

Fifty years from the publication of the first two papers on Chilean rocky intertidal assemblages: Honoring Professor Eric R. Guiler

Cincuenta años desde la publicación de los dos primeros trabajos sobre el intermareal rocoso de Chile: Homenaje al Profesor Eric R. Guiler

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Resumen.- En este trabajo, reviso y rindo honor a los principales hallazgos científicos del investigador australiano, Profesor Eric R. Guiler, quien en 1955 visitó las costas de Chile y realizó trabajos pioneros sobre zonaciones bióticas intermareales. Producto de ello publicó los dos primeros trabajos sobre las comunidades intermareales rocosas de Chile norte y central: Guiler 1959a, b. Además, destaco sus principales observaciones e hipótesis sobre el funcionamiento de estas comunidades en relación con sus estructuras y dinámicas. En particular, resalto las observaciones realizadas por Guiler al interior de la bahía de Antofagasta y las contrasto con trabajos experimentales de terreno recientes. Finalmente, destaco las extensas contribuciones en esta línea de investigación realizadas por investigadores chilenos y su elevado reconocimiento internacional.

Palabras clave: Primeros trabajos publicados, ensambles, especies intermareales, Chile central y norte

Abstract.- In this paper I review and honor the scientific rocky intertidal findings made by the Australian investigator Professor Eric R. Guiler, who visited Chile in 1955. He pioneered this line of research in the country and published the first two papers on the Chilean rocky intertidal biotic zonation for northern and central Chile: Guiler 1959a, b. I remark Guiler's main observations and hypotheses about the structure and dynamics of these systems. I highlight the observations made by Guiler inside the Bay of Antofagasta and contrast them with recent experimental ecological work carried out inside this bay. Finally, I refer to the extensive and significant contributions made by Chilean researchers in this line of research and international recognition.

Key words: First published papers, intertidal species, assemblages, central and northern Chile

Introduction

Professor Eric R. Guiler, University of Tasmania, Australia, with the support of the Rockefeller Foundation and the Royal Society of Tasmania, visited the coast of central and northern Chile in the summer of 1955. He carried out intertidal observations and worked on rocky intertidal biotic fringes, comparing Chilean intertidal patterns with those described for other latitudes. The visit was supported by Professor Parmenio Yañez, Head of the Estación de Biología Marina de Montemar, Universidad de Chile at Viña del Mar. Guiler participated in an oceanographic expedition to northern Chile, where he visited four ports on board of the Corvette Papudo under Commander P. Woolvett. Following the trip he remained at Montemar, central Chile, and carried out a series of observations on rocky intertidal biotic zoning. As a product of this work Guiler published two papers on northern and central Chile rocky shores: Guiler (1959a,

b). To the best of my knowledge these are the first two comprehensive papers published about this biotic system for Chile.

This work celebrates the 50 year publication of these papers and honors the work carried out by Guiler in Chile, under the frame of the 60 years celebration of the Revista de Biología Marina y Oceanografía. I revisit Guiler's papers and highlight key observations about the rocky shore systems in Chile, particularly those related with my own lines of research in Antofagasta and central Chile, about the structure and dynamics of rocky intertidal systems.

Professor Eric R. Guiler: A marine ecologist from the Department of Zoology, University of Tasmania, Australia and the development of rocky intertidal ecology in Chile

Early, in the decade of the 1950's, Professor Guiler started publishing on rocky intertidal biotic fringe zoning patterns in Tasmania (Guiler, 1950, 1951a,b, 1952a,b,c, 1953, 1955).

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This, undoubtedly, within the scientific framework developed by rocky intertidal pioneer ecologists as Coleman (1933), Stephenson (1936), Chapman (1938) and Doty (1946). Stephenson & Stephenson (1949) synthesized our early knowledge about the universal features of biotic fringes between tidemarks of rocky coasts. Initially, the causes behind the biotic intertidal patterns were understood almost exclusively based on physical factors such as the tides, desiccation, isolation, wave splash, exposition or the geographical orientation of the shores. These works were continued, among others, by Lewis (1955), Pérès & Picard (1955), Doty (1957), Southward (1958) and Guiler (1960). On turns, in the 1960 and early 1970's two rocky intertidal researchers organized and synthesized the information and contributed to the further development of this line of research: Lewis (1964) and Stephenson & Stephenson (1972). Furthermore, rocky intertidal experimentalists appear in scene: a work represented by the papers of Connell (1961) and Paine (1966) (although many more rocky intertidal field experimentalists contributed to this approach). Now, rocky intertidal biotic interactions were exacerbated, but also combined with physical forces. Indeed, new findings in these ecological systems made a significant contribution to the development of general ecological theory (see Paine 1994).

In Chile, during the 1970 and 1980's there was an active production of rocky intertidal papers dealing with species assemblages and the ecology of community structure and dynamics. Furthermore, this research activity translated in the 1990 and 2000 into an explosive line of rocky intertidal experimental (manipulative) research in the country, overwhelmingly done by Chilean researchers. This was followed by creation (on top of the Estación de Biología Marina at Montemar Research Station, Universidad de Chile) of two new coastal marine stations and coastal reserves: The Estación Mehuín in southern Chile (Universidad Austral de Chile) and the Estación Costera de Investigaciones Marinas, Las Cruces in Central Chile (Pontificia Universidad Católica de Chile). A sample of those publications are: Alveal (1971), Alveal *et al.* (1973), Castilla (1976a,b), Romo & Alveal (1977), Viviani (1979), Castilla & Bahamonde (1979), Santelices (1980, 1981), Santelices *et al.* (1980, 1981), Montalva & Santelices (1981), Oligier & Santelices (1981), Castilla (1981, 1985), Castilla & Moreno (1982), Moreno & Sutherland (1982), Moreno & Jaramillo (1983), Jara & Moreno (1984), Moreno & Jara (1984), Moreno *et al.* (1984, 1986), Santelices & Ojeda (1984), Ojeda & Santelices (1984a,b), Castilla & Durán (1985), Paine *et al.* (1985), Bahamondes & Castilla (1986), Castilla & Paine (1987), Durán & Castilla (1989) (also see reviews by Santelices 1991, Castilla 2000). In this paper I am not summarizing the major Chilean research contributions to this line of research done from the middle 1990's to present.

To discover and understand the dynamics of biotic zoning fringes in Chilean rocky shore systems has been for me a fascinating scientific trip. Therefore, it has not been difficult, even though I did not meet Professor Guiler, to imagine his excitement in the rocky shores of this country more than 50 years ago. Also, it has been easy to understand the support of the Rockefeller Foundation to Guiler's trip to Chile, since the same Foundation enthusiastically supported Patricio Sánchez Reyes (P. Universidad Católica de Chile; Castilla & Santelices 1999) to develop marine coastal research and the training of young scientists in Chile (1960-1967). Among the important lessons in this area of research in Chile we have learned along these years is that the development of basic, elemental and solid science, has truly served the country and society, not only via the development of new ideas and the test of ecological hypotheses (as examples, see Santelices 1991, Power *et al.* 1996, Castilla 2000), but for the science of marine conservation and the rational use of marine coastal resources (Castilla *et al.* 1998a, Castilla & Fernández 1998, Castilla & Gelcich 2008).

Professor Guiler in Chile: Oceanographic expedition to northern Chile

In the summer of 1955 Professor Guiler, on board of the Papudo Corvette, left Valparaíso, as part of a northern Chile (Valparaíso - Arica) oceanographic expedition organized by the Estación de Biología Marina de Montemar and financed by the Corporación de Fomento de la Producción (CORFO), in the company of Professor P. Yañez. The Papudo, in its expedition made short stops at four ports: Coquimbo (20th February), Antofagasta (22nd February), Iquique (25th February) and Arica (26-28th February), and in its return to Valparaíso at Antofagasta (2nd March). The main objectives of the expedition were to obtain oceanographic information, but Guiler went ashore and visited and worked in the rocky shores around the mentioned ports. His paper, Guiler (1959a), is the product of those visits. He published, for the first time, comprehensive descriptions of the biotic assemblages in those rocky shores, as well as their biotic zoning patterns. Further, in his paper he reviewed and commented the known literature on Chilean oceanic currents, winds, salinity and tides of northern Chile, making comparisons with the information at hand from Peru and other latitudes.

Professor Guiler in the Antofagasta's intertidal rocky shore: Six key observations

As a result of my own scientific work on the structure and dynamics of rocky shores inside the Bay of Antofagasta (Castilla & Guiñez 2000, Castilla *et al.* 2000, 2004) I have decided to concentrate the analysis of Guiler



Figure 1

Dense matrices of *Pyura praeputialis* in the rocky intertidal of Antofagasta (low tide) A = at AAA platforms (see text); B = at El Way platforms. C and D = formation of biofoam in intertidal pools and rocky shores on top of *Pyura* matrices (Castilla *et al.* 2007)

Matrices densas de *Pyura praeputialis* en el intermareal rocoso de Antofagasta (marea baja). A = en plataformas de AAA (ver texto); B = en plataformas de El Way. C and D = formación de bio-espuma en pozas intermareales en los roqueríos sobre las matrices de *Pyura* (Castilla *et al.* 2007)

(1959a) paper on six observations he made when working on the rocky intertidal platforms inside this bay. These observations and hypotheses formulation (made more than 50 years ago) on the structure and possible dynamic interactions regarding the unique intertidal biotic system inside the Bay of Antofagasta, have always amazed me. They were done just based on a few tidal excursions. Guiler's observations were keen and the questions asked very inquisitive. Guiler included a photograph of the rocky shores he worked at Antofagasta (22nd February, 1955), the so called Playa Blanca, opposite to the Artillery Barracks, beyond the southern end of the town (at that time), on the road to the Automobile Club of Antofagasta (Asociación Automovilística de Antofagasta, AAA). In this paper I am including four photographs taken in the

Antofagasta rocky intertidal shores, close to the sites worked by Guiler (Fig. 1A, B, C, and D). In my view the following six observations, descriptions and hypotheses, are worth to be distinguished from Guiler (1959a) paper:

Observation 1. On describing the rocky intertidal zonation at Antofagasta, Guiler (1959a, pp. 46-47) highlights the unique presence of a dense intertidal covering of an ascidia (Fig. 1A, B) and a red turf coralline: *Pyura-Corallina* belt, that replaces the traditional intertidal barnacle belt present in other intertidal localities in Chile (we can deduce that he also referred this covering as replacing the mussel intertidal belt, see p. 49). He wrongly identified the ascidia as *Pyura chilensis*. The species was rightly identified, more than 55 years later, by Castilla *et al.* (2002a), as *Pyura praeputialis*. Further,

Guiler (1959a) indicates that the ascidia may be considered as an intertidal indicator of warm water conditions, pointing out that in warm temperate seas in Australia, an ascidia as this one, also forms intertidal extensive and ecologically very similar belts. Indeed, Castilla *et al.* (2002a) based on DNA analyses showed that the Australian and the Antofagasta intertidal *Pyura* were the same species, most probably having arrived to the Antofagasta Bay from Australia. The pronounced presence of this biotic belt in Antofagasta along miles of the rocky shore, and its inland (supralittoral) extension was also highlighted by Guiler. The uniqueness in Chile, of this intertidal belt formation scheme, found exclusively inside this bay, powerfully called Guiler's attention.

Observation 2. Guiler (1959a) described how the Antofagasta *Pyura* individuals were closely (Fig. 1A) united into coalesced masses offering strong resistance to wave action, and how the space between the ascidians and the rock offered shelter and habitat for more delicate organisms: which it may be interpreted as suggesting an intertidal increase of microhabitats and local biodiversity. He indicated that species such as the loco *Concholepas concholepas*, chitons and key-hole limpets were fairly common in the infralittoral fringe as well as under the *Pyura* beds. Cerda & Castilla (2001) and Castilla *et al.* (2004) showed that indeed the Antofagasta *Pyura* matrices generated a new tridimensional microhabitat that enhances local invertebrate biodiversity (and biomass) inside the bay, as compared with sites from outside the bay.

Observation 3. Guiler (1959a) based on preliminary meteorological observations in the port of Antofagasta concluded that there were physical factors inside the bay that produced somewhat warmer conditions at sites on either side of the bay. This is a remarkable observation, since recently and using remote sensing techniques, it was demonstrated the existence, inside the Bay of Antofagasta, of one of the strongest and more persistent upwelling shadows occurring along the southeastern Pacific coast (for upwelling shadows see Graham *et al.* 1992, Graham 1993, Graham & Largier 1997), and which translates in an increase of the temperature of the bay's water of up to 2-3°C. Moreover, Escribano & Hidalgo (2001) and Castilla *et al.* (2002) demonstrated the existence of cyclonic circulation inside the Bay of Antofagasta and suggested this as a retentive mechanism, which may help plankton retention, and leading to spatial variation in recruitment of intertidal invertebrates (Lagos *et al.* 2008)

Observation 4. One of the most important observations made by Guiler (1959a), during the two days visit to Antofagasta's rocky shores, was the description of the shore being covered with an abundant white foam: 'which

acts as a very efficient protection from the sun and filled the clefts and gulley in the rocks and covered all the shore from top of the barnacle belt down...and wave actions did not disturbed it'. Guiler included a photograph (22nd February, 1955) illustrating the white foam deposited on intertidal rocks in front of the Artillery Barracks. Interestingly, Castilla *et al.* (2007) re-described the existence of abundant biofoams on the rocky shores of Antofagasta (Fig. 1C, D), resulting from the synchronous mass spawning of *Pyura praeputialis*, both male and female gametes, into aerated and turbulent inshore waters. It was experimentally demonstrated that *Pyura* gametes decreased the surface tension of the water, inducing the formation of the biofoam, which enhanced *Pyura* fertilization success and larval retention on the rocky shore inside the bay.

Observation 5. Guiler (1959a) observed that the *Pyura* belt extended from the midlittoral down to the infralittoral fringe, commenting that in other localities in northern Chile the infralittoral fringe is dominated by the large Pheophyceae *Lessonia nigrescens* (while in central Chile is also present *Durvillaea antarctica*, 'cochayuyo'). He offered two explanations for this species replacement: a) That in the Bay of Antofagasta there exist some set of local conditions which do not favor the growth of large Pheophyceae in the infralittoral fringe; b) That some catastrophe befell these algae (it may have been El Niño?) and that they were replaced in the shore by the ascidians, which became so numerous that the algae were unable to compete in their accustomed habitat. Guiler specifically argued about the possibility of *Pyura* outcompeting *Lessonia* (also see Paine 1986). So far, our own observations (unpublished results) indicate that *Lessonia* kelps transplanted (see *Lessonia* transplanting techniques in Correa *et al.* 2006) from sites outside the Bay of Antofagasta to intertidal rocks inside the bay, show a significant reduction in growth, survival and photosynthesis, expressed as enhanced photoinhibition and low recovery capacity, after light stress; when compared with *Lessonia* kelps simultaneously transplanted outside the bay. In Antofagasta, we have not yet explore direct competition interactions between *Pyura* and *Lessonia*.

Observation 6. Obviously, the unique Chilean-Peruvian muricid gastropod *Concholepas concholepas* did not escape Guiler's curiosity. He described its presence in the rocky infralittoral and sublittoral fringes of Antofagasta and recognized that as the species approaches the northern ends of its range (northern Chile and the border with Peru) decreases in size, as compared with central and southern Chile specimens. Nevertheless, ecologically, he mistakenly thought that *Concholepas* was

an algae grazer and that in Chile this mollusk appeared to fill the niche of *Haliotis*. Nevertheless, it has to be taken into account that only about 25 years later Castilla and collaborators produced solid evidence for the carnivore status of *C. concholepas* (Castilla & Guisado 1979, Castilla *et al.* 1979). Furthermore, it took another 15-20 years to demonstrate the key-stone species ecological role of *Concholepas* in Chilean rocky shores (Castilla & Durán 1985, Power *et al.* 1996, Castilla 1999).

Professor Guiler in central Chile rocky shores: Montemar and nearby sites

I have been unable to obtain information about Guiler's stay in Montemar, even the time he worked at the Marine Biological Station of Montemar, one of the first marine coastal stations established in South America in 1948 (including an intertidal reserve zone, Castilla 1996). Professor Nibaldo Bahamonde remembers Guiler 'as a tall, thin and gentle Australian marine shore researcher'. They interchanged letters about Chilean invertebrate taxonomical aspects. Nevertheless, what it can be said is that Guiler spent enough time at Montemar and surrounding shores to produce his second paper about the Chilean intertidal rocky shores: Guiler (1959b), specifically on the Montemar area (*ca.* 32°57'S, 71°33'W). He analyzed tidal, oceanographic, hydrological and climatic information for the area and carried out rocky intertidal biotic zonations in exposed and sheltered rocky sites. He called the attention that in central Chile the rocky shores were extremely exposed. He stated that by sheltered he meant sites '*sheltered from the main forces of the waves*'. Indeed, this is a characteristic for most of the rocky shore sites in central Chile, along hundred of kilometers (Castilla *et al.* 1998b). Guiler described the rocky shore biotic fringes with details and presented the first rocky intertidal fringe zoning kite-like figure (Guiler 1959b, p. 178).

In this section I would like to highlight a series of intertidal biotic fringe zoning observations and comparative analyses between the Montemar shore and nearby sites, north and south of Montemar, carried out by Guiler. Similar observations were done later on, independently, by me and students (also in central Chile rocky shores), and they form part of the core of my lines of research. Moreover, some of those key observations lead me to the establishment of the Estación Costera de Investigaciones Marinas, Las Cruces, in 1982 (Castilla 1996). Guiler (1959b, pp. 179-181) described rocky intertidal assemblages for two interesting sites: Laguna Verde (*ca.* 20 km south of Montemar) and Punta Curaumilla (*ca.* 10 km south of Laguna Verde), at that time '*only accessible by walking or by transport over a*

very rough road', (this is to say with little or no human interference). Guiler indicates that in the infralittoral, about 1km south of Laguna Verde, the intertidal zonation changes sharply. Among other observations, he reports that the *Lessonia nigrescens* belt is becoming replaced by a belt of *Durvillaea antarctica* (in Chile an edible macroalgae). Nevertheless, *Lessonia* continues present only in relatively shelter zones, particularly in those behind beds of *Macrocystis pyrifera*. He suggests, correctly, that subtidal shallow *Macrocystis* beds may exert a considerable effect in lowering the strength of the waves on the rocky shore. Nevertheless, south of Punta Curaumilla, *Durvillaea* becomes very common and is the dominant kelp in the infralittoral fringe. The dominance of *Durvillaea* in this fringe is also reported for Las Ventanas (*ca.* 25 km north of Montemar), a site also with a strong wave action; nevertheless, at Pichidangui (*ca.* 120 km north of Montemar), a site also with strong wave action, the dominance goes back to *Lessonia*. Guiler then asks the question: Why then is *D. antarctica* almost absent from the Laguna Verde-Montemar-Quinteros area? He rejects two hypotheses: a) That the exposure and wave strength may be the cause, since wave action at Montemar is much stronger than for instance in Laguna Verde; b) That the influence of fresh water may be the cause, since in the studied area that influence is negligible, though may be important at Concon. He concluded, rightly, that the only factor offering any explanation of this peculiarity in the distribution and dominance of *D. antarctica*, between Punta Curaumilla and Pichidangui (*ca.* 200 km of coast line) would be the effect of human interference, since *Durvillaea* is in considerable demand for food. Guiler suggests the existence of a strong competition between the two species of algae and baptized *D. antarctica* as a '*wave action loving species*'. Several decades after, in the 80 and 90's, several ecologists in Chile tackled these and related problems (i.e., Santelices *et al.* 1980). Furthermore, Castilla & Bustamante (1989), Bustamante & Castilla (1990) re-addressed the human interference/exploitation hypothesis regarding populations of *D. antarctica* in central Chile (actually they used Punta Curaumilla as a focal study area). More recently, Castilla *et al.* (2007) have demonstrated that human exploitation heavily diminished populations of *D. antarctica* in central Chile rocky shores, and that the populations may be re-established, provided human extraction is strictly controlled.

A second careful observation made by Guiler (1959b) at Montemar refers to one of the most remarkable fishes, *Syngnathus sanguineus* ('pejesapo'). *Syngnathus* is transported by waves and is found on steep-sloping rocks in exposed crevices and gullies. The fish clings to the rocks, when the strong surf recedes, using a ventral powerful sucker

Table 1

List of intertidal algae and invertebrates recorded by Guiler (1959a, b). Species in parenthesis are no valid combinations; valid combinations are included below the parenthesis

Listado de especies de algas e invertebrados intermareales en Guiler (1959a, b). Las especies entre paréntesis son combinaciones no válidas; las combinaciones válidas son indicadas abajo del paréntesis

SPECIES	Northern Chile Guiler (1959a)	Montemar (Central Chile) Guiler (1959b)	SPECIES	Northern Chile Guiler (1959a)	Montemar (Central Chile) Guiler (1959b)
PHAEOPHYTA			CNIDARIA		
<i>Adenocystis utricularis</i>		✓	<i>(Sagartia chilensis)</i>		✓
<i>Colpomenia sinuosa</i>	✓	✓	<i>Anthothoe chilensis</i>		✓
<i>Durvillaea antarctica</i>		✓	<i>(Phymactis clematis)</i>		✓
<i>Ectocarpus</i> sp.	✓		<i>Phymactis papillosa</i>		✓
<i>Endarachne binghamiae</i>	✓		POLYCHAETA		
<i>Glossophora kunthii</i>	✓		<i>Potamilla</i> sp.		✓
<i>(Halopteris horadacia)</i>	✓		<i>Cirriiformia</i> sp.	✓	
<i>Halopteris paniculata</i>			<i>Dasybranchus</i> sp.	✓	
<i>Lessonia nigrescens</i>	✓	✓	(no valid for Chile)		
<i>Macrocystis integrifolia</i>		✓	<i>Demonax</i> sp.		✓
<i>(Scytosiphon lomentarius)</i>	✓	✓	<i>Eulalia personata</i>	✓	
<i>Scytosiphon lomentaria</i>			(no valid for Chile)		
RHODOPHYTA			<i>Euphrosine</i> sp.		✓
<i>Centroceras clavulatum</i>		✓	<i>Halosydna fuscomarmorata</i>	✓	
<i>(Corallina chilensis)</i>			(no valid for Chile)		
<i>Corallina officinalis</i>	✓	✓	<i>Hemipodus simplex</i>		✓
var. <i>chilensis</i>			<i>Lepidasthenia virens</i>	✓	
<i>(Gelidium filicinum)</i>			<i>Lumbrineris</i> sp.	✓	✓
<i>Gelidium filicinum</i>		✓	<i>Lumbrineris tetraura</i>	✓	
(no valid for Chile)			<i>Marphysa sanguinea</i>		✓
<i>(Iridaea laminarioides)</i>			(no valid for Chile)		
<i>Mazzaella laminarioides</i>		✓	<i>Nereis grubei</i>	✓	
<i>(Lithothamnia sp.) lithothamnioides</i>	✓	✓	<i>Nerides</i> sp.		✓
(no valid for Chile)			(no valid for Chile)		
<i>(Plocamium pasificum)</i>			<i>Pherusa</i> sp.	✓	
<i>Plocamium cartilagineum</i>	✓		<i>Phragmatopoma moerchi</i>	✓	✓
<i>(Porphyra columbiana)</i>			<i>Platynereis magalhaensis</i>		✓
<i>Porphyra columbina</i>		✓	<i>Pseudonereis gallapagensis</i>	✓	✓
<i>Rhodymenia corallina</i>	✓		<i>Scoloplos</i> sp.		✓
CHLOROPHYTA			<i>Spirorbis</i> sp.	✓	✓
<i>Ulva lactuca</i>	✓	✓	<i>Thelepus concinnatus</i>		✓
<i>(Enteromorpha intestinalis)</i>	✓		(no valid for Chile)		
<i>Ulva intestinalis</i>			<i>Thelepus</i> sp.	✓	✓
<i>(Enteromorpha sp.) Ulva</i> sp.	✓	✓	MOLLUSCA		
<i>Codium dimorphum</i>		✓	<i>Acanthopleura echinata</i>	✓	
<i>Chaetomorpha linum</i>	✓		<i>(Chiton latus)</i>	✓	
<i>Gigartina lessonii</i>	✓		<i>Chiton magnificus</i>		
PORIFERA			<i>Chiton cumingsi</i>	✓	✓
<i>Haliclona sordida</i>		✓	<i>Chiton granosus</i>		✓
<i>Halichondria panicea</i>		✓	<i>Chaetopleura peruviana</i>		✓
			<i>Enoplochiton niger</i>	✓	
			<i>(Acmaea sp.)</i>	✓	
			<i>Scurria</i> sp.		

(Table 1 Cont.)

SPECIES	Northern Chile Guiler (1959a)	Montemar (Central Chile) Guiler (1959b)	SPECIES	Northern Chile Guiler (1959a)	Montemar (Central Chile) Guiler (1959b)
<i>(Acmaea viridula)</i>			<i>Leptograpsus variegatus</i>		✓
<i>Scurria viridula</i>	✓		<i>Acanthocyclus gayi</i>		✓
<i>(Acmaea araucana)</i>			<i>Acanthocyclus hassleri</i>		✓
<i>Scurria araucana</i>	✓		<i>Amphoroidea typa</i>	✓	
<i>(Collisella araucana)</i>			<i>(Cancer polyodon)</i>	✓	
<i>Scurria araucana</i>	✓		<i>Cancer setosus</i>	✓	
<i>Scurria scurra</i>	✓	✓	<i>Pachycheles grossimanus</i>	✓	✓
<i>(Brachidontes granulatus)</i>			<i>Pagurus edwardsi</i>		✓
<i>Brachidontes granulata</i>	✓	✓	<i>Paraxanthus barbiger</i>	✓	✓
<i>(Brachidontes purpuratus)</i>			<i>(Petrolisthes angulosus)</i>	✓	✓
<i>Perumytilus purpuratus</i>	✓	✓	<i>Allopetrolisthes angulosus</i>	✓	
<i>Mytilus</i> sp.	✓		<i>Petrolisthes tuberculatus</i>	✓	
<i>(Mytilus chorus)</i>			<i>(Petrolisthes spinifrons)</i>		✓
<i>Choromytilus chorus</i>	✓		<i>Allopetrolisthes spinifrons</i>		
<i>(Fissurella concinna)</i>			<i>(Petrolisthes patagonicus)</i>	✓	
<i>Fissurella maxima</i>	✓		<i>Liopetrolisthes patagonicus</i>		
<i>Fissurella costata</i>	✓	✓	<i>Taliepus dentatus</i>		✓
<i>Fissurella crassa</i>		✓	<i>(Gaudichaudia gaudichaudii)</i>	✓	
<i>Fissurella limbata</i>	✓		<i>Gaudichaudia gaudichaudi</i>		
<i>(Littorina peruviana)</i>			<i>Pilumnoides perlatus</i>	✓	✓
<i>Echinolittorina peruviana</i>	✓	✓	<i>(Pinnotheres chilensis)</i>		✓
<i>Siphonaria laeviuscula</i>	✓	✓	<i>Pinnaxodes chilensis</i>		
<i>(Siphonaria lessoni)</i>			<i>(Pisoides edwardsii)</i>		✓
<i>Siphonaria lessonii</i>	✓		<i>Pisoides edwardsi</i>		
<i>Tegula atra</i>	✓	✓	<i>Platypodiella</i> sp.		✓
<i>(Turbo niger)</i>			(no valid for Chile)		
<i>Prisogaster niger</i>	✓	✓	<i>Betaeus emarginatus</i>		✓
<i>Nacella magallanica</i>		✓	<i>Synalpheus spinifrons</i>		✓
<i>Thais chocolata</i>	✓	✓	<i>Emerita analoga</i>		✓
<i>Concholepas concholepas</i>	✓	✓	<i>Rhynchocinetes typus</i>	✓	✓
<i>(Polypus fontanieanus)</i>			ECHINODERMATA		
<i>Robsonella fontaniana</i>	✓		<i>Loxechinus albus</i>		✓
CRUSTACEA			<i>Tetrapygus niger</i>	✓	
<i>(Chthamalus cirratus)</i>			<i>Meyenaster gelatinosus</i>		✓
<i>Jehlius cirratus</i>	✓	✓	<i>Patiria chilensis</i>		✓
<i>(Balanus flosculus)</i>			<i>Patiriella</i> sp.		✓
<i>Notobalanus flosculus</i>	✓	✓	<i>Stichaster striatus</i>	✓	✓
<i>(Balanus laevis laevis)</i>			<i>Heliaster helianthus</i>	✓	
<i>Balanus laevis</i>	✓	✓	ASCIDEACEA		
<i>(Balanus psittacus)</i>			<i>Pyura chilensis</i>	✓	✓
<i>Austromegabalanus psittacus</i>	✓	✓			

and can tolerate thermal stress and desiccation. Guiler described *Syciases* feeding on algae attached to the rocks using powerful incisor teeth. Emersion behavior of this extraordinary Gobiesocidae fish and its foraging ecology where tackled later on by Paine & Palmer (1978). *S. sanguineus* is a unique trophic generalist, which consumes at least 17 species of macroalgae and 43 species of invertebrate (Cancino & Castilla 1988).

Species of intertidal macroalgae and invertebrates identified by Guiler (1959 a,b) in Chile

Table 1 shows the list of species of intertidal macroalgae

and invertebrates identified by Guiler (1959a,b), as product of field trips during the oceanographic expedition to four ports of northern Chile and those for the coast of central Chile (Punta Curaumilla to Pichidangui). In Guiler's species' identification endeavor he was helped by Chilean and foreign taxonomists. He mentions taxonomical expertise received in the Montemar Station from Professors P. Yañez and H. Etcheverry and from international institutions from Drs. O. Hartman, D. P. Henry, L. B. Holthuis, M. Burton, F.A. Chance, D. Ingram and I. Bowman.

In the first column of Table 1 there is a list the species

recorded by Guiler (1959a) in northern Chile shores: 16 species of macroalgae and 55 species of invertebrates. In the second column are those recorded by Guiler (1959b) from central Chile shores: 17 species of macroalgae and 58 species of invertebrates. When possible, I have indicated known changes of specific denominations. Most probably, this is the first list of intertidal macroalgae and invertebrate assemblages published for the central and northern coast of Chile. Before, the Lund-Chile expedition to southern Chile (Brattström & Dahl 1951) had completed a comprehensive survey of the marine biota, particularly south of 40°S.

Final remarks

It is my view that these two papers of Guiler (1959a,b) on the Chilean intertidal rocky ecosystems did set part of the stage for the future development of this discipline in the country, which 50 years later shows a strong school of thought and has received international recognition. Professor Eric R. Guiler was a sharp rocky intertidal observer. He knew the discipline, most probably enjoyed field work, and in no doubt was inspired by the great school of thought of intertidal ecologists of that time. More than that, undoubtedly he formed part of the 1940's and 1950's rocky intertidal scientific school of thought. Looking back, we as future Chilean rocky intertidal ecologists, profited enormously from Guiler's visit to Chile, above all due to the formulation of advanced and challenging hypotheses on the structure and dynamics of northern and central Chile rocky shore assemblages. It is more than proper to honor the 50 year anniversary of Eric R. Guiler (1959a, b)'s rocky intertidal papers.

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