west from Cape Horn. Additionally, the Kerguelen Islands are approximately 3,500 km from the nearest continental landmass, making it one of the most isolated places on Earth (Blott et al. 1988). Also, other species with direct development has been found in isolated islands (e.g., Easter Island, the Juan Fernández Islands, and Kerguelen Island) at higher proportion than usual (McDowall 1968)

Vicariance (H1) and epiplanktonic larval dispersal (H2) hypotheses: *G. trapesina* lacks a free-living larval stage, therefore the epiplanktonic larval dispersal hypothesis could be discarded. However, it is possible that founding of isolated island populations may have occurred through dispersal of larvae with an extended planktotrophic phase (pelagic development) from the original populations, provided that this developmental mode was loss afterwards in both populations. Prior to1984 the oldest record for *Gaimardia* was from the late Pleistocene of New Zealand. Nevertheless, Zinsmeister (1984) reported the presence of *Gaimardia flemingi*, that resembles *G. trapesina*, in the upper Eocene at La Meseta Formation, Seymour Island from the Antarctic Peninsula. He suggested that *Gaimardia*

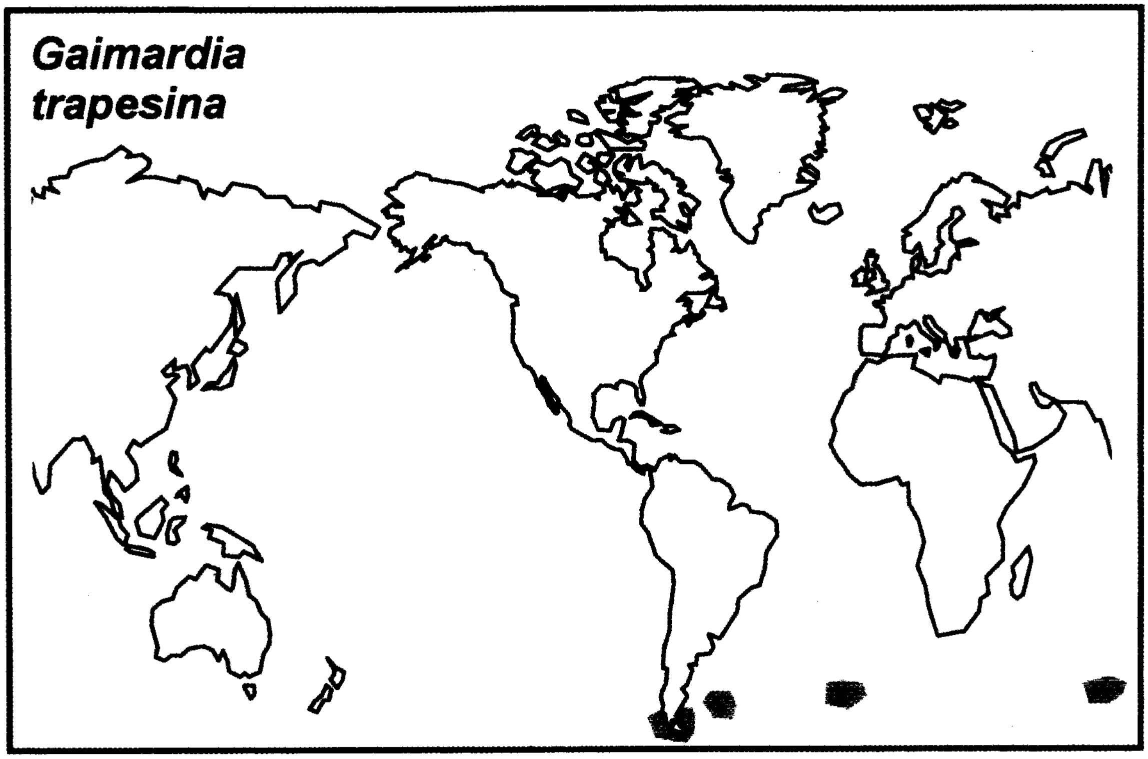

Fig. 1. Southern hemisphere extant disjoint geographical distribution of the bivalve *Gaimardia trapesina* (see stippled areas).

Distribución geográfica disyunta de las poblaciones actuales del bivalvo *Gaimardia trapesina* en el hemisferio sur (ver áreas achuradas).

originated in the southern hemisphere around Antarctica during the Paleogene (Paleocene-Oligocene). Further, it has been argued that during the late Miocene, at the beginning of markedly cooler conditions, species moved northward into lower latitudes (Zinsmeister & Feldman 1984). Thus the vicariance hypothesis and/or the independent evolution of a common development mode may explain the present pattern of geographic distribution exhibited by *Gaimardia trapesina*.

The juvenile/adult dispersal (H3) and anthropogenic dispersal (H4) hypotheses: Helmuth et al. (1994) presented evidence of long-distance (approximately 1,300 to 2,000 km) dispersal for this brooding bivalve in the Southern Ocean: Cape Horn, the Falkland Islands, and South Georgia. *G. trapesina* is a common component of kelp-bed communities (Dell 1964, Ralph & Maxwell 1977, Ojeda & Santelices 1984, Castilla 1985). Therefore, it is possible that the species might be transported offshore via kelp-rafting. In fact, Helmuth et al. (1994), on a cruise between South Georgia and Punta Arenas, Chile, made observations and collections of 43 kelps from three rafts. The rafts were made almost entirely of individual plants of *Macrocystis pyrifera* and the relative abundance of *G. trapesina* on kelp stipe was highly variable, showing no significant trend with distance from South America. The authors also found that *G. trapesina* bivalves were able to survive transport across distances between South Georgia and South America, maintaining brooded young during this time. The authors suggested that dispersal by rafting can occur over geological and ecological time scales and could potentially serve as a significant way of genetic exchanges between populations. The adult dispersal hypothesis (H3) and the vicariance hypothesis (H1) cannot be discarded even when the Scotia Arc, the Falkland Islands, South Georgia, Marion Island and the Kerguelen Islands were probably completely covered by ice between the late Miocene and the Early Pliocene (Knox 1980, Graft 1994).

Ostrea chilensis: a brooding species with short-lived planktonic larvae

Present disjoint biogeographical distribution: The classification of the New Zealand dredge oyster *Ostrea lutaria* (Hutton, 1873) and the Chilean oyster *Ostrea chilensis* (Philippi, 1845) is controversial. Wakamatsu (1975) described *O. chilensis* as occurring along the West Coast of South America and around New Zealand. Korringa (1976) suggested that *O. lutaria* [according to Buroker et al. (1983) was wrongly referred as *O. angasi* (Sowerby, 1871)] and *O. chilensis* were closely related species. Chanley & Dinamani (1980) compared the larval characters of ostreid species around the world and found that *O. chilensis* and *O. lutaria* differed from all other ostreids and proposed the creation of a new genus, *Tiostrea,* including two species: *Tiostrea chilensis* and *Tiostrea lutaria.* However, Buroker et al. (1983) using protein-gel electrophoresis found that both taxa were different geographical populations of a single species. Harry (1985) extended the classification of the living species of oysters beyond that proposed by Stenzel (1979) and divided the genus *Ostrea* (Ostreidae, Ostreinae, Tribe Ostreini) into two subgenera: *Ostrea s.s.* and *Eostrea* Ihering, 1907. He proposed that *Eostrea* have a single species: *Ostrea* (*Eostrea*) *puelchana* Orbigny, 1841, including as junior synonyms the following: *Tiostrea* Chanley and Dinamani, 1980, *Ostrea lutaria* Hutton, 1873, *Ostrea chilensis* Philippi, 1845, *Ostrea angasi* Sowerby, 1871 and *Ostrea algoensis* Sowerby, 1871. Harry (1985) suggested that *O. puelchana* is a circumglobal species, extending between 35° and 50°S latitude, including coasts of South America, southern New Zealand, southern Australia, and South Africa. Additionally, Carriker et al. (1994) proposed *O. puelchana* as a synonym for *O. chilensis.* According to Toro (1995) the taxonomic status of these oysters is still obscure, particularly because neither the proposition of Harry (1985) nor that of Carriker et al. (1994) have considered the presence of significant differences in the reproductive biology among them (Fernández Castro 1988, Toro & Chaparro 1990, Pascual et al. 1992, Toro 1995). Consequently, in this paper we follow Toro (1995) and continue referring to the Chilean oyster as *Ostrea chilensis*: a species showing a disjoint distribution spanning New Zealand and Chile (Fig. 2).

In New Zealand, *O. chilensis* is found throughout the nearshore including the Chathman Islands, between 34° and 47°S of latitude (Buroker et al. 1983, Jeffs & Creese 1996). The main population of *O. chilensis* in New Zealand is present in Foveaux Strait, in the South Island, and supports a valuable dredge fishery (Cranfield & Michael 1989). In Chile, the distribution of the species shows a restricted geographical range between, 41° and 47° S of latitude, but is found mainly between 41° to 42°, from shallow waters down to depths of approximately 11m (Buroker et al. 1983, Winter et al. 1984, Guiñez & Galleguillos 1985, Toro 1995). The main beds are located in Gulf of

Quetalmahue and Guaitecas Islands (Solís 1967, Winter et al. 1984, Guiñez & Galleguillos 1985, Toro & Chaparro 1990). The Chilean oyster population within its northern range has sustained an important fishery, but has also suffered strong declines due to overfishing (i.e. Pullinque bed: Toro & Chaparro 1990). Presently the Chilean oyster production is sustained mainly through oysterculture (Lépez 1984, Toro & Chaparro 1990).

The prevailing hypotheses accounting for the *O. chilensis* disjoint biogeographical distribution have been recently discussed and scrutinized by Ó Foighil et al. (1999) and encompass the four types of hypotheses defined by us in the Introduction.

The vicariance-historical hypothesis (H1): It may be expected that both Chilean and New Zealand oyster populations are Gondwanaland relicts. The species has been documented for the New Zealand Pliocene (Beu & Maxwell 1990) but fossil oysters from pre-Holocene Chilean strata are unknown (Herm 1969, Ó Foighil et al. 1999). Therefore, it is possible that the species does not belong to the Gondwanaland fragmentation (Weissel & Hayes 1977). The fossil and genetic evidence information obtained through isoenzymes and mitochondrial DNA does not support the vicariance hypothesis. Buroker et al. (1983) compared the genetic structure of oysters from New Zealand and Chile and concluded, on the basis on 29 structural loci, that both taxa were almost indistinguishable. They suggested that the Chilean and New Zealand oysters represent disjoint geographical populations of the same species. The same conclusion was reached by Ó Foighil et al. (1999), using 609 nucleotide fragment of the cytochrome oxidase I (COI) mtDNA gen. They found a difference of four nucleotide substitutions between samples from the North Island (New Zealand) and Chiloé island (Chile), implying a 0.6% sequence divergence.

In conclusion, fossil and genetic information allows concluding that the hypothesis of vicariance through a Gondwanaland connection does not explain the trans-Pacific disjoint distribution of the Chilean and New Zealand oysters. The evidence suggests that the New Zealand oyster population is the ancestral one (Ó Foighil et al. 1999). Other hypotheses must be used to explain the present geographical distribution.

The oceanic epiplanktonic larval dispersal hypothesis (H2): The Chilean oyster broods its larvae within the mantle cavity for approximately 8

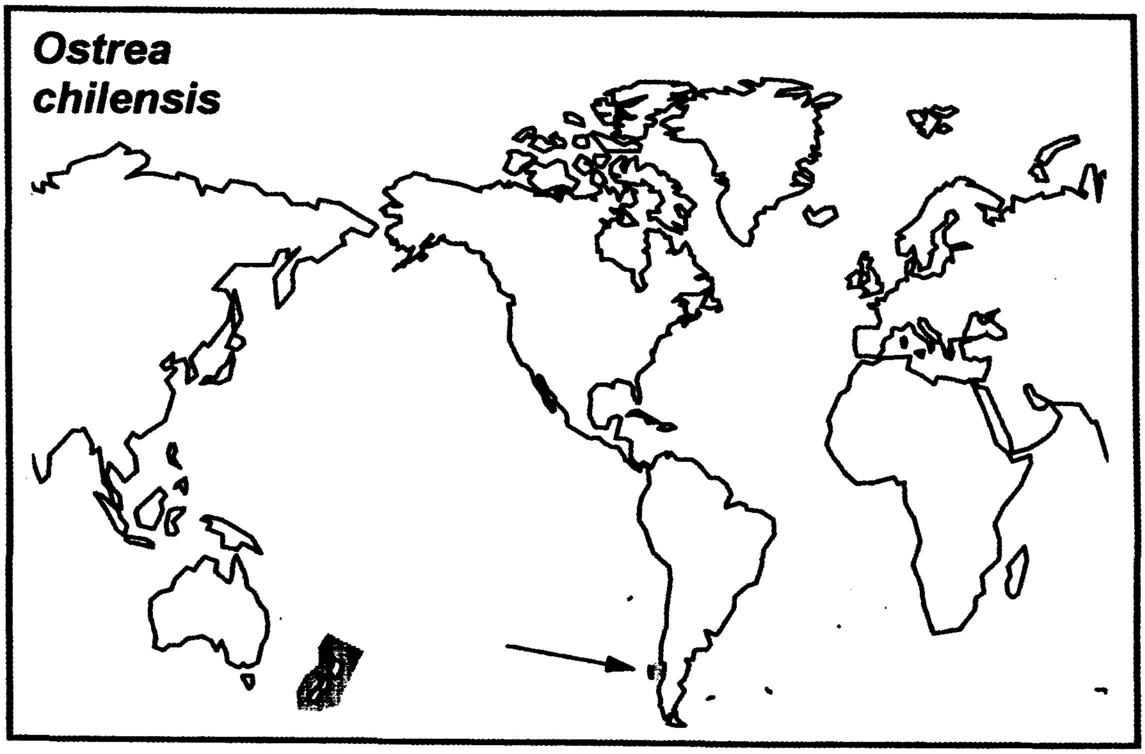

Fig. 2. Southern hemisphere extant disjoint geographical distribution of the bivalve *Ostrea chilensis* (see stippled areas). The arrow indicates the Chiloé island, Chile.

Distribución geográfica disyunta de las poblaciones actuales del bivalvo *Ostrea chilensis* en el hemisferio sur (ver áreas achuradas). La flecha indica la isla de Chiloé, Chile.

weeks, longer than any other oyster species. The veligers are not lecitothrophic, but remove ingested particles suspended in the mantle cavity of the mother. The larvae are released at a very advanced stage of development (approximately >450 μm diameter) and settle within a few hours (DiSalvo et al. 1983, Winter et al. 1984, Toro & Chaparro 1990, Chaparro et al. 1993). Therefore, the oceanic larval dispersal hypothesis cannot be called for. However, Ó Foighil et al. (1999) discussed a possible variant of this hypothesis: the Chilean population may have been established from New Zealand via the transoceanic dispersal of larvae with extended planktotrophic pelagic development, with a posterior and independent loss of this developmental mode in both populations. Ó Foighil et al. (1999) examined a juvenile fossil folding from New Zealand (late Pliocene strata, 1.6-2.0 mya) through scanning electron micrographs of prodissoconch and found that their structure is identical to that of modern specimens. This suggests that the species had fully evolved the present day larval development prior to the Pleistocene. In Chile, there is no fossil evidence of this species from the Pliocene/Pleistocene (Herm 1969, Ó Foighil et al. 1999). Radiocarbon techniques giving an age estimates (95 % confidence intervals) of 953-1,238 and 2,998-3,383 years before the present (y BP) have dated the first subfossils found in Chile. The juvenile fossils preserved had the present larval development (Ó Foighil et al. 1999). The phylogenetic parsimony search of COI including the South and North Islands of New Zealand and Chiloé island (Chile) indicated that the New Zealand North Island and Chilean samples belong to sister lineages with the New Zealand South Island branching off earlier. This implies an additional restriction to the variant hypothesis of loss of the extended pelagic larval period, since it would require three independent homoplasies after the respective branching of the N. Zealand South Island, North Island and (pre-Pleistocene and post-trans-Pacific colonization) Chilean lineages (Ó Foighil et al. 1999). The evidence and arguments discussed preclude the oceanic larval dispersal hypothesis (H2).

Oceanic dispersal of juvenile or adult (H3) and anthropogenic dispersal (H4) hypotheses: The evidence discussed above suggests that the founder oyster population in Chile occurred at least 2,000 y BP and originated from N. Zealand North Island. It is known that the first human settlement in New Zealand occurred unequivocally about 950 y BP (McGlone et al. 1994). Then, the anthropogenic oyster introduction or dispersal hypothesis can be discarded (Ó Foighil et al. 1999). Rafting has been suggested as the most probable explanation for the present disjoint trans-Pacific distribution of the Chilean oyster (Buroker et al. 1983, Ó Foighil et al. 1999). In fact, given that hypotheses H1, H2 and H4 have been rejected as plausible explanations for the disjoint present distribution of the Chilean oyster, the conclusion of Ó Foighil et al. (1999), is that dispersal by rafting is by far the most likely explanation. They suggested that pumice may have served as the subscase for transport. It is known that pumice have been released by repeated eruptions of the New Zealand North Island Taupo Volcanic Zone since the Pliocene (Wilson et al. 1986, Ó Foighil et al. 1999).

Pyura stolonifera taxonomic complex of species: larvae with a short free-swimming planktonic period

Present disjoint biogeographical distribution: Large barrel-shaped filter-feeding tunicates, such as *Pyura* species, are found as dominant rocky intertidal and shallow water organisms exclusively along the shores of South Africa, Australia and Chile (Fig 3). So far, the taxonomic nomenclature of these taxa is confounded and the phylogeny is not well understood (but see below). According to Kott (1997) the following subspecies may be distinguished: (1) *P. stolonifera stolonifera* (=*P. stolonifera* Heller, 1878) (see Day 1974, Fielding et al. 1994), known in S. Africa as "red bait" and present in the lower intertidal rocky shore fringe and shallow subtidal, along several 1,000´s of km of coastline, from Cape Town to Natal; (2) *P. stolonifera praeputialis* (= *P. praeputialis* Heller, 1878) (see Fairweather 1991), known in Australia as "cunjevoy" and present in the mid and low intertidal rocky shore fringes and shallow subtidal along several 1,000´s of km of coastline, in New South Wales, Victoria and Tasmania; (3) *P. stolonifera bradleyi* (= *P. bradleyi* Van Name, 1931) (=*P. praeputialis* Heller, 1878; see Paine & Suchanek 1983, Castilla 1997a, Clarke et al. 1999), known in Chile as "piure de Antofagasta" and present in the mid and low rocky intertidal fringes and shallow subtidal exclusively inside the Bay of Antofagasta Chile, along approximately 70 km of coast (Clarke et al. 1999, Castilla et al. 2000). *P. bradleyi* (Van Name, 1931) was collected only once, in 1931, in Zorritos, northern Peru. Since then, the species has not been collected. Two expeditions to Peru aiming specifically to Zorritos´ site, have not succeeded to locate the species (see Clarke et al. 1999). Recently, Kott (1998) has suggested that species in the *Pyura* *stolonifera* complex from South Africa, Australia and Chile are conspecific, returning to her previous opinion (Kott 1985).

The vicariance (H1) hypothesis: Tunicates, in spite of the hard tunicin protein-like of their tunic, do not fossilize well. In the case of this complex of subspecies there is not known fossil record. The prevailing hypothesis accounting for their disjoint biogeographical distribution, specially between the Australian and Chilean pyurid populations, was suggested by Kott (1985). The author proposed that the Chilean *Pyura* populations may be a Gondwanaland species relict, remaining since the late Mesozoic, when the Australian and South African *Pyura* populations diverged (Kott 1985). In order to test the taxa status and phylogenetic relationships between the southern hemisphere *Pyura stolonifera* complex (Castilla et al., unpublished data), DNA was extracted from either gill-sac or siphon tissue of *P. stolonifera* collected from Botany Bay (Sydney, Australia), from the Bay of Antofagasta (Chile) and from Cape Town (South Africa). As outgroup, the authors analyzed subtidal individuals of *Pyura chilensis* (Molina 1872) (Pyuridae), *Molgula ficus* (MacDonald 1859) (Molgulidae) and *Asterocarpa humilis* (Heller 1878) (Styelidae) (Clarke & Castilla 2000) all collected in Antofagasta (Chile). J.C. Castilla did field collections in all sites with the exception of Cape Town, where Prof. G. Branch collected tunicates.

A summary of the methodology used for the tunicate´s sequence of COI mitochondrial genes is the following: double-stranded products for the COI mitochondrial gene were amplified via PCR using primers from Folmer et al. (1994). They were cycle-sequenced using the Thermo Sequenase Dye Terminator Cycle Sequencing Premix Kit (Amersham). Sequences were generated from electrophenograms using ABI Prism RRR 377 software and analyzed with Sequence Navigator RRR (ABI). Each amplified mtDNA product was sequenced in both directions and compared by overlap to assure accuracy. COI were translated to aminoacids, based on the mitochondrial code for invertebrates, with ascidians exceptions (Yokobori et al.1993), via MacVector RRR (IBI) and aligned by eye. Additionally, the COI sequence of a pyurid species *Halocynthia roretzi* was available from Gen Bank (acc. N°

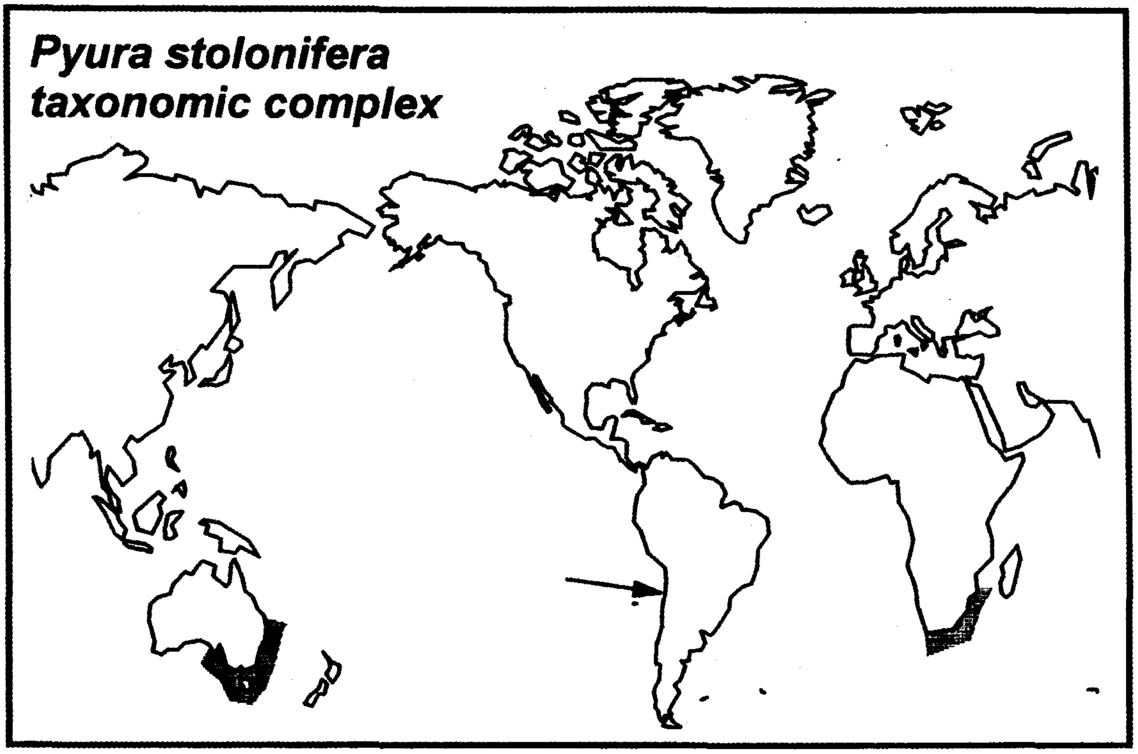

Fig. 3. Southern hemisphere extant disjoint geographical distribution of the tunicate *Pyura stolonifera* taxonomic complex (see stippled areas and taxonomical discussion in the text). The arrow indicates the Bay of Antofagasta, Chile.

Distribución geográfica disyunta de las poblaciones actuales del complejo de especies del tunicado *Pyura stolonifera* en el hemisferio sur (ver áreas achuradas y discusión taxonómica en el texto). La flecha indica la Bahía de Antofagasta, Chile.

S54796). The resulting data matrix for analyses totaled a length of 588 bases for 11 individuals/taxa. The data were analyzed using PAUP* 4.0 (Swofford 1998). Tree searches were conducted with optimality criteria of parsimony, maximum likelihood, and minimum evolution (= 1,000 replicates). The degree of transition: transversion bias was estimated using maximum likelihood. Parsimony searches were done with and without transversion bias corrections by differential weighing. Maximum likelihood searching, with 10 replicates, for optimal trees with simultaneous estimation of the T-ratio (= 3.01), gamma shape parameter (= 0,305), the shape of the distribution of substitution rates across the COI sequences were done. A Bremer´s node (Bremer 1988, 1994) on the consensus ten most parsimonious phylogenetic trees was applied.

For the phylogenetic analysis, we calculated, (Castilla et al., unpublished data) a distance matrix for the COI sequence data yielded the following results: (1) the *P. stolonifera* COI sequence from the Australian specimen differed from those of the Chilean specimens by 0.34%, 0.51%, 0.68%, and 1.03%, respectively; (2) none of the 4 Chilean *P. stolonifera* specimens had identical sequences and the variation ranged between 0.17% and 1.03%; (3) a much greater difference in COI sequences, 18.81%, was observed between *P. stolonifera* from Australia and *P. stolonifera* from South Africa; and (4) a similar difference in COI sequences, ranging between 18.81 and 18.82%, was observed between *P. stolonifera* from Chile and *P. stolonifera* from South Africa. Other results were: (1) the two COI sequences for *M. ficus* were identical, and they differed from the other COI species sequences between 36.78 and 39.69%; (2) the COI sequence for *H. roretzi* differed from the other COI sequences between 24.35 and 37.59%; (3) the COI sequence for *A. humilis* differed from the other COI sequences between 22.76 and 38.63%; and (4) the COI sequence for *P. chilensis* differed from the other COI sequences between 23.26 and 37.98%.

We demonstrated, (Castilla et al., unpublished data) a very close genetic similarities between the *P. stolonifera* from Australia and *P. stolonifera* from Chile (of the same order of magnitude than those found in Chilean intrapopulations), and conversely large genetic differences between them and *P. stolonifera* from South Africa. Therefore, we propose to keep the specific name of *Pyura praeputialis* for the Australian and Chilean pyurid populations and *Pyura stolonifera* for the South African pyurids. According to these results, and observed genetic distances, the authors suggested that given the extensive range of geographical distribution of *P. praeputialis* in Australia and the extremely restricted one in Chile, the Australian population is more likely to be the ancestral stock. It appears plausible that the "piure of Antofagasta" represents a population of *Pyura praeputialis*, introduced from Australia and not a Gondwanaland relict.

The larval dispersal hypothesis (H2): Clarke et al. (1999) published information on the reproduction, early embryology, larval development and metamorphosis for *P. stolonifera* from Antofagasta. In the laboratory the mean active free-swimming period for the tadpole larvae (ranging from 1080 to 1380 mm) was of 2:35 h (SD= 0:59 h). This period was similar to what Anderson et al. (1975) reported for the active free-swimming tadpole larvae of *P. stolonifera* from Australia: 1:00-2:00. Griffiths (1976) reported that for *P. stolonifera* from South Africa the tadpole free-swimming period lasted "few hours". The short-lived larval phase of this taxonomic complex of *Pyura* species does not support the hypothesis of an oceanic large-scale epiplanktonic larval dispersal through drifting and thereby oceanic interchanges between the disjoint populations.

The juvenile/adult dispersal hypothesis (H3) and anthropogenic dispersal hypotheses (H4): Monniot & Bittar (1983), Monniot (1994), Monniot & Monniot 1994 and Clarke et al. (1999) have suggested that the Chilean population of *P. stolonifera* may have been recently introduced to the Bay of Antofagasta, via accidental anthropogenic or non-anthropogenic dispersal agents (i.e. ships' fouling, drifting objects). In fact, the results of the molecular genetic data discussed above suggests that the hypotheses of oceanic dispersal of adults, via rafting (H3), or the accidental anthropogenic (i.e. ship's fouling) dispersal hypotheses (H4) are both likely. We don't have evidence to reject either.

Aulacomya ater: a species with a long free-swimming planktonic larvae period

Trans-Atlantic disjoint distribution: The ribbed mussel, *Aulacomya ater*, is widespread (Fig. 4) on both Atlantic and Pacific coasts of South America, from El Callao (Perú) to Estrecho de Magallanes (Chile), from southern Brazil to Tierra del Fuego (Argentina), the Falkland Islands, and the Kerguelen Islands (Soot-Ryen 1955, 1959, Lozada 1968, Osorio & Bahamonde 1968, Cancino & Becerra 1978, Suchanek 1986, Linse 1999). Also, the species is found in the Atlantic coast of

Africa, from Rocky Points in northern Namibia to Port Alfred in the southeastern coast (van Erkom Shuring & Griffiths 1990).

The vicariance (H1) and the anthropogenic dispersal (H4) hypotheses: Fossil for *A. ater* in South America and South Africa shores are known from Pleistocene deposits (at least 2 million years ago) but not from the Pliocene deposits (Herm 1969, Pether 1997). However, the genera *Aulacomya,* represented by fossils of *Aulacomya anderssoni* (Zinsmeister 1984, Stilwell & Zinsmeister 1992) were reported from the late Eocene (approximately 42-33 mya) from La Meseta Formation (Antarctic Peninsula). *A. anderssoni* is also known from the late Eocene-early Oligocene from the San Julian Formation, Patagonia (Crame 1999). This suggests that the genera originated in the southern hemisphere, around Antarctic, during the Paleogene, and therefore, a vicariance explanation (H1) cannot be rule out. However, the above allows us to reject the anthropogenic dispersal hypothesis (H4).

The larval (H2) and the juvenile/adult dispersal (H3) hypotheses: As most of mussels, *A. ater* larvae are expected to spend two to four weeks in the free-swimming planktotrophic stage (Ramorino & Campos 1983, Suchanek 1986), so the larval dispersal hypothesis (H2) can be considered as a possible explanation for the disjoint geographical distribution of the species.

The ribbed mussel is usually found as a common component of nearshore kelp-bed communities and algae holdfasts in central Chile, subantarctic and Antarctic waters (Ojeda & Santelices 1984, Vásquez & Santelices 1984, Castilla 1985) and South Africa (van Erkom Shuring & Griffiths 1990). So, it is possible that juveniles or adults of the species could also be dispersed by kelp-rafting. Therefore, the vicariance hypothesis (H1), and/or the juvenile (H2) or adult hypothesis (H3) are plausible explanations for the present disjoint distribution of the species. The anthropogenic related hypotheses can be discarded as explanations for the present disjoint distribution of *A. ater*.

Concholepas concholepas: a species with a long–lived pelagic and planktotrophic larvae

Present, paleobiogeographical distributions and the vicariance hypothesis (H1): The present geographical distribution of the "loco" *C. concholepas* (Gastropoda: Muricidae), the only

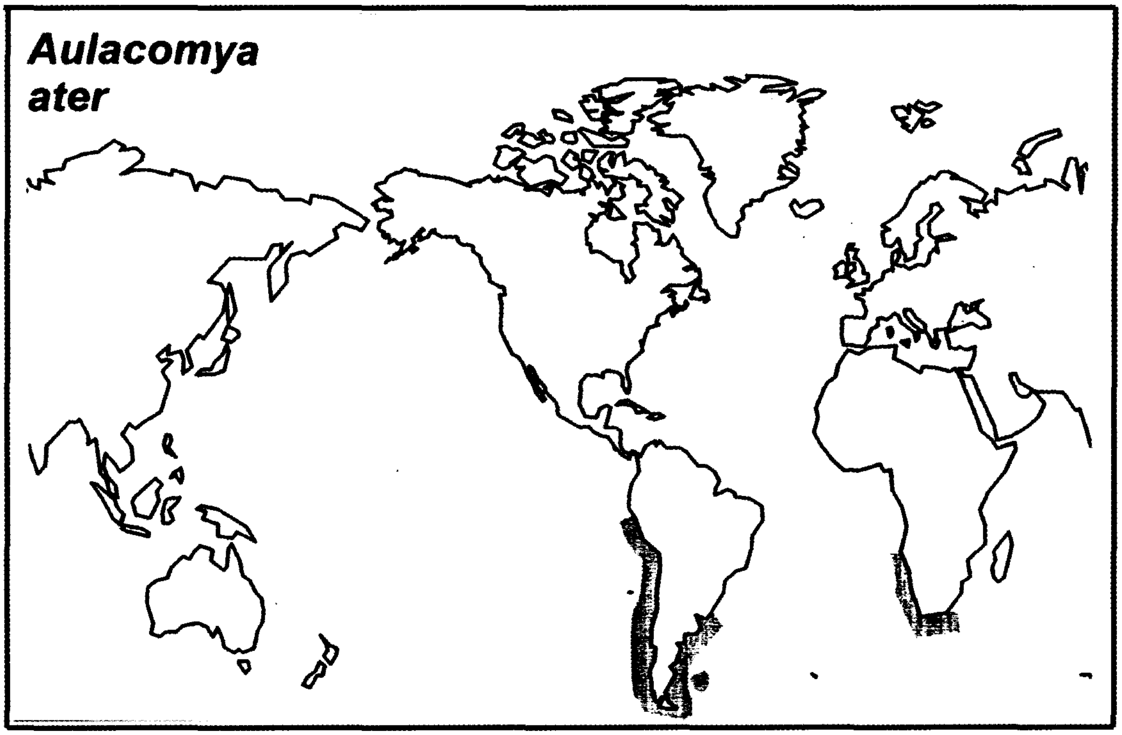

Fig. 4. Southern hemisphere extant disjoint geographical distribution of the bivalve *Aulacomya ater* (see stippled areas).

Distribución geográfica disyunta de las poblaciones actuales del bivalvo *Aulacomya ater* en el hemisferio sur (ver áreas achuradas).

living species in the genus, is restricted to South America, from Islas Lobos de Afuera in Peru, 6° 27′ S (Sánchez Romero 1973) to Cape Horn, Chile, and in the Juan Fernández Islands (Stuardo 1979) (Fig. 5). DeVries (1995) published information showing that there are 4 South American fossil species in the genus *Concholepas* Lamarck, 1801, extending from the middle Miocene up to the Holocene: (1) *C. ungis* DeVries, 1995 (middle Miocene, from Lomitas, Peru); (2) *C. kieneri* Hupe, 1854 (late Miocene to Pliocene, from Peru and Chile); (3) *C. nodosa* Moricke, 1896 (middle and late Pliocene, from Peru and Chile) and (4) *C. concholepas* (Bruguière, 1789) (Quaternary, in the Pleistocene and Holocene, from South Africa, Peru and Chile). The author suggested that the South American and South African species of *Concholepas* should be considered an endemic lineage and that 4 extra non-South American species originally referred to *Concholepas* (i.e. Beu 1970, Vokes 1972) are not closely related taxa. On the other hand, Vermeij (1998) described *Edithais* as a sister genus of *Concholepas* Lamarck, 1801, for the 4 non-South American Cenozoic fossils of muricids, designating *Concholepas drezi* Vokes, 1972 as the type species. The four *Edithais* species listed by Vermeij (1998) are: (1) *Edithais drezi*, Vokes, 1972 (=*Concholepas drezi*: Burdiglian, from the early Miocene, Chipola formation, Florida, North America); (2) *E. deshayesi* Rambur, 1862 (= *Concholepas deshayesi*: Helvetian, from the middle Miocene, Touraine, France); (3) *E. antiquata* Tate, 1894 (=*Concholepas antiquata*: Balcombian, from the middle Miocene, Victoria, Australia) and (4) *E. pehuensis* (= *Lippistes pehuensis* Marwick,1926: Tongaporutuan, from the late Miocene, Nort Taranaki, New Zealand).

In our opinion, the taxonomic and phylogenetic problems described for the genera *Concholepas* and *Edithais* complex have not yet been solved (see Discussion below). Nevertheless, in this paper we follow DeVries (1995) and Vermeij (1998) preliminary conclusions. In doing so, it appears that the fossil complex of species of *Edithais* have been found in the southern hemisphere in New Zealand (*E. pehuensis*, in the late Miocene) and approximately during the middle Miocene, in Australia (*E. deshayasi*); in France (*E. deshayesi*) and in Florida (*E. drezi*), and also around the middle Miocene. So far, no explanation about this rather odd paleobiogeographical distribution of *Edithais* species has been offered. Nevertheless, such odd paleo-biogeographical distributions are not uncommon. For example, fossil relatives to extant species of the genus *Lyreidus* de Haan, 1839 (Crustacea, Decapoda, Ranididae), with western North Atlantic and Indo-West Pacific

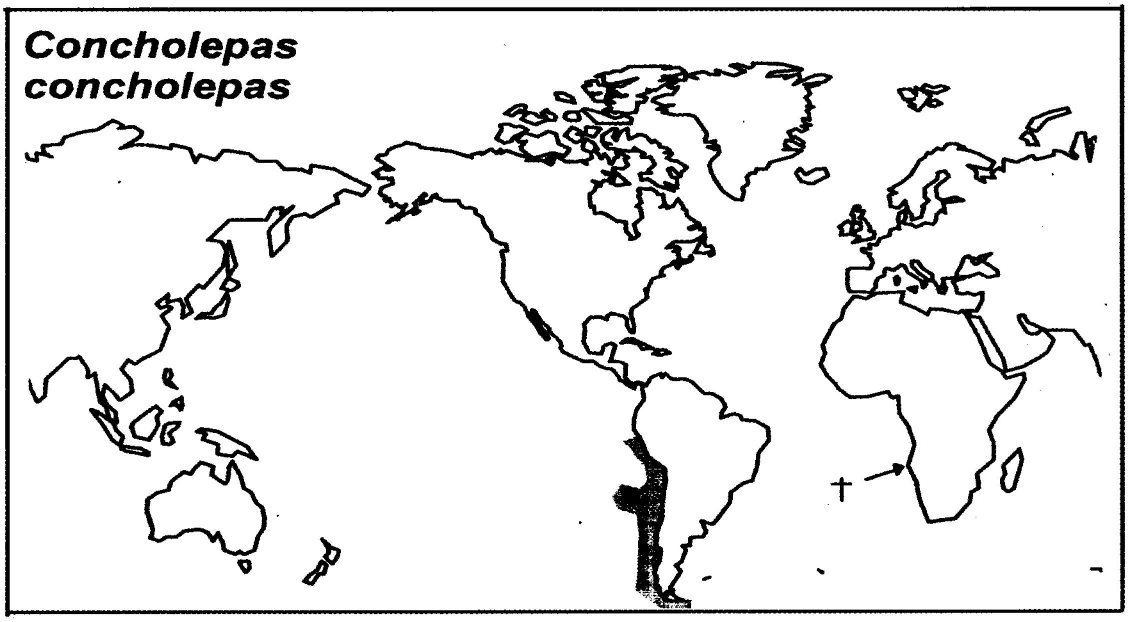

Fig. 5. Southern hemisphere extant disjoint geographical distribution of the gastropod *Concholepas concholepas* (see stippled areas and discussion in the text). The arrow indicates the presence of Pleistocene and Holocene fossils of *C. concholepas* in South Africa.

Distribución geográfica disyunta de las poblaciones actuales del gastrópodo *Concholepas concholepas* en el hemisferio sur (ver áreas achuradas y discusión en el texto). La flecha muestra la presencia de fósiles de *C. concholepas* en el Pleistoceno y Holoceno en Sud Africa.

distribution, can be traced as relict from Miocene related species showing an Atlantic-Tethyan distributional pattern, and from related species from the late Eocene in the southern hemisphere (see Fig 14, Feldmann 1992).

On the other hand, the South American *Concholepas* complex of species appears to conform an endemic lineage of fossils: *C. ungis* > *C. kieneri* > *C. nodosa* > *C. concholepas* in sites of Peru and Chile, from the middle Miocene up to the Holocene (DeVries 1995). Nevertheless, during the late Pleistocene and Holocene *C. concholepas* fossils showed a notorious disjoint paleobiogeographic distribution in the southern hemisphere, represented by fossils found in Peru-Chile and West South Africa-Namibia (Kensley 1985, De Vries 1995). According to Kensley (1985) the South African *C. concholepas* fossils are indistinguishable from those in South America. (J.C. Castilla examined the set of 5 South African *Concholepas* fossils, deposited in the South African Museum, Cape Town and agrees with Kensley, 1985). Furthermore, the South Africa fossil shells do not differ from the approximately 8,000-9,000 years archeological shell midden excavated *C. concholepas*, from central Chile (Jerardino et al. 1992).

Kensley (1985) suggested that the *Concholepas* South African fossils represented a chance short-lived pioneer population, probably established via larvae drifting from South America, following the West Wind Drift (see Shannon et al 1989, Schafer & Krauss 1995, Florenchie & Verron 1998, Stutzer & Krauss 1998 and Stramma & England 1999 for main oceanic drifting directions between the southern tip of South America and South Africa). However, this seems problematic as the Benguela current it is not a continuation of the West Wind Drift, but it is separated by the well marked Subtropical Convergence. Nevertheless, Shannon et al. (1989) has suggested that perturbations occurring in the Subtropical Convergence are likely to be important for the transfer of biota between the Southern and Atlantic oceans. In any case, according to present knowledge the vicariance Gondwanaland explanation for the amphiatlantic disjointed biogeographical distribution of this species must be rejected.

The epiplanktonic larval dispersal (H2) and the juvenile/adult dispersal (H3) hypotheses: *C. concholepas* shows internal fertilization (copulation); females cement egg capsules to rocky substrates year-round, with two peaks: January/February and May/July (Castilla 1979). Laboratory observations indicate that the number of larvae inside the capsules (no nutritious eggs present) varies between 600 and 14,000, depending on the capsule size. Hatching time ranged between 36-128 days (Gallardo 1973, Castilla & Cancino 1976). Spontaneously eclosed *C. concholepas* veliger larvae cultured in laboratory conditions, fed on monospecific cultures of microalgae, grow from an initial protoconch shell length of approximately 250 mm to near 1700 mm in 111-124 days (DiSalvo 1988). According to DiSalvo & Carriker (1994)´s laboratory experiments the metamorphosis of competent *C. concholepas* larvae is slow and the modification of its veliger behavior, from a long-lived natatorial independent planktonic stage, to a benthic slow crawling, shell-boring carnivore individual, can be delayed for hours, days or weeks before a suitable settling site is identified and the teleconch starts to form. On the contrary, our own experience (laboratory conditions) with competent *C. concholepas* veligers collected from the plankton in central Chile (P. Manríquez personal comm.) indicates that competent larvae collected from the superficial plankton (once the protoconch of the larva reaches approximately 1,800-1,900 mm) readily settles within minutes to a few hours in presence of settlement surfaces such as glass, plastic, mussel and loco's shells, granitic rock or on substratum offered at the water surface. Laboratory cultures indicate that after 3-month period juveniles of *C. concholepas* reach 10-20 mm maximum diameter of the peristome (DiSalvo 1988).

Undoubtedly, after several months of free-swimming planktonic life, and with the possibility of a delay in the metamorphosis and settlement (see above), this species is a candidate to advocate larval dispersal through planktonic drifting in the southern hemisphere (i.e. Kensley 1985, Pether 1997). Nevertheless, taking into account: (a) the characteristics of the planktonic larvae of *C. concholepas*, (b) the predominant surface oceanic circulation in the area and (c) the unlikeness that the South African-Namibian fossils represent a relict population of the late Cretaceous that included the west and south-west coasts of the separating masses of South America and Africa (Kensley 1985), it appears odd that so far only 2 fossil records of *C. concholepas* have been located in South Africa (-and none for the 3 South American former middle and late Miocene *Concholepas* paleo-species-). Probably *Concholepas* larvae drifting along the West Wind Drift could not be the only (and/or the most important) mechanism for dispersal of extant or paleo populations of the loco. This view would contradict the prevailing hypothesis about the mechanisms behind the disjoint paleogeographical distribution of *C. concholepas* in the southern hemisphere. We feel that such a mechanism for dispersal should include not only the larvae characteristics of the species, but also the potential for adult/juvenile dispersal through drifting agents and the biological characteristics of the snail such as its trophic ecology.

The biology and the trophic ecology of *C. concholepas* was reviewed by Castilla (1982, 1988, 1997b). Castilla (1999) summarized the ecological role of species such as the loco in the rocky intertidal of central Chile. The species is a carnivore, limpet-like, slow moving muricid, preying predominantly on mussels, barnacles and ascidians (DuBois et al. 1980). In its early life stages (less than approximately 20 mm) *C. concholepas* is a shell-boring species (Méndez & Cancino 1982). Later on develops more efficient prey-attacking behavioral strategies (Castilla et al.1979). Laboratory and field observations indicate that for *Concholepas* to perform successfully any of its prey-attacking strategies, the individual needs to be strongly attached to the substratum (Castilla et al. 1979). Therefore, from the trophic point of view *Concholepas* differs substantially from the filter feeders (bivalves and tunicates) analyzed in this paper.

Hereby we suggest that *Concholepas* larvae drifting via the West Wind Drift might not be an efficient dispersal agent, as could be the case for the mytilid *A. ater*. Otherwise, we don't see the reason why more fossil or present species of *Concholepas* have not been found in the West Coast of Africa, as for example it is the case of *A. ater*. Instead, we suggest that *Concholepas* egg capsules may raft by themselves or that adult or juvenile *Concholepas* specimens may be rafted on solid/consolidated substrates, such as the holdfast of kelps. Nevertheless, these dispersal mechanisms make the transoceanic crossing between the tip of South America and Africa less likely (Nelson 1994). There are evidences for the recruitment and establishment of juvenile and adult *Concholepas*, mussels, barnacles and ascidians inside the holdfast of the South American kelp *Lessonia nigrescens* (Cancino & Santelices 1981, 1984, Vásquez & Santelices 1984). Newly settled individuals of *Concholepas* inside these holdfasts encounter a permanent solid substrate and abundant prey items (mussels, barnacles, ascidians, crabs etc). If this is so, *C. concholepas* may be kelp-rafted throughout *Lessonia* or others macroalgae across oceanic routes (but see Nelson 1994). Furthermore, we suggest that there exist the possibility that the fossils of *C. concholepas* excavated in South West Africa-Namibia shores may not represent a short-lived pioneer population, started from larvae transported from Chilean waters, but that they may represent a case(s) of rare event of juvenile/adult group of *Concholepas* arriving to the western African coast via some consolidated drifting substrata. The scarcity of *Concholepas* fossils reported from South West Africa-Namibia shores, which presents rich oceanographic upwelling characteristics similar to those of the Humboldt Current System in Chile and Peru, suggests that the arrival of *Concholepas* to that continent may represent a rare/unusual dispersal event. The other possibility is that there is not enough paleo excavations in the west coast of South Africa. Nevertheless, this is unlikely since the African coast from which *Concholepas* fossils were discovered, is extensively known from its paleo record due to diamond mining operations (Kensley 1985).

GENERAL DISCUSSION AND FUTURE DIRECTION

With reference to the southern hemisphere extant and paleo biogeographical disjoint distribution of the 5 species discussed: (a) the vicariance (H1) hypothesis can be almost completely discarded for *O. chilensis, Pyura stolonifera* taxonomic complex and *Concholepas concholepas.*. This is no so for *G. trapesina* and *A. ater*. (b) The epiplanktonic larval hypothesis (H2) appears as a likely explanation for *A. ater* and less so for *C. concholepas*. (c) The juvenile/adult dispersal hypotheses (H3) by rafting, alone or in conjunction with other hypotheses, can not be rejected for the 5 species analyzed and (d) the anthropogenic dispersal hypothesis (H4) is hereby rejected for *O. chilensis*, *A. ater* and *C. concholepas*.

Vicariance hypothesis (H1): The southern origin of *G. trapesina* and *A. ater,* associated to the evolution of the Antarctic continent, has been well documented in the literature (see Zinsmeister 1984). Previous to the discover of the occurrence of both genera in the upper Eocene at La Meseta Formation, Seymour Island (Antarctic Peninsula), the oldest known occurrences were from the late Pleistocene of New Zealand (*Gaimardia*) and South America and South Africa shores (*A. ater*). This lead to Fleming (1963) to suggest that some Neoaustral taxa (southern Pacific taxa that first appear along the southern circum-Pacific during the late Neogene) originated from tropical or subtropical stocks, that during the late Neogene entered the southern oceans from Australasia, South Africa, or South America. According to this author these immigrants were then distributed around the southern hemisphere by the West Wind Drift . However, the Eocene occurrence of *Gaimardia*, *Aulacomya* and other bivalves

(*Gomphina* and *Eurhomalia*) around Antarctic demonstrates that these taxa originated around the Antarctic and suggests that not all Neoaustral taxa followed the Flemming's proposition. On the contrary, according to Zinsmeister & Feldman (1984) and Zinsmeister (1984), derived Neoautral taxa originated in the Antarctic moved northward into the lower latitudes during the late Miocene, at the onset of markedly cooler conditions in the southern hemisphere (Neogene) and eventually dispersed along the West Wind Drift. Thus, the actual geographical distribution pattern exhibited by *Gaimardia* and *Aulacomya* may reflect a complex history of vicariance, geographical range shifts and dispersal events.

Epiplanktonic larval (H2) vs. juvenile/adult dispersal (H3) hypothesis: The disjoint biogeographical transoceanic distribution is the common characteristics of the five selected species, which present different development strategies, ranging from strictly brooder (*G. trapesina*) to a several months long-lived free-swimming planktonic veliger (*C. concholepas*). This permits to postulate that the transoceanic disjoint distribution is not only determined by the larval dispersal capacity as expected (Mileikovsky 1971, Scheltema 1978, 1986a, Crisp 1978, Jablonski 1986), but also other mechanisms must be considered.

The planktonic larval has been generally assumed to cause most of the dispersal of these organisms; such larvae can be routinely transported over 10s to 1,000s of kilometers during their pelagic development (Crisp 1958, Ó Foighil 1989), and are even capable of transoceanic dispersal (Scheltema 1971, Pechenik et al. 1984). For instance, among central Pacific islands it has been proposed that the colonization has been accomplished by means of planktonic larval dispersal (using information from 210 plankton tows collected over a period of 26 years, between 1953 and 1979; Scheltema 1986b). A comparable collecting effort is lacking in the southern hemisphere. On the other hand, it has been proposed that species with planktotrophic larvae have greater geographic range (for a review, see Ó Foighil 1989), but this prediction does not explain the disjoint transoceanic distribution of at least three of the five selected species: *G. trapesina*, *O. chilensis* and *P. praeputialis*, nor other species (Jokiel 1984, 1989, Jackson 1986, Johannesson 1988, Safriel & Hadfield 1988, Ó Foighil 1989). Johannesson (1988) discussed the decreasing density effects that mortality and diffusion can produce on larvae with extended planktonic larvae period, able to cross-oceans. Furthermore, the author argued that if the founder group belongs to a species with direct development or which produces very short-lived planktonic larvae, the low mobility of all life-stages will maintain the population within a restricted area so that mates will be likely to encounter each other. The opposite may occur to a species with long-lived planktonic larvae, such as *C. concholepas*. This can be considered as an alternative explanation for the reduced success of a *C. concholepas* founder populations across the southern oceans.

Rafting is an alternative dispersal mechanism potentially available for species without or with reduced larval development time, which has been proposed as more effective (100s to 1,000s of km) than planktonic larval development (Jokiel 1984, 1989, Highsmith 1985, Jackson 1986, Johannesson 1988, Ó Foighil 1989, Ó Foighil et al. 1999). Fell (1962) using inferential evidence based on species of benthic echinoderms showing southern circumpolar ranges, proposed that individuals adhered to macroalgae might complete trans-Pacific oceanic dispersal by means of the Antarctic Circumpolar West Wind Drift, moving unidirectionally from west to east. This mechanism has also been suggested to explain the eunicemorph polychaete annelids distribution in Antarctic and subantarctics areas (Orensanz 1990), and for *O. chilensis* thought the northern deflection of the West-Wind Drift along the coast of Chile, known as the Humboldt Current (Buroker et al. 1983) . Rafting by macroalgae (kelp rafting) has been shown to occur in *Gaimardia trapesina* (Helmuth et al. 1994). The authors suggested that this mechanism probably accounts for the widespread distribution of the species. As *G. trapesina* is found in rafts and also associated to kelp-beds and kelp holdfast (Castilla 1985), also other species associated to kelp beds may be subjected to kelp rafting. According to our field experience, we predict that in the southern Atlantic it may be possible to discover juvenile/adult specimens of *A. ater* and *C. concholepas* being rafted by kelps holdfast of *Durvillaea antarctica* or *Macrocystis pyrifera* (Ojeda & Santelices 1984, Castilla 1985). The rafting via *L. nigrescens* probably is not as likely as via *Durvillea* or *Macrocystis*, because the *Lessonia's* plants have solid non-buoyant blades and stipes (Nelson 1994). Nevertheless, according to the time elapsed for drifting kelps to become negatively buoyant (particularly in open ocean situations, see Edgard 1987) we also predict that those probabilities will increase between relatively short coastal-oceanic distances within the southern tip of South America (i.e. between the Beagle Channel or the Magellan Strait and the Falkland Islands), and that they will decrease over extensive open oceanic routes. It might be an extremely unlike event for a drifting kelp to cross the oceanic distance separating the southern tip of South America and the South West coast of South Africa, particularly for a carnivore species. This may also explain the scarcity of founder populations and fossils of *Concholepas* reported for the west coast of Africa-Namibia. Since the present populations of *C. concholepas* are abundant in Chile, and *A. ater* in Chile and Argentina, future analysis on kelp drifting associated invertebrate fauna in the high latitudes of the southern Atlantic ocean may help to enlighten cases as the above. Dispersion by infrequent chance rafting events have been suggested for the occurrence of South African and Indian late Miocene fossil taxa of the Genera *Bullia* (Gastropoda: Nassariidae) (Allmon 1990) and also for the occurrence of subfossil shells of three locally extinct molluscs: *Tawera philomela*, *Sassia philomelae* and *Pareuthria fuscata,* with Subantarctic affinities, found in the Benguela region off southwestern Africa (Pether 1993).

Rafting on pumice was suggested by Ó Foighil et al. (1999) as the more probable dispersal mechanism for the trans-Pacific range extension of *O. chilensis.* According to Jokiel (1989) major pumice rafting episodes frequently result from volcanic eruptions, so volcanism continually injects large volumes of floating pumice in the ocean basins. We think that the broader significance of pumice as an invertebrate transoceanic transport mechanism has been overlooked. For example, pumice from the 1962 submarine eruption (see Fig. 4 from Jokiel 1989) in the South Sandwich Islands drifted to southern Australia shores, to New Zealand, South America and Africa and probably dispersed over the entire world ocean. However, we do not have direct evidence for tunicates (*P. praeputialis*), oysters (*O. chilensis*) nor the other species analyzed in this paper, being found on pumice. Furthermore, related drifting mechanism could be linked to other natural drifting materials, such as driftwood, charcoal, seeds (coconut, cycad, mangrove) and heavily fouled floating nautilus shell, where it has been observed corals, calcareous algae, fleshy algae, oysters, barnacles, polychaetes, forams, bryozoans, tunicates, anemones and teredos (Jokiel 1989). These information reinforce the suggestion made by Helmuth et al. (1994) that dispersal by rafting (via macroalgae, pumice or floating debris) can occur over geological and ecological time scales.

Anthropogenic dispersal hypothesis (H4): Anthropogenic passive and active transportation of marine flora and fauna is an emergent and growing mechanism for NSBI dispersal, that is changing the species composition of many marine communities (Carlton 1987). Among the major mechanism for this kind of dispersal are shipping (fouling and ballast water) and the transportation of commercial shellfish and fish. Tunicates are among the species of invertebrate which are most readily transported by ships as fouling organisms (Monniot & Bitar 1983, Carlton 1987, Monniot & Monniot 1994) or in ballast seawater (water taken in a port and released on ports of call, Carlton & Geller 1993). Both dispersal agents may explain, through the species invasion mechanism, the particular disjoint and odd geographical distribution of *P. praeputialis* in Australia (along 1,000´s of km of coast) and in Antofagasta, Chile (along only 70 km of coast; Clarke et al. 1999, Castilla et al. 2000). Ó Foighil et al. (1999) suggested that careful analysis of Chilean taxa with reduced or absents pelagic larval development, including ascidians, may reveal additional cryptic rafted immigrants from New Zealand.

FUTURE DIRECTIONS

We have shown the utility of incorporating techniques of molecular genetics in the study of marine populations, which may provide evidence for temporal frameworks for species divergence, and phylogenetic reconstruction (see *O. chilensis* and *P. stolonifera* taxonomic complex sections). We propose that the incorporation of this kind of research is needed no only to advance in the phylogenetic relationships and systematic of the species analyzed here, but also in the genetic structure of donors and receiver populations.

According to studies in progress in our laboratory the taxonomic and evolutionary problem of *Concholepas* and *Edithais* as reported by DeVries (1995) and Vermeij (1998), has not yet been solved. For instance, along the geographical gradient of extant *C. concholepas* (more than 7,000 km of coast line and oceanic islands) there is much more morphological variation than what DeVries (1995) and Vermeij (1998) used to arrive to their conclusions regarding: thickness, the sunking of the spire below adapical margin of the outer lip, sculpture, and the presence-absence of a parietal tooth (Manríquez and Castilla, personal observations). In the future we will incorporate *Concholepas*´s shell morphological characteristics to describe the range of morphological variation along its geographical range. This, together with reported genetic differences between populations (Guiñez et al. 1992) may help to understand the geographical distribution of the species.

With regards to the population genetic structure of *O. chilensis*, even when Ó Foighil et al. (1999) have confirmed the results of Buroker et al. (1983), we suggest caution if the findings are going to be extrapolated to the natural populations. In fact, Buroker et al. (1983) in their analysis used 36 Chilean oysters obtained from oysterfarm facilities at Coquimbo (29° 53' S, 71° 18' W), out of the natural range distribution of the species. They did not report from which natural bed the oysters came from. So, the reported putative founder effect occurring in the Chilean oyster "population", with a lower level of genetic variation than the New Zealand oyster population, may be explained because a small effective population number of oysters was used, which were obtained from a farming facility. Guiñez & Galleguillos (1985) reported evidence for population genetic differentiation of oysters within their natural range of distribution in Chile (also see Toro & Aguila 1996). This suggests that even when the species may have arrived recently (see *O. chilensis* section) to Chile, it has experienced genetic changes, which could be due to selection post-settlement (Guiñez & Galleguillos 1985, Toro & Vergara 1995). Furthermore, Fujio et al. (1983) described the genetic variability of oysters in New Zealand (same locality as Buroker et al. 1983) and reported 67% polymorphic loci and 21.6% of heterozygosity. This is contradictory from the 27.6% polymorphic loci and 6.7% heterozygosity reported by Buroker et al. (1983) for the same species. We have evidences for even lower levels of polymorphism and heterozygosity from oysters collected in the Chilean Pullinque oyster bed (population protected by law); than those reported by Buroker et al. (1983). Therefore, we suggest that more genetic analyses are needed to gain a comprehensive understanding of the colonization dynamics process and on the phylogenetic and systematic relationships of *O. puelchana* and *O. chilensis* (Harry 1985, Carriker et al. 1994, Toro 1995).

ACKNOWLEDGMENTS

The paper is dedicated to the late Professor Patricio Sánchez Reyes, teacher, tutor and friend. We are especially grateful to Dr. J.M. (Lobo) Orensanz for constructive criticisms that permitted to improve importantly this paper. The paper is part of the Cátedra Presidencial en Ciencias awarded to J.C. Castilla in 1997. We appreciate suggestions made by Dr. M. Fernández. Art work by M. Bobadilla.

LITERATURE CITED

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Invited Editor J.C. Castilla