A review of longnose skates Zearaja chilensis and Dipturus trachyderma (Rajiformes: Rajidae)

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Abstract

Longnose skates may have a high intrinsic vulnerability among fishes due to their large body size, slow growth rates and relatively low fecundity, and their exploitation as fisheries target-species places their populations under considerable pressure. These skates are found circumglobally in subtropical and temperate coastal waters. Although longnose skates have been recorded for over 150 years in South America, the ability to assess the status of these species is still compromised by critical knowledge gaps. Based on a review of 185 publications, a comparative synthesis of the biology and ecology was conducted on two commercially important elasmobranchs in South American waters, the yellownose skate Zearaja chilensis and the roughskin skate Dipturus trachyderma; in order to examine and compare their taxonomy, distribution, fisheries, feeding habitats, reproduction, growth and longevity. There has been a marked increase in the number of published studies for both species since 2000, and especially after 2005, although some research topics remain poorly understood. Considering the external morphological similarities of longnose skates, especially when juvenile, and the potential niche overlap in both, depth and latitude it is recommended that reproductive seasonality, connectivity and population structure be assessed to ensure their long-term sustainability.

Keywords: conservation biology; fishery; roughskin skate; South America; yellownose skate

Introduction

Global threats to sharks, skates and rays have been increasing due to direct and indirect fishing effects (Pauly et al. 2002, Worm et al. 2006, Dulvy et al. 2014). Important declines in exploited populations and species have been documented, particularly in larger and less resilient species (Stevens et al. 2000, Baum et al. 2003, Myers et al. 2007, Dulvy et al. 2008, 2014, Ferretti et al. 2008).

Skates (Family Rajidae) are the most diverse group of batooids, with 27 genera and about 245 species distributed worldwide (McEachran & Miyake 1990, Ebert & Compagno 2007) representing about 25% of all extant chondrichthyan species (Compagno 2005a,b).
Rajids mostly inhabit marine environments from the sublittoral zone to depths of about 3,000 m and exhibit high species diversity in high latitudes and deep waters (McEachran & Miyake 1990, Ebert & Compagno 2007).

In general, longnose skates (Tribe Rajini) present unique challenges for fishery management (Stevens et al. 2000) and conservation (Robert & Hawkins 1999, Dulvy & Reynolds 2002) due to large adult body size, low fecundity, late age at sexual maturity, relatively high longevity and large offspring size (Du Buit 1968, Holden 1977, Frisk et al. 2001, Dulvy & Reynolds 2002, Myers & Worm 2005, Dulvy et al. 2014). The biology and ecology of longnose skates is poorly known and requires further morphological, taxonomic and molecular research in spite of them being one of the largest taxa within batoids (Compagno 1999, Ebert & Compagno 2007, Séret & Last 2008) and have been subject to intense fishery exploitation (Baum et al. 2003, Myers & Worm 2005, Myers et al. 2007, Dulvy et al. 2008, 2014, Ferretti et al. 2008). Intense local fisheries with unmanaged landings are often accompanied by a lack of biological information required to maintain a healthy fishing stock (Ferretti et al. 2008, 2010), and it has been suggested that longnose skates are generally vulnerable to stock collapse even when subjected to low levels of fishing pressure (Agnew et al. 2000). Large population declines and local extinctions of longnose skates have been documented over recent years. The common skate Dipturus batis (Linnaeus, 1758), barndoor skate D. laevis (Mitchell, 1818), white skate Rостrora аlba (Lacepède, 1803), thornback ray Raja clavata L., 1758, smooth skate D. innominatus (Garrick & Paul, 1974) and longnosed skate D. oxyrinchus (L., 1758), are among the best documented examples of local extinctions in cartilaginous fishes as a result of fishing activities (Casey & Myers 1998, Francis et al. 2001, Dulvy et al. 2008, Dulvy & Forrest 2010).

Relatively few fisheries specifically target clasmobranch fishes in Chilean waters and among those, the yellownose skate Zeаraja chilenis (Guichenot, 1848) and the roughskin skate Dipturus trachyderma (Krefft & Stehmann, 1975) are the most valuable species (Bustamante et al. 2012, SERNAP, 2012). Although there are basic identification keys and field guides for longnose skates of the southeast Pacific, poor species identification and the lack of specific landing records are big issues for fishery management and quota allocation, impairing conservation management. In particular, these two commercially important species, Z. chilenis and D. trachyderma, have an additional vulnerability as both are endemic to southern South America, occurring in temperate-cold waters (De Buen 1959, Leible & Stehmann 1987, Agnew et al. 2000, Menни & Stehmann 2000, Gomes & Picado 2001, Bustamante et al. 2014 b).

From a taxonomic perspective, the genus Zeаraja was described in 1939 from a monotypic species, Z. nasuta (Müller & Henle, 1841), which was relocated from the genus Raja. Later, Stehmann (1990) synonymised this taxon within Dipturus, but Last & Yearsley (2002) resurrected Zeаraja as a subgenus by the relocation of two species (Z. chilenis and Z. nasuta) and suggested that zeаrazids are likely to be generically distinct from raijids due to skeletal differences, e.g., in clasper, neurocranium, pelvic and pectoral girdle morphologies. Last & Gledhill (2007) suggested the upgrade of Zeаraja to a genus based on key features of the external and internal anatomy, i.e., disc width/length ratio (giving it the familiar sub-rhomboid shape), presence of a strong rostral cartilage, orbital and midline thorn patterns and all the skeletal characteristics previously mentioned. Currently, the genus Zeаraja includes three valid species: Z. nasuta from New Zealand, Z. chilenis from Chile and Argentina, and Z. maugeana Last & Gledhill (2007) recently described from Tasmanian waters in Australia. However, these changes to the genus Zeаraja are one part of the taxonomic and systematic issues of genera within the Family Rajidae (Eschmeyer & Fong 2011).

Longnose skates of the genus Dipturus have a widespread distribution including waters of the Caribbean (Compagno 1999, Gomes & Picado 2001), northwestern Atlantic Ocean (McEachran & Carvalho 2002, Gedamke et al. 2005, Schwartz 2012), off South America (Gomes & Picado 2001, Soto & Mincaronе 2001, Díaz de Astarloa et al. 2008, Bustamante et al. 2014 b), Australasia (Last et al. 2008 a, Last & Alava, 2013), western Europe and Africa (Ellis et al. 2005 a, b, Ebert & Compagno 2007, Cannas et al. 2010). The genus Dipturus Rafinesque, 1810 was described using Raja batis (L. 1758) as the type species and initially was considered a subgenus within genus Raja (Stehmann 1973, Ishihara & Ishiyama 1986, Ishihara 1987,
Pequeño 1989, Séret 1989, Pequeño & Lamilla 1993, Jacob & McEachran 1994, Lopez et al. 1996, Bizikov et al. 2004), but was resurrected to generic level by McEachran & Dunn (1998). The genus includes 45 valid and several undescribed species (Séret 1989, McEachran & Dunn 1998, Ebert & Compagno 2007, Last 2008, Last et al. 2008a, Séret & Last 2008, Last & Alava 2013, Ebert et al. 2013). Eight species of the genus Dipturus are present in South American waters: D. ecuadoriensis (Beebe & Tee-Van, 1941) in the Pacific Ocean, D. argentinensis Díaz de Astarloa, Mabragaña, Hanner & Figueroa 2008, D. bullisi (Bigelow & Schroeder, 1962), D. dieibli Soto & Mincarone 2001, D. leptocauda (Krefft & Stehmann, 1975), D. menni Gomes & Paragó, 2001 and D. teevani (Bigelow & Schroeder, 1951) in the Atlantic Ocean, and D. trachyderma in both Pacific and Atlantic Oceans. All South American longnose skates have been reported on the continental shelf and slope between 100 – 450 m and are heavily fished over their entire range (Leible & Stehmann 1987, Lloris & Rucabado 1991, Gomes & Picado 2001, Soto & Mincarone 2001, Diaz de Astarloa et al. 2008).

Overall, peer-reviewed literature regarding the basic biology and taxonomy of longnose skates is scarce. For example, no additional information (molecular or morphological) has been produced to appraise the genus re-assignment of Last & Gledhill (2007). Recent changes in the taxonomic status of longnose skates has resulted in confusion that is of considerable importance in the context of South American fisheries management, where two sympatric and morphologically similar species, originally in the genus Dipturus, are now in two separate genera, Dipturus and Zearaja (Menni & Lopez 1984, Agnew et al. 2000, Bustamante et al. 2012).

Materials and Methods

A reference matrix was constructed using specialised search engines, i.e., Google Scholar, ScienceDirect, SharkReferences and worldwide academic libraries by a combination of fuzzy matching keywords for any scientific and common names regarding the species Zearaja chilensis and Dipturus trachyderma (in Spanish and English), e.g., ‘Raja’, ‘Zearaja’, ‘Dipturus’, ‘Trachyderma’, ‘Trachydermus’, ‘Chilensis’, ‘Roughskin skate’, ‘Yellownose skate’, ‘Raya volantín’, ‘Raya espinosa’, ‘Raya de vientre áspero’. Query matches were filtered by content and only those focused somehow on the target species were included in the matrix. An additional filter was applied to exclude references that lacked observational data or analysis. Remaining matches were counted only once and separated into seven categories based on their content. The seven categories (and sections) are: Anatomy and morphology (body size, colouration, dermal denticles, dentition, skeletal components, egg cases); Checklists and biological inventories (distribution ranges); Habitats and feeding habits; Life-history patterns (reproduction, age, growth and longevity); Fisheries (southeast Pacific, southwest Atlantic); Genetics; and Parasites.

Results and Discussion

A total of 185 articles were found regarding the biological entities Zearaja chilensis (Figure 1a) and Dipturus trachyderma (Figure 1b). An additional 32 articles were excluded from the matrix as the species received only nominal mention. For Z. chilensis, 77% of the articles correspond to scientific publications and 23% to ‘grey literature’ (e.g. non peer-reviewed and ‘popular’ media) that comprised mostly fishery reports, covering almost 170 years since the original description. A similar division between published scientific and grey literature was found for D. trachyderma, 75% and 24% respectively.

The most studied category for both species was ‘Checklist and biological inventories’ with at least one article per year, with 54 publications for Z. chilensis and 33 for D. trachyderma (Figure 2). While some publications contained specific information about taxonomic identity and sampling data, most papers reported historical and observation records without mention of the diagnostic features used for species recognition, and therefore were considered as doubtful reports.

‘Genetics’ was the least represented category for both species (Figure 2), which may reflect that relevant and accessible genetic approaches for species identification, stock structure and population analysis do not have a long research history (Dudgeon et al. 2012), and hence research has yet to address these topics. ‘Habitat and feeding habits’ was also poorly
represented in the literature (Figure 2), which may indicate a lack of resources or imperative to conduct research in these areas even though both species are of high economic value to South American economies. Undoubtedly, the study of many aspects of the biology of longnose skates is challenging due mainly to difficulties in access to these deep-water species, a dependency on fishing activity for sample collection across their extensive ranges and associated issues with the handling of large, economically valuable animals. There was a marked increase in the number of published studies for both species from 2000 and especially after 2005, when both species became an important asset to Chilean economy as

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**Fig. 1.** Cumulative number of peer-reviewed papers, books and government reports separated into seven categories for: (A) *Zearaja chilensis* and (B) *Dipturus trachyderma.*
fishing interest increased along with the creation of new landing species-specific categories for *Z. chilensis* and *D. trachyderma* (Figure 3). However, opportunities for future research in many of the categories remain, especially on population size and structure, short and long-term movements or migrations, feeding ecology and habitat use, and reproduction. To avoid near-future population collapse due to incomplete or inappropriate management measures, there is an urgent need to fill these information gaps.

The yellownose skate: *Zearaja chilensis*

Order RAJIFORMES Berg, 1940
Family RAJIDAE Blainville, 1816
Genus *Zearaja* Whitley, 1939

*Zearaja chilensis* (Guichenot, 1848) (Figure 4)

*Raia chilensis* Guichenot, 1848

*Raja chilensis* Philippi 1892, Delfín 1900, De Buen 1959, De Buen 1960, Carvajal 1971, Carvajal & Goldstein 1971, Bahamonde & Pequeño 1975, Carvajal & Dailey 1975, Pequeño 1975, Pequeño 1977, Ojeda 1983, Fernández & Villalba 1985, Pequeño & Lamilla 1985, Villalba & Fernández 1985, Sielfeld & Vargas 1999, Gili et al. 1999, Buschmann et al. 2005.

*Raja flavirostris* Philippi 1892, Delfín 1900, Garman 1913, Gotschlich 1913, Quijada 1913, Fowler 1916, Fowler 1926, Norman 1937, Fowler 1941, Oliver 1943, Fowler 1945, Hart 1947, Fowler 1951, Bahamonde 1953, Bigelow & Schroeder 1953, Mann 1954, De Buen 1957, Angelescu et al. 1958, Bigelow & Schroeder 1958, Ringuelet & Aramburu 1960, López 1963 a, b, Hulley 1966, Olivier et al. 1968, Hulley 1970, Menni 1971, Ringuelet & Aramburu 1971, Hulley 1972, Castello & Tapia-Vera 1973, Sadowsky 1973, Gósztonyi 1979, Menni & López 1979, Gósztonyi 1981, Menni 1981, Menni et al. 1981, Menni & Gósztonyi 1982, Menni & López 1984, Menni et al. 1984, Raschi 1986, Threlfall & Carvajal 1986, Prenski & Sánchez 1988, Sánchez & Prenski 1996, García de la Rosa 1998, Agnew et al. 2000, Jo et al. 2004, Wakeford et al. 2005, Buschmann et al. 2005.

*Raja oxyptera* Philippi 1892, Delfín 1900, Lönnberg 1907, Garman 1913, Gotschlich 1913, Quijada 1913.

*Raja latastei* Delfín, 1902

*Raja brevicaudata* Marini, 1933

*Raja (Dipturus) flavirostris* Stehmann 1970, Menni 1972, Menni 1973, Stehmann 1978, Leible 1984, Leible 1987, Leible & Stehmann 1987, Leible 1988,

Fig. 2. Number of published studies for *Zearaja chilensis* (1848–2014) (black bars) and *Dipturus trachyderma* (1975–2014) (grey bars) by research category.
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Fuentesalba & Leible 1990, Fuentesalba et al. 1990, Leible et al. 1990, López et al. 1996.

*Raja (Dipturus) chilensis* Pequeño 1989, Lloris & Rucabado 1991, Pequeño & Lamilla 1993, Sáez & Lamilla 1997, Bizikov et al. 2004.

*Dipturus chilensis* Bahamonde et al. 1994, Bahamonde et al. 1996, 1997, McEachran & Dunn 1998, Meneses & Paesch 1999, Paesch 1999, Paesch & Meneses 1999, Cousseau & Perrotta 2000, Cousseau et al. 2000, Lucifora et al. 2000, Koen Alonso et al. 2001, Gomes & Picado 2001, Soto & Mincarone 2001, Lamilla et al. 2002, Last & Yearsley 2002, Nion et al. 2002, Sánchez & Mabragaña 2002, Calderón et al. 2003, Lamilla & Sáez 2003, Meneses & Paesch 2003, Buren 2004, García de la Rosa et al. 2004, Massa et al. 2004, Smith et al. 2004, Acuña et al. 2005, Céspedes et al. 2005, Compagno 2005 a, b, Lamilla & Bustamante 2005, Quiroz & Wiff 2005, Oddone et al. 2005, Araya & Cubillos 2006, Lamilla et al. 2006, Licandeo et al. 2006, Concha et al. 2007, Cousseau et al. 2007, Ebert & Bizarro 2007, Ebert & Compagno 2007, Licandeo

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Fig. 3. Total annual numbers of published studies for (A) *Zearaja chilensis* and (B) *Dipturus trachyderma*.
Fig. 4. Morphotypes for *Zearaja chilensis*. (A) Original description, female, 750 mm TL, Chile (Philippi 1892). (B) Mature male, 975 mm TL, Chile (Delfín 1902). (C) Adult male, Argentina (Norman 1937). (D) Immature male, 374 mm TL, Argentina (Bigelow & Schroder 1958). (E) Mature male, Argentina (Llotis & Rucabado 1991). (F) Female, Falkland Islands, British Overseas Territory (Bizikov et al. 2004). (G) Female, 690 mm TL, Los Vilos, Chile (Melo et al. 2007). (H) Mature female, 770 mm TL, Valdivia, Chile.

& Cerna 2007, Licandeo et al. 2007, Melo et al. 2007, Aburto et al. 2008, Andrade & Pequeño 2008, Arkhipkin et al. 2008, Díaz de Astarloa et al. 2008, Domingo et al. 2008, Lamilla et al. 2008, Paesch & Oddone 2008, Quiroz et al. 2008, Reyes & Torres-Flores 2008, Mabragaña et al. 2009, Quiroz et al. 2009, Ruarte et al. 2009, Silveira 2009, Quiroz et al. 2010, Zavatteri 2010, Aversa et al. 2011, Mabragaña et al. 2011 a, Quiroz et al. 2011, Cortes & Cueto 2012, San Martin & Trucco 2012, Colonello & Cortes 2013, Silveira et al. 2014.

**Dipturus flavirostris** Menni & Stehmann 2000, Cedrola et al. 2005, Bovcon & Cochía 2007.

**Dipturus (Zearaja) chilensis** Estalles et al. 2011, Kyne & Sympfendorfer 2007, Lamilla et al. 2009.

**Zearaja chilensis** Kyne et al. 2007, Last & Gledhill 2007, Menni & Lucifora 2007, Kyne & Sympfendorfer 2010, Lamilla et al. 2010, Vargas-Caro 2010, Lamilla & Flores 2011, Lamilla et al. 2011, Mabragaña et al. 2011 b, Perier et al. 2011, Queirolo et al. 2011, Arkhipkin et al. 2012, Bustamante et al. 2012, Concha et al. 2012.
The yellownose skate (Zearaja chilensis) was first described in 1848 and since then the species identity has caused confusion within the scientific community. Guichenot (1848) described the species from a male of 836 mm total length (TL) collected in Quinteros Bay, Chile. Although this report may be considered brief, the author provided information about external features and highlighted the fact that it was very abundant on local markets. Later, Philippi (1892) described Raja flavirostris (Figure 4a) based on two females of 750 mm average TL and Raja oxyptera from a mature male of 1080 mm TL from the same locality (Quinteros Bay), and provided a comprehensive description including morphometric measurements and detailed external morphology. On this occasion the author considered R. flavirostris and R. oxyptera as separate species mainly for having different thorn patterns on the caudal region, but did not include a comparison with the previously described R. chilensis. Delfín (1902) provided a description of a new species, Raja latastei (Figure 4b), based on a male (795 mm TL) and a female (567 mm TL) specimen of an ostensible R. chilensis from Coquimbo, Chile. Garman (1913) synonymised R. latastei as R. flavirostris and provided a comparison between R. flavirostris and R. oxyptera suggesting that apparent changes in external morphology due to sexual maturity and ontogenetic changes may be used to separate two morphotypes of a single species, with the relocation of R. flavirostris and R. oxyptera to the same nominal species. Norman (1937) subsequently published a comprehensive review of skates (rajids) of the Argentinian Patagonia, supporting Garman’s hypothesis and suggesting that the ‘nominal species’ is R. flavirostris and relocating R. chilensis as a major synonymy. Interestingly, De Buen (1959) provided a description and comparisons of Chilean longnose skates using specimens (males and females) collected from the R. chilensis type locality, and concluded that R. flavirostris, R. oxyptera and R. latastei should be synonyms of R. chilensis supplementing Guichenot’s original description with different morphotypes. De Buen’s suggestions were supported by Leible (1984, 1987) and Leible et al. (1990), who described R. chilensis as a polymorphic species and distinguished at least three clear morphotypes in central and southern Chile, agreeing with observations by Pequeño & Lamilla (1985), Pequeño (1989), and Lloris & Rucabado (1991) (Figure 4e). Following the Principle of Priority of the International Code of Zoological Nomenclature (ICZN), it is appropriate to use and apply the name R. chilensis, rather than R. flavirostris, to the nominal species recognised as the ‘yellownose skate’ in Chilean waters. The use of change of ranks and combinations (Article 23c, ICZN 1964) and plenary power (Article 79b, ICZN 1964) to consider R. chilensis as a senior synonym of R. flavirostris (Menni & Stehmann 2000) was incorrect, as a modification of the Code that would have seen a valid change from chilensis to flavirostris, based on 50 years without references to a species name, occurred after the reference to R. chilensis by De Buen (1959).

The phylogenetic analysis provided by MeEachran & Dunn (1998) proposed the elevation of the subgenus Dipturus (formerly under Raja) to genus level by using internal anatomy and external morphology of the family Rajidae, as suggested by Stehmann (1970). Recently, Last & Yearsley (2002), resurrected Zearaja as a subgenus (from Dipturus), and Last & Gledhill (2007) raised Zearaja to genus level based on key features of the external morphology and internal anatomy of the clasper. As a consequence, the name Zearaja chilensis (Guichenot 1848) is valid to date, and is suggested the relocation of Raja latastei, R. flavirostris and R. oxyptera as junior synonyms.

The roughskin skate: Dipturus trachyderma

Order RAJIFORMES Berg, 1940
Family RAJIDAE Blainville, 1816
Genus Dipturus Rafinesque, 1810
Dipturus trachyderma (Krefft & Stehmann, 1975) (Figure 5)

Raja (Dipturus) trachyderma Krefft & Stehmann 1975, Krefft 1978, Leible 1984, Leible & Stehmann 1987, Leible 1988, Pequeño 1989, Lloris & Rucabado 1991, Pequeño & Lamilla 1993, López et al. 1996, Bizikov et al. 2004.

Raja trachyderma Menni & Gosztonyi 1977, Menni & Gosztonyi 1982, Sielfeld & Vargas 1992, Sielfeld & Vargas 1999, Gili et al. 1999, Buschmann et al. 2005, Thiel et al. 2009.
**Dipturus trachydermus** López et al. 1989, Compagno 1999, Knoff et al. 2001 b, Knoff et al. 2002, López et al. 2002, Oyarzún et al. 2003, Knoff et al. 2004, Cedrola et al. 2005, Compagno 2005 a, Kyne & Simpfendorfer 2007, Lamilla & Massa 2007, Menni & Lucifora 2007, Reyes & Torres-Flores 2008, Muniz-Pereira et al. 2009, Quiroga et al. 2009, Kyne & Simpfendorfer 2010, Menni et al. 2010.

**Dipturus trachyderma** Stehmann 1978, Menni et al. 1984, Mould 1997, McEachran & Dunn 1998, Menni & Stehmann 2000, Cousseau et al. 2000, Gomes & Picado 2001, Soto & Mincarone 2001, Knoff et al. 2001 a, Nion et al. 2002, Lamilla & Sáez 2003, Smith et al. 2004, Céspedes et al. 2005, Compagno 2005 b, Lamilla 2005, Lamilla & Bustamante 2005, Lamilla et al. 2006, Licandeo et al. 2006, Bovcon & Cochia 2007, Ebert & Compagno 2007, Cousseau et al. 2007, Licandeo et al. 2007, Melo et al. 2007, Arkhipkin et al. 2008, Díaz de Astarloa et al. 2008, Domingo et al. 2008, Jeong & Nakabo 2008, Lamilla et al. 2008, Quiroz et al. 2008, Santos et al. 2008, Góngora et al. 2009, Lamilla et al. 2009, Mabragaña et

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**Fig. 5.** Morphotypes of *Dipturus trachyderma*. (A) Original description, female, 1135 mm TL, off Argentina (Krefft & Stehman 1975). (B) Male, 2000 mm TL, Chile (Leible & Stehmann 1987). (C) Male, 2075 mm TL, Beagle Channel, Argentina (Lloris & Rucabado 1991). (D) Female, Falkland Islands, British Overseas Territory (Bizikov et al. 2004). (E) Male, 2007 mm TL, Valdivia, Chile.
al. 2009, Lamilla et al. 2010, Quiroz et al. 2010, Vargas-Caro 2010, Estalles et al. 2011, Lamilla & Flores 2011, Lamilla et al. 2011, Mabragaña et al. 2011 a, b, Moreira et al. 2011, Perier et al. 2011, Queirolo et al. 2011, Sáez & Lamilla 2012, Arkhipkin et al. 2012, Concha et al. 2012, Lamilla et al. 2012 a, b, Bovcon et al. 2013, Lamilla et al. 2013, Bustamante et al. 2014 a, b.

The roughskin skate (Dipturus trachyderma) was described by Krefft & Stehmann (1975) (Figure 5 a), using an immature male of 1135 mm TL as the holotype. This specimen was collected during the cruises of the R/V Walther Herwig to South America in 1971, particularly off southern Argentina (49° S, 60° 52' W) at the outer shelf edge (195 – 200 m depth). Authors provided general information about the external morphology, neurocranium and pelvic girdle of the species. Considering that the specimen was an immature, a detailed description of secondary sexual characters, i.e. clasper morphology, and of dorsal thorns in general, is absent. Additional specimens from Argentinian waters were collected, but unfortunately due to the large size of these animals only general external measurements (e.g. TL) were recorded, and in some cases body parts were preserved and kept for reference and further investigations (Menni & Gosztonyi 1977, 1982). The species description was supplemented through specimens collected in Chile (Leible & Stehmann 1987) (Figure 5b). Even with some incomplete specimens, the authors were able to provide a detailed description of the neurocranium and pelvic girdle, including information on meristics, morphometrics, and variations of shape and squamation. Also, Leible & Stehmann (1987) provided the first description of the scapulocoracoid cartilage and external and internal morphology of claspers. Unfortunately, since then no other study has addressed morphological characters. General additional information about descriptive demography can be found in checklists, reference books and field guides (Lloris & Rucabado 1991, Cousseau et al. 2000, Bizikov et al. 2004, Lamilla & Bustamante 2005, Cousseau et al. 2007).

**Diagnosis:** Zearaja chilensis is characterized by the combination of the following characters: Disc broader than long, anterior margins undulated. Long and strong rostral cartilage with white-yellow rostrum. Dorsal surface of disc dark brown, ocelli present on each pectoral fin. Dorsal side of disc smooth, denticles irregularly scattered over body, thorns on orbital, rostrum, nuchal, tail, alar and malar (in males) areas. Ventral surface with whitish and brownish areas, reddish brown colour at posterior disc margins; most of disc, pelvic fins and tail pale to medium brown. Alar thorn patch well developed with 1 – 3 rows on each pectoral fin. Tail with 1 – 3 rows (one median and two laterals) in males, up to 5 rows in females with a maximum of 47 thorns; 1 – 5 interdorsal thorns. Tooth rows in upper jaw 30 – 46.

Dipturus trachyderma is characterized by the combination of the following characters: Disc broadly rhombic; anterior margin of disc concave and posterior margin convex with rounded inner corner to level of pelvic fins. Snout hard, long and pointed. Dorsal surface of disc dark brown without a pattern or distinct ocelli; only mucus pores coloured black. Ventral surface as dark as dorsal side in large areas, reddish brown colour at posterior disc margins; gill slits and cloaca creamy white. Both dorsal and ventral sides completely covered by dermal denticles, with exception of a smooth belly. Ocular and spiracular thorns present, nuchal thorn absent, no other thorns on the disc. Alar thorn patch very well developed with 4 – 5 rows on each pectoral fin. Tail with 1 – 3 rows (one median and two laterals) in males, up to 5 rows in females with a maximum of 43 thorns; 1 – 4 interdorsal thorns. Tooth rows in upper jaw 36 – 44.

**Description:** Most studies on the taxonomy, growth, maturity, maximum size, and species demography rely on measurements of all or parts of the body (Francis 2006). Hubbs & Ishiyama (1968) found that skates commonly have interspecific differences in the relative size of the head, trunk, tail and fins as well as between sexes. As a consequence, researchers have used a variety of measurements, making the accurate comparison among studies almost impossible and in some cases leading to invalid data comparison and incorrect conclusions (De Buen 1959, Francis 2006, Last et al. 2008 b).

As skate body morphology is likely to vary inter and intra specifically (between sexes and with body size), a standardised measurement protocol is necessary for specimen comparisons. Hubbs & Ishiyama (1968) defined a large number of body measurements for skate identification, including disc, tail, fins, head, trunk and cranial areas. They recommended that disc width (DW) be used as the independent variable when calculating
relative proportions of body measurements, as tail length, which is part of TL, exhibited negative allometry. The use of total length was considered problematic in embryonic and small juvenile skates because of a non-linear scaling with body mass (Templeman 1987). However, TL has been used as the standard reference measurement for body proportions of the Rajidae, as greater variation in proportions was noted if DW was used (Hulley 1970, Stehmann 1970). Disc width measurements of *Batyrja richardsoni* (Garrick, 1961) in fresh condition have been shown to be highly variable, lack repeatability and are sensitive to inter-observer error (Templeman 1973). Regarding preserved material, DW depends on the shape in which the specimen was preserved, which highlights the importance of making measurements on unfixed specimens (Ishiyama 1950). A comprehensive review of the methods used for measuring chondrichthyans recommended the use of TL as the reference for batoids (Francis 2006), and a standard methodology for measuring skates proposed the use of 46 measurements and the use of TL as reference for body size (Last et al. 2008 b).

The literature that pre-dates this proposal has, however, variably used TL or DW; in seven studies on *Z. chilensis* between 13 and 23 variables were measured (Philippi 1982, Delphin 1902, De Buen 1959, Menni 1973, Pequeño & Lamilla 1985, Leible 1987, lloris & Rucabado 1991) and 15 – 20 variables were used in three studies of *D. trachyderma* (Krefft & Stehmann 1975, Leible & Stehmann 1987, lloris & Rucabado 1991). Many of these authors used a variety of measurements as ‘body descriptors’ and not only TL was used as the standard reference, making comparisons between studies difficult or virtually impossible.

The minimum and maximum sizes reported for *Z. chilensis* are 156 mm and 1580 mm TL, respectively, with females growing to larger sizes than males (Norman 1937, Bahamonde 1953, De Buen 1959, Leible 1987, Fuentealba & Leible 1990, Leible et al. 1990, García de la Rosa 1998, Cousseau et al. 2000, 2007, Gomes & Picado 2001, Cedrola et al. 2005, licandeo et al. 2006, licandeo & Cerna 2007, Paesch & Oddone 2008, Estalles et al. 2011, Lamilla et al. 2012 a, b). A single reference that suggested *Z. chilensis* could attain a maximum size of 2480 mm TL for females and 2220 mm TL for males in Argentinian waters (Koen Alonso et al. 2001) is likely to be a misidentification of *D. trachyderma* (Leible 1987, Cedrola et al. 2005, Iglesias et al. 2010, Estalles et al. 2011).

**Colouration:** The dorsal body surface of batoids may be plain or patterned and is generally brown, grey, black, or yellowish, although red, blue, and green colours also occur in some species, whereas the ventral skin is usually lighter and of a uniform colour (Kemp 1999). Colour patterns of skates may reflect different habitat occupancy within both horizontal and vertical ranges, with the possibility that interspecific colour variation may be influenced by environmental factors additional to phyletic relationships. Overall, multiple factors have to be considered before an assumption of intraspecific and ontogenetic colour variations can be made, such as whether (or not) colour of the integument is uniform or spotty, variation of dorsal and ventral surfaces when fresh or preserved, presence of colour markings or patterns on either surface of the body and, presence of pectoral ocelli (Ishiyama 1958 b). Body colouration can be an important feature for species identification, as colour patterns in different body regions on both the dorsal and ventral surfaces are often diagnostic (Hubbs & Ishiyama 1968).

Colouration of *Z. chilensis* is red-brownish when fresh, usually with irregular dark spots on the dorsal surface which appear to fade after a few hours post-capture. Both sides of the rostral cartilage are yellowish and translucent, and in some individuals a large circular dark ocellus is present at the base of each pectoral fin. The ventral surface is dark brown with a creamy white abdomen, and pelvic fins have a white base and are reddish around their edges. Numerous blackish pores are also present grouped around the mouth and gill opening on the ventral surface. In mature males, the terminal section of the claspers has a reddish-brown colour (Norman 1937, De Buen 1959, Leible 1987, lloris & Rucabado 1991, Bizikov et al. 2004, Cousseau et al. 2007). In *D. trachyderma* the dorsal surface is uniformly dark brown and supports numerous pores that appear blackish. The ventral surface has a base colour reddish to dark brown especially at posterior disc margins, abdomen, posterior pelvic lobes and underside of tail. However,
in fresh specimens large areas may appear blackish, due to a layer of mucus over the skin. Jaws, gill slits and cloaca are creamy white in appearance. Ventral mucus-filled pores appear black, although they are indistinct due to dark base colour of the skin. In mature males the terminal section of the claspers has a light reddish-brown colour (Krefft & Stehmann 1975, Leible & Stehmann 1987, Lloris & Rucabado 1991, Cousseau et al. 2000, 2007). Some colour variations are suggested to relate to ontogenetic development, sex of individuals and environmental conditions (Ishiyama 1958 b, Leible 1988).

**Dermal denticles:** Dermal denticles (placoid scales) are a characteristic of the skin of chondrichthyan fishes and cover the entire body in sharks, but are usually distributed discontinuously in batoids and chimaeras (Reif 1985, Kemp 1999). Each dermal denticle comprises a basal plate embedded in the dermis, a neck, and an exposed spiny crown (Kemp 1999). Overall, dermal denticles can differ dramatically among species and even body regions of an individual and their morphology is usually associated with functional roles such as protection from predators, reduction of mechanical abrasion and hydrodynamic drag (Reif 1985, Bushnell 1991, Raschi & Tabit 1992, Lang et al. 2012). Skates have an impressive array of dermal denticles on the dorsal and ventral disc, around the head, trunk, pectoral and pelvic fins, and the tail. Small denticles < 3 mm in length are referred as prickles and may cover either the dorsal or ventral disc surfaces, or both (Ishiyama 1958 b, Stehmann & Bürkel 1984, Leible 1988, Deynat 2000 a, Gravendeel et al. 2002). Medium-sized denticles or thorns < 3 mm long have a circular or star-like basal plate. Thorns are generally located on the dorsal surface and can be separated into ‘series’ according to the body region, i.e. orbital, rostral, nuchal, scapular and caudal series (Hubbs & Ishiyama 1968, Stehmann & Bürkel 1984, Gravendeel et al. 2002). The distribution, number and basal plate edge morphologies of thorns are usually diagnostic features for species identification (Hubb & Ishiyama 1968, Leible 1988, Gravendeel et al. 2002, Last et al. 2008 b). The number of thorns reported to occur in different body areas of longnose skates from Chilean waters is summarised in **Table 1**, although values may vary according to sex and maturity of individuals. For example, mature males develop their alar series, while mature females have more thorns in the caudal zone than males (Leible 1988). The presence of a nuchal thorn in *Z. chilensis* was originally considered to be a diagnostic character that separated it from *D. trachyderma* (Leible 1987), but *Z. chilensis* was later recognised as a polymorphic species and the nuchal thorn was not always present (Leible et al. 1990). However, the fact that the presence of a nuchal thorn is not a diagnostic character has been overlooked in several field guides (Cousseau et al. 2000, Lamilla & Sáez 2003, Lamilla & Bustamante 2005, Cousseau et al. 2007), which generates an unfortunate uncertainty for rapid species identification. Adult male series of large and curved denticles, or hooks, in the alar and malar regions can vary among species in the number of transverse and lengthwise rows. Alar hooks are erectile and are grouped near the pectoral fin margins, while the non-erectile malar hooks are aligned near the margin of the disc lateral to the eyes (Bigelow & Schroeder 1953, Hubb & Ishiyama 1968). While caudal thorns and other dermal denticles have been used for species identification of some extant and fossilised rajids (Stehmann & Bürkel 1984, Gravendeel et al. 2002), few studies have been used dermal denticles morphology for taxonomic and phylogenetic purposes (Deynat & Séret 1996, McEachran & Konstantinou 1996, Deynat 1998, 2000 a, b). Caudal thorns have also been sectioned and used to determine the age of some skates and rays (Gallagher & Nolan 1999, Henderson et al. 2004, Gallagher et al. 2006, Davis et al. 2007, Matta & Gunderson 2007, Moura et al. 2007).

| Body series | Range |
|-------------|-------|
| **Z. chilensis** | **D. trachyderma** |
| Orbital | 1 – 9 | 1 – 7 |
| Spiracular | 1 – 2 | n/a† |
| Nuchal | 0 – 1 | 0 |
| Alar | 9 – 33 | 17 – 48 |
| Alar rows | 1 – 3 | 4 – 5 |
| Caudal | 10 – 47 | 11 – 43 |
| Interdorsal | 1 – 5 | 0 – 4 |
| Caudal rows | 3 – 5 | 3 – 5 |

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*Ishiyama sex of individuals and environmental conditions are suggested to relate to ontogenetic development.*

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**Table 1.** Variation in the number of dermal denticles of the yellownose skate *Zearaja chilensis* and roughskin skate *Dipturus trachyderma* (Modified after Guichenot 1848, Philippi 1892, Delfín 1902, Norman 1937, De Buen 1959, Menner 1973, Leible 1987, Leible & Stehmann 1987, Lloris & Rucabado 1991, Bizikov et al. 2004). † There is no available information in the literature mentioning this series.
The body surfaces of *Z. chilensis* are relatively smooth (excluding the rostral area), with sparse prickles on the dorsal surface and without obvious denticles on the ventral surface. In contrast, both dorsal and ventral surfaces in *D. trachyderma* are covered with prickles when mature, except for a smooth patch around the abdominal area (in general *Dipturus* species are covered with dermal denticles with the dorsal surface rougher than the ventral surface) (Krefft & Stehmann 1975, Leible & Stehmann 1987, Leible 1988).

**Dentition:** Dental morphology is widely used in taxonomic, biological and fossil studies of cartilaginous fishes (e.g. Herman et al. 1995, 1996, Kemp 1999, Adnet & Cappetta 2001, Lamilla & Sáez 2003, Sáez & Lamilla 2012), and while most studies provide descriptions of tooth morphology (Du Buit 1978, Pequeño & Lamilla 1985, Leible 1987, 1988, Zorzi & Anderson 1988, Herman et al. 1995, 1996, Delpiani et al. 2012), relatively few address variation in tooth number and arrangement, mono- or dignathic heterodonty, malformation, dental sexual dimorphism and ontogenetic change or their relation to dietary intake (Bigelow & Schroeder 1953, Leible, 1988, Motta 2004, Gutteridge & Bennett 2014).

Description of the dentition of *Z. chilensis* and *D. trachyderma* includes the number of tooth rows: 30 – 46 rows in *Z. chilensis* (Philippi 1892, Delphin 1902, Norman 1937, Leible 1987, 1988) and 36 – 44 in *D. trachyderma* (Krefft & Stehmann 1975, Leible & Stehmann 1987, Lloris & Rucabado 1991). Information about how tooth row number varies with ontogeny is not available, although this will impact the usefulness of row count for taxonomic purposes. Sexually dimorphic dentition has been reported in *Z. chilensis*, with sharp and conical (spike-shaped) teeth in mature male skates, while females have blunt ‘oval shaped’ teeth (Leible 1987). Such sexual dimorphic dentition was hypothesised to correlate with different diets between the sexes in batooids (Feduccia & Slaughter 1974), but has since been shown to facilitate the male grasp of the female pectoral fins to aid in the act of copulation (McEachran 1977, Gutteridge & Bennett 2014). Although no further studies have been published regarding dental morphology or dental formulae for longnose skates in South America, both features are widely, if uncritically, used as diagnostic characters in cartilaginous fishes.

**Skeletal components:** Studies of the anatomy and systematics of batoids have revealed significant variation among chondrichthyes (Compagno 1977, Miyake 1988, Miyake & McEachran 1991). The neurocranium, pectoral and pelvic girdles and the male reproductive organs may provide useful diagnostic skeletal features for species identification (Ishiyama & Hubbs 1968, Hulley 1970, Stehmann 1970, Hulley 1972, McEachran 1982, 1983). According to Ishiyama (1958 b), differences in clasper skeletal components “provide excellent generic and specific features and insights about phylogenetic relationship within groups and fully discriminative analyses even between closely related species”. Clasper morphology was the main feature used to resurrect *Zearaja* to genus level (Last & Yearsley 2002), and used to relocate *Z. chilensis* and *Z. nasuta* to the genus (Last & Gledhill 2007). External differences in clasper morphology occurs between longnose skate; for example, the shield is short and robust in *Zearaja*, but long and slender in *Dipturus*, and the distal lobe is spatulated in *Zearaja*, but rounded in *Dipturus*. Internally, clasps may differ in their structural components by the presence or absence of cartilages (Last & Gledhill 2007). Menni (1971) described the internal components of the clasper of *Z. chilensis* which was later supplemented with an external anatomical comparison (Leible 1987). However, the presence of the accessory terminal I cartilage (Atr1) was erroneously reported by Menni (1971) and Leible (1987), as there is no equivalent structure in *Zearaja* species (Last & Gledhill 2007). Leible (1987) also described the neurocranium, pelvic girdles and scapulocoracoid of *Z. chilensis*, and suggested that intra-specific variation occurs among Chilean longnose skates populations, highlighting the need of further investigation. For *D. trachyderma*, the original (Krefft & Stehmann 1975) and subsequent description (Leible & Stehmann 1987) included details of external and internal structures, such as neurocranium, pelvic girdles, scapulocoracoid and clasper; and where the presence of Atr1 and the sentinel (both absent in *Zearaja*) were reported. Moreira et al. (2011) found differences in the neurocranium, scapulocoracoid and clasper between *D. menni* and *D. trachyderma*, which was consistent with there being two separate species, even though some specimens of *D. menni* were originally identified as *D. trachyderma* (Gomes & Picado 2001). The taxonomic revision of South American batoids by Leible in 1988 highlights that most species exhibit...
marked morphological variation, mainly related to sex and maturity. However, as clasper morphology and that of other skeletal components has not been addressed in the past 25 years, and given the relative importance of these structures in taxonomic and phylogenetic studies, a revision of the internal skeletal components of longnose skates is deemed necessary.

**Egg cases:** All skates utilise extended oviparity in which fertilised eggs are encapsulated in a structurally complex egg case that protects the embryo during an often long development, which occurs primarily outside of the mother (Hamlett & Koob 1999, Hamlett 2005). Longnose skates are single ovi-parous, bearing one egg capsule per oviduct at a time (Mabragaña et al. 2011 b, Concha et al. 2012), with a marked synthetic synchrony of the nidamental gland activity, consistent with other rajoid species (McEachran & Aschliman 2004, Ebert & Compagno 2007). The morphology of egg cases is considered to be genus- and species-specific, and has been used as a taxonomic tool for species identification and systematics (e.g. Ishiyama 1950, 1958 a, b; Ebert 2005, Ebert & Davis 2007, Ishihara et al. 2012). It is, however, imperative that morphological descriptions of egg cases are performed where the species identity is known unambiguously; such as egg cases collected from a mother's uterus or those that have been laid in an aquarium that contains a single oviparous species (Ebert & Davis 2007, Bustamante et al. 2013). Variations in egg case morphology among oviparous species may relate to the structure in which they are deposited, for example, the presence of long tendrils may suit deposition in a structurally complex habitat (Ebert et al. 2006) and provide information about the reproductive strategy (Dulvy & Reynolds 1997, Didier 2004, Kyne & Simpfendorfer 2010).

Egg cases of longnose skates are generally rectangular in shape with a horny process in each corner (Mabragaña et al. 2011 b). The egg cases of *Z. chilensis* and *D. trachyderma* have been described from specimens from the southwest Atlantic (Paesch & Oddone 2008, Mabragaña et al. 2011 b) and southeast Pacific (Concha et al. 2012). For *Z. chilensis* the egg case is dark brown in colour with a smooth surface, finely striated and without ridges, and has a capsule length (CL) of 94 – 158 mm and capsule width (CW) of 64 – 76 mm. For *D. trachyderma* the deposited egg case is a golden-brown colour, and is possibly the largest of any cartilaginous fish at 197 – 230 mm CL and 100 – 163 mm CW (Mabragaña et al. 2011 b, Concha et al. 2012). The egg case has well developed aprons and a strong lateral keel, similar to the shape of egg cases from other *Dipturus* species e.g. giant skate *D. gigas* (Ishiyama, 1958), longnosed skate *D. oxyrinchus* (L., 1758) (Ishiyama 1958 b), and wedgenose skate *D. whitleyi* (Iredale, 1938) (Treloar at al. 2006). In comparison to the egg case of *Z. chilensis*, that of *D. trachyderma* has smaller horns, located closer to the terminal zone of the apron (Concha et al. 2012).

**Checklists:** Although *Z. chilensis* was described in 1848 (as *R. chilensis*), there are no further records of its presence in Chile until after 1900. Several authors documented the presence of *Z. chilensis* (but identified as *R. flavinotris*) in the South Pacific and South Atlantic between 1900 and 1960 (Delfín 1900, 1902, Lönnberg 1907, Garman 1913, Gotschlich 1913, Quijada 1913, Fowler 1926, Norman 1937, Oliver 1943, De Buen 1960). In Chilean waters, checklists and field guides reported the presence of *R. chilensis* from 1959 onwards (De Buen, 1960, Bahamonde & Pequeño 1975, Pequeño 1977, 1989). *Dipturus trachyderma* was added subsequently to the Chilean ichthyofauna (Pequeño 1989), and both species of longnose skates were documented to occur in Chilean waters by Pequeño & Lamilla (1993), Sielfeld & Vargas (1999), Lamilla & Sáez (2003), Lamilla & Bustamante (2005) and Bustamante et al. (2014 a, b).

In the southwest Atlantic *Z. chilensis* is reported in systematics lists and field guides for marine fishes of Argentina and Uruguay (Ringuelet & Aramburu 1960, López 1963b, Menni et al. 1984, López et al. 1989, 1996, Lloris & Rucabado 1991, Nion et al. 2002, Bovcon & Cochía 2007, Ruarte et al. 2009). Both *Z. chilensis* and *D. trachyderma* were identified as part of the chondrichthyan fauna of Argentina and Uruguay (Menni & Lucifora 2007, Cousseau et al. 2000, 2007, Perier et al. 2011), and from Falkland Island waters (Bizikov et al. 2004). In Brazilian waters, the presence of *D. trachyderma* has been made indirectly, through taxonomic lists (Gomes & Picado 2001) and parasite studies (Knoff et al. 2001 a, b, 2002, 2004). The misspelling of *D. trachyderma* (as *D. trachydermus* by López et al. 1989) and the incorrect citation of the year of its original description may lead to confusion in the literature (Compagno 1999, 2005 a, b, Kyne & Simpfendorfer 2007, 2010).

**Distribution:** Of the two genera of longnose skates, *Zearaja* is restricted to the Southern Hemisphere
(Beentjes et al. 2002, Cousseau et al. 2007, Last & Gledhill 2007, Bustamante et al. 2014 b), while Dipturus has a worldwide distribution (Gomes & Picado 2001, Soto & Mincarone 2001, McEachran & Carvalho 2002, Gedamke et al. 2005, Ellis et al. 2005 a, b, Díaz de Astarloa et al. 2008, Last et al. 2008 a, Cannas et al. 2010, Schwartz 2012, Last & Alava 2013, Bustamante et al. 2014 b). The greatest species diversity of longnose skates occurs on the continental slope, but they are also present in demersal areas of the continental shelf worldwide (Ebert & Compagno 2007).

In the southeast Pacific, Z. chilensis occurs in cold-temperate waters off Chile between 32° S and 56° S (Figure 6), although there are dubious records around 29° S (Delfín 1902), and the type locality Quinteros Bay (32° S), central Chile (Philippi 1892). The historical absence of records between 1848 and 1892 may be explained by the relative undeveloped fishing activities in the region where the skates may occur that later provided most of the observations. The known range of Z. chilensis in Chile currently includes the central and austral zones (Figure 6). The presence of D. trachyderma

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**Fig. 6.** Distribution of the yellownose skate *Zearaja chilensis* in South America. The numbers represent documented records following (1) Philippi (1892), (2) Delfín (1902), (3) Lührnberg (1907), (4) Gotschlich (1913), (5) Norman (1937), (6) De Buen (1959), (7) Carvajal (1971), (8) Menni (1973), (9) Sadowsky (1973), (10) Ojeda (1983), (11) Raschi (1986), (12) Fernandez & Villalba (1985), (13) Leible (1987), (14) Leible et al. (1990), (15) Lloris & Rucabado (1991), (16) Lucifora et al. (2000), (17) Gomes & Picado (2001), (18) Koen Alonso et al. (2001), (19) Cespedes et al. (2005), (20) Licandeo et al. (2006), (21) Cousseau et al. (2007), (22) Licandeo & Cerna (2007), (23) Aburto et al. (2008), (24) Díaz de Astarloa et al. (2008), (25) Quiroz et al. (2009), (26) Silveira (2009), (27) Arkhipkin et al. (2012), (28) Bustamante et al. (2012), (29) Deli Antoni et al. (2012), (30) Bustamante et al. (2014 a). Filled circle indicates the holotype locality.
in Chile was documented from specimens collected in central and south Chile by Leible & Stehmann (1987), although its current range also includes waters off Patagonia and austral Chile (Figure 7). Overall, *Z. chilensis* and *D. trachyderma* seem to have the same distribution in Chilean waters (32° S – 56° S), but this range may be biased considering that most documented records come from the demersal longline fishery which operates over this latitudinal range. Fishery independent surveys northwards of 32° S and southwards of 56° are required to confirm latitudinal boundaries (Bustamante et al. 2014 a). No longnose skates have been reported from around Chile’s oceanic islands in the southeast Pacific although the areas have been sampled (Andrade & Pequeño 2008).

In the southwest Atlantic, the presence of *Z. chilensis* is documented along the Argentinian coast, from 34° S to 54° S, and including the Falkland Islands (Figure 6). Early records suggested that *D. trachyderma* in the southern Atlantic was restricted to Argentinian waters (Krefft & Stehmann 1975, Menni & Gosztonyi 1977, 1984). The numbers represent documented records following (Fig. 7. Distribution of the roughskin skate *Dipturus trachyderma* in South America. The numbers represent documented records following (1) Krefft & Stehmann (1975), (2) Menni & Gosztonyi (1977), (3) FRV “Walther Herwig” (1978), (4) FRV “Holmberg” (1983), (5) Menni et al. (1984), (6) Leible & Stehmann (1987), (7) Lloris & Rucabado (1991), (8) Cousseau et al. (2000), (9) Gomes & Picado (2001), (10) Knoff et al. (2001), (11) Cedrola et al. (2005), (12) Cespedes et al. (2005), (13) Díaz de Astarloa et al. (2008), (14) Lamilla et al. (2010), (15) Perier et al. (2011), (16) Arkhipkin et al. (2012), (17) Lamilla et al. (2012 a), (18) Lamilla et al. (1995), (19) Bustamante et al. (2014 b). Filled circle indicates the holotype locality.
Menni et al. 1984), but recent records show that it co-occurs with *Z. chilensis* around the Falkland Islands (Figure 7), and *D. trachyderma* has also been documented off southern Brazil (Gomes & Picado 2001, Knoff et al. 2001), although the occurrence of the species north of 40° S needs to be further explored.

*Dipturus trachyderma* has been characterised as an endemic species of the Magellanic Province (see Bustamante et al. 2014 b), which is a relatively stable biogeographic region with cold water masses distributed from latitude 42° to 56° S in Chile and Argentina (Camus 2001), but with an influence across the continental slope up to 36° S (Balech & Ehrlich 2008). The thermal barrier produced by the warm tropical water masses of the Argentinian Province (Menni et al. 2010), which extends from Rio de Janeiro (23° S) to Valdes Peninsula (42° S), may restrain ‘Magellanic Province species’ to the continental shelf of Argentina. The absence of records of *D. trachyderma* from latitude 32° S to 41° S in the southwest Atlantic raises questions about its proposed presence in Brazilian waters (Gomes & Picado 2001) 1.500 km north of confirmed Argentinian records. As such, records of *D. trachyderma* northwards Río de la Plata are considered of doubtful validity and specimens from Brazil may represent a misidentification of species of similar appearance, such as *D. menni*.

**Habitat:** The longnose skates, *Z. chilensis* and *D. trachyderma*, are distributed in cold-temperate waters of South America, inhabiting the continental shelf and slope of central Chile to southern Brazil at depths of 14 – 477 m (Norman 1937, Leible & Stehmann 1987, Agnew et al. 2000, Menni & Stehmann 2000, Gomes & Picado 2001, Bustamante et al. 2014 b). Sea temperature and salinity preferences for these species in the southwest Atlantic are reported to be 3.5 – 14 °C and 32.2 – 34.3 parts per thousand (ppt) respectively for *Z. chilensis* (Menni 1973, Menni & Lopez 1984, García de la Rosa 1998), and 4.0 – 8.2 °C and 33.1 – 33.6 ppt for *D. trachyderma* (Krefft & Stehmann 1975, Menni & Gosztonyi 1977, Menni et al. 2010, Arkhipkin et al. 2012).

*Zearaja chilensis* appears to be relatively common at depths of 14 – 100 m (Menni & Lopez 1984, Leible et al. 1990, García de la Rosa 1998, Concha et al. 2012), it is abundant at 150 – 350 m (Menni & Gosztonyi 1977, Menni & Lopez 1984, Leible 1987, Leible et al. 1990, Licandeo et al. 2006, Quiroz et al. 2009, Arkhipkin et al. 2012), but can be found at depths of up to 450 m (Ojeda 1983, Menni & Lopez 1984, Fuentecolba & Leible 1990, García de la Rosa 1998). In contrast, *D. trachyderma* appears less abundant in shallow waters (a single specimen reported at 20 – 22 m in the Beagle Channel (Lloris & Rucabado 1991), and catches reported at 87 – 97 m in San Jorge Gulf (Cedrola et al. 2005)), seems most common at 180 – 350 m (Krefft & Stehmann 1975, Menni & Gosztonyi 1977, Bizikov et al. 2004, Lamilla et al. 2010, Menni et al. 2010, Arkhipkin et al. 2012), but there are records from 400 – 500 m (Leible & Stehmann 1987, Gomes & Picado 2001).

**Feeding habits:** Diet, food consumption and feeding habits of longnose skates have been studied for a number of species, mainly from by-catch fisheries of Patagonia (Koen Alonso et al. 2001), Tasmania (Treloar et al. 2007), Barents Sea (Dolgov 2005), South Africa (Ebert et al. 1991), the north-west Atlantic Ocean (Templeman 1982), and south-west Atlantic Ocean (Lucifora et al. 2000). In their analysis of skate diets, Ebert & Bizarro (2007) showed that five species of *Dipturus* had estimated trophic levels of between 3.52 and 4.06, whereas *Z. chilensis* had a trophic level of 4.22, with the prey category ‘teleost fishes’ of the greatest dietary importance (81.8%) followed by ‘squid’ (11.6%). Although *Z. chilensis* had the highest trophic level of all of the 60 skate species examined, the estimated level probably reflected a sampling bias for larger specimens as it is well-known that the diet and trophic level of many elasmobranchs often changes with body size. For *Z. chilensis* it has been shown that crustaceans form the main prey category for skates of < 50 cm TL (Bahamonde 1953, De Buen 1959, Sánchez & Prenski 1996, Koen Alonso et al. 2001), which would result in a trophic level of about 3.5. Whereas, as *Z. chilensis* increases in size the importance of ‘teleost fishes’ (particular Argentinian hake *Merluccius hubbsi*) in the diet increases dramatically (Sánchez & Prenski 1996, García de la Rosa 1998, Lucifora et al 2000, Koen Alonso et al. 2001, Sánchez & Mabragaña 2002), which would likely result in a higher trophic level.

While there is information on the diets of various species in the genus *Dipturus* that suggests that they feed primarily on decapod crustaceans and, secondarily, on teleost fishes (Ebert & Bizarro 2007, Treloar et al. 2007, Kyne et al. 2008, Simon et al. 2009, Yigin & Ismen 2010, Forman & Dunn 2012), the only information for
D. trachyderma is from a single individual of 242 cm TL in which four hake (M. hubbsi), one sand skate (Psammobatis sp.) and the remains of Antarctic king crab (Lithodes sp.) were found (Cousseau et al. 2007).

Reproduction: All members of the family Rajidae are oviparous (Wourms 1977, Carrier et al. 2004), and mature females of both Z. chilensis and D. trachyderma have two functional ovaries and paired uteri. For Z. chilensis the ovaries initiate development of vitellogenic oocytes, indicative of maturity, when females reach 940 – 1039 mm TL, whereas males mature at 760 – 900 mm TL (Fuentalba & Leible 1990, Licandeo et al. 2006, Paesch & Oddone 2008, Quiroz et al. 2009, Bustamante et al. 2012). For D. trachyderma, the oviducal glands and uteri enlarge when females mature at about 2000 mm TL. In males maturity occurs at around 1860 mm TL based on clasper size and calcification (Licandeo & Cerna 2007).

Oviparity as occurs in skates is a specialized strategy since it is based on the advantages of producing small numbers of large eggs and competent newborns (Wourms 1977). Information related to ovarian fecundity is rare, but oocyte counts for Z. chilensis of 70, 22 – 62, and 24 – 84 have been made by Fuentealba & Leible (1990), Licandeo et al. (2006) and Licandeo & Cerna (2007) respectively. For D. trachyderma, ovarian fecundity is 28 – 68 follicles (Licandeo et al. 2007). Only one egg capsule per oviduct has been documented for both species, and it is assumed that there is a single embryo per egg case as there are only rare exceptions to this (big skate Beringraja binoculata (Girard, 1855) and mottled skate Raja pulchra Liu, 1932 which have up to four embryos per egg case (Ebert & Winton 2010)).

Gestation period for Z. chilensis and D. trachyderma has not been reported, but incubation periods for oviparous batoids may last from a few months to over a year (Carrier et al. 2004). There are no reports on the mating behaviours of Z. chilensis or D. trachyderma.

Age, growth and longevity: Estimation of age-at-maturity, longevity, and growth rate, coupled with knowledge of reproductive output, are mainstays for stock assessment and demographic models that allow for the estimation of intrinsic productivity, resilience, vulnerability, and how populations may change over time (Ricker 1975, Cailliet et al. 1986, Cailliet & Goldman 2004). A variety of mineralised structures may be used for age and growth estimation in chondrichthyans, i.e., vertebrae (Francis et al. 2001, Gedamke et al. 2005, Ainsley et al. 2014, Natanson et al. 2014), dermal denticles (Moura et al. 2004, Campana et al. 2006, Serra-Pereira et al. 2008), and caudal thorns (Henderson et

| Species | Sex | L_∞ (mm TL) | k | t₀ | t_max | t₅₀ | L₅₀ (mm TL) | Reference |
|---------|-----|-------------|---|----|-------|----|-----------|-----------|
| Zearaja chilensis | ♀ | 1456 | 0.084 | -1.534 | 24 | – | 1068 | Céspedes et al. 2005 |
| | ♂ | 1248 | 0.972 | -1.655 | 21 | – | 822 | Céspedes et al. 2005 |
| | ♀ | 1283 | 0.112 | -0.514 | 27 | 14 | 1060 | Licandeo et al. 2006 |
| | ♂ | 1078 | 0.134 | -0.862 | 23 | 11 | 860 | Licandeo et al. 2006 |
| | ♀ | 1364 | 0.104 | -0.669 | 21 | 13.49 | 1031 | Licandeo & Cerna 2007 |
| | ♂ | 1179 | 0.116 | -1.056 | 17 | 10.74 | 879 | Licandeo & Cerna 2007 |
| | ♀ | 1496 | 0.087 | -1.266 | 22 | 12.75 | 1035 | Licandeo & Cerna 2007 |
| | ♂ | 1220 | 0.11 | -1.263 | 19 | 10.31 | 871 | Licandeo & Cerna 2007 |
| Dipturus trachyderma | ♀/♂ | 2848 | 0.067 | -0.443 | 27 | – | 1940 | Céspedes et al. 2005 |
| | ♂ | – | – | – | – | – | 1540 | Céspedes et al. 2005 |
| | ♀ | 2630 | 0.079 | -1.438 | 26 | 17 | 2150 | Licandeo et al. 2006 |
| | ♂ | 2465 | 0.087 | -1.157 | 25 | 15 | 1951 | Licandeo et al. 2006 |
al. 2004, Francis & Ó Maolágin 2005, Arkhipkin et al. 2008, Francis & Gallagher 2009). A popular ageing technique in elasmobranchs is the sagittal-sectioning of vertebral centra from the thoracic region (Cailliet et al. 2006). Generally, growth band pairs are visible, to a greater or lesser degree, within each centrum from anterior vertebrae of sharks (Goldman 2004) and posterior vertebrae of batoids (Francis et al. 2001, White et al. 2001, Licandeo et al. 2006, Pierce & Bennett 2010).

Age and growth of *Z. chilensis* may be influenced by the geographic location, based on life-history trait differences found for this species in southern Chile (Licandeo & Cerna 2007). Estimated maximum age for females is 21 – 27 years, and 17 – 23 years for males (see Table 2), which is considerably older than the 9 years reported for the congeneric species *Z. nasuta* (Francis et al. 2001). However, estimates of age for *Z. chilensis* conducted prior to 2000 may have been confounded by inclusion of *D. trachyderma* specimens among the samples examined (Fuentealba & Leible 1990, Fuentealba et al. 1990, Bahamonde et al. 1994, 1996, Gili et al. 1999). The estimated maximum age of *D. trachyderma* in Chilean waters, determined through the use of the same vertebral analytical approach, was 26 years for females and 25 years for males (Licandeo et al. 2007), which is consistent with an estimated maximum age of 27 years for the sexes combined (Céspedes et al. 2005) (Table 2).

Fig. 8. Spatial distribution of the *Zearaja chilensis* and *Dipturus trachyderma* fishery in Chile, indicating main fishing locations and the extension of the artisanal (dark green) and industrial fisheries (light green).
Dipturus trachyderma grows to a large size for a skate and has a preference for cold-water habitats, the combination of which might be expected to be reflected in considerable longevity. The estimated maximum age of D. trachyderma in Chilean waters, determined through the use of the same vertebral analytical approach as for Z. chilensis is 26 years for females and 25 years for males (Licandeo et al. 2007), which is consistent with an estimated maximum age of 27 years for the sexes combined (Céspedes et al. 2003) (Table 2). Other large skate species, such as Bathyraja griseocauda (Norman, 1937) (Arkhipkin et al. 2008), D. batis (Du Buit 1972), D. innominatus (Francis et al. 2001), B. binoculata and Raja rhina Jordan & Gilbert, 1880 (McFarlane & King 2006) also live to over 20 years of age. The concern is that larger species that have slow growth rates and are long lived are particularly vulnerable to population collapse, as has been suggested for Z. chilensis (Agnew et al. 2000, Bustamante et al. 2012).

Fisheries in the southeast Pacific: In Chile the directed fishery for skates started in 1979 and initially targeted Z. chilensis. However, until 2004 at least six skate species including Z. chilensis and D. trachyderma were landed under the generic category of ‘skate’ in official records (Gili et al. 1999, Roa & Ernest 2000). Recently, the take of skates as bycatch in demersal fisheries for southern hake Merluccius australis (Hutton, 1872) and pink ling Genypterus blacodes (Forster, 1801) has become an attractive economic activity for many artisanal fishermen as a result of the commercial value and market demand for large skates. Overall, the skate fishery is geographically extensive, covering around 20 degrees of latitude from San Antonio to Punta Arenas (Figure 8), but with most of the fishing effort between Valdivia and Aisén. The Chilean Fishing Authority identifies two main components within the fishery: (1) Industrial vessels (over 18 m length) that have restricted fishing zones outside of five nautical miles off the coast. These vessels operate southward 41°28.6’ S and can only land skates as bycatch; (2) Artisanal vessels (12 – 17 m length), that are managed through fishing quotas.

Landings and fishing effort have increased steadily since 1993, when the fishery was opened to the Asian market. The artisanal fleet expanded due to international investment and, together with the industrial fishery, reported 3000 tonnes (t) in landings in 1994 (Figure 9). This artisanal fleet with approximately 1900 vessels accounts for 70% of national landings, whereas only 5 vessels in the industrial trawling fleet that targets hake are authorised to land skates as bycatch, which represents 20 – 25% of total catch. In 1997, fishing management measures were established that included annual catch

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**Figure 9.** Total longnose skate landings in Chile between 1979 and 2012 by fishery and species. Total catch is represented by the solid line. Artisanal (dashed line) and industrial (dotted line) landing are indicated for the ‘skates’ landing category (black), Dipturus trachyderma (green) and Zearaja chilensis (blue). [Note: Z. chilensis and D. trachyderma were officially separated into different landing categories by the Fishing Authority in 2004].
quotas between the Concepción and the parallel 41°28.6´S (Figure 8). During the Asian financial crisis in 1998, skate landings increased considerably peaking at 4000 t and 5193 t in 2000 and 2003 respectively, where approximately 85% was caught solely by the artisanal fleet (Figure 9). Skate landings subsequently decreased by about 40% (to about 1500 t per annum) over the following decade (SERNAP, 2012).

The yellownose skate *Z. chilensis* is caught in Chile as a target species, but also as a secondary target species in teleost and shark fisheries, i.e. South Pacific hake *Merluccius gayi* (Guichenot, 1848), pink ling *G. blacodes*, sand flounder *Paralichthys micros* (Günther, 1881), corvina drum *Cilus gilberti* (Abbott, 1899), black ling *Genypterus maculatus* (Tschudi, 1846) and spiny dogfish *Squalus acanthias* L., 1758, (Lamilla et al. 2008, 2010, Bustamante et al. 2012). However, the roughskin skate *D. trachyderma* is only observed as a ‘secondary target’ species (>25% of total catch by mass per fishing trip) in yellownose skate and pink ling fisheries, and apparently peaked at about 60 t in 2006 (Figure 10). However, landing records of *D. trachyderma* are underestimated as adult skates (>10 kg) are processed on-board and only their fins are landed (Lamilla 2005), while *Z. chilensis* is landed and sold complete (ungutted). Although only target skates (*Z. chilensis* and *D. trachyderma*) are identified and recorded in landing records, at least another four skates, *Bathyraja albomaculata* (Norman, 1937), *B. brachyurops* (Fowler, 1916), *B. griseocauda* and *Rajella sadowskii* (Krefft & Stehmann, 1974) are landed as bycatch and reported in a generic category without taxonomic identity which represents 5% of the national landings (Lamilla et al. 2010).

After 2006, a temporal fishing closure was imposed on the artisanal fleet which operates during the austral summer months (December – February) to protect ‘possible reproductive events’ (Lamilla 2005). Subsequently, in 2009 – 2011, a total fishing closure was imposed on the entire fishery in response to landing size and overall biomass decline, but despite these ‘closures’, the government continues to allocate national catch quotas of up to 700 t annually as a result of political pressures and lobbying.

The current skate fishery in Chile is considered to be ‘fully exploited’; however, information on stock structure of longnose skates is lacking, which confounds assessment, management and resource allocation. The high percentage of juveniles present in catches, the decreasing trend of the catch size, as well as the constant fishing effort and landings, are symptoms of a fishing collapse as suggested for *Z. chilensis* (Bustamante et al. 2012). Sustainable harvest requires management strategies based on comprehensive knowledge of the

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Fig. 10. Total landings of *Dipturus trachyderma* between 2004 and 2012 by fishery type: artisanal (black) and industrial (green).
biology and ecology of biological stocks, especially for longnose skates that have intrinsic life history patterns that make them highly susceptible to commercial over-exploitation (Dulvy et al. 2000, 2014, Dulvy & Reynolds 2002, Frisk 2010).

**Fisheries in the southwest Atlantic:** A different situation is observed for the zone that includes waters off Argentina, Uruguay and the Falkland Islands where longnose skates are only caught as bycatch in several trawl fisheries (Paesch & Oddone 2008). An analysis of landing records of marine fishes in Argentina from 1898 to 2010 conducted by Sánchez et al. (2012) has little information about *Z. chilensis* which only appears in catch records after 2008, and nothing about *D. trachyderma* which is not reported in any landing category.

Some information is available however, from incidental capture records for *Z. chilensis* and *D. trachyderma* in the Patagonian red shrimp *Pleoticus muelleri* (Spence Bate, 1888) and the Argentine hake *M. hubbsi* Marini, 1933 fisheries (Angelescu et al. 1958, Cedrola et al. 2005, Estalles et al. 2011). Falkland Islands fisheries have reported *Z. chilensis* as an abundant species since 1993, where it is caught in the multi-species skate fishery, with approximately 16 other skate species (Agnew et al. 2000, Falkland Islands Government 2014). Cedrola et al. (2005) reported that the skate bycatch (1.6 – 1.9% of the total catch) in the *P. muelleri* fishery in San Jorge Gulf comprises seven species, included *Z. chilensis* as the most frequently caught, with a total biomass of 2,135 kg (55.6% of the bycatch by mass). *Dipturus trachyderma* was only present in 9.3% of hauls, with a total biomass of 829 kg (55.6% of the bycatch by mass).

**Genetics:** Molecular analysis has become a standard tool in the study of elasmobranch populations, and is used predominantly to estimate phylogenetic relationships and to define population structure (Heist 2004 a, Portnoy 2010, Dudgeon et al. 2012). Genetic methods have been increasingly used to analyse stock structure and connectivity, to identify specimens to species level (considering the presence of sister and cryptic species) and to identify body parts, such as shark fins from markets (Lavery & Shaklee 1991, Shivji et al. 2002, 2005, Heist 2004 a, Clarke et al. 2006, Griffiths et al. 2010), aiding fisheries management and conservation (Heist 2004 b, Ovenden et al. 2009, 2010). The first application of molecular/genetic methods in relation to *Z. chilensis* and *D. trachyderma* was to identify species through protein electrophoresis and DNA molecular markers, based on 100 individuals from Chilean waters (Céspedes et al. 2005). Using protein electrophoresis, the authors were able to match species to field identification in most cases (88%), but failed to amplify nuclear and mitochondrial regions through PCR, arguing a lack of species-specific primers and that the species are very closely related. Later, Díaz de Astarloa et al. (2008) attempted to sequence the *cox1* region of the mitochondrial DNA (mtDNA) from five specimens of *Z. chilensis* and two of *D. trachyderma* from Argentinian waters. The authors were able to distinguish *Z. chilensis* from other *Dipturus* species, but *cox1* gene amplification for *D. trachyderma* failed ‘as a result of mutational differences within the primer sites’, indicating that *D. trachyderma* possessed a significantly divergent *cox1* haplotype of its own. Using primers for *nad1*, eight specimens of *Z. chilensis* were sequenced from a single locality in Chile (Naylor et al. 2012), and they were able to differentiate them from the congeneric species *Z. nasuta*, and also from the biological entity identified as ‘*Z. flavirostris*’ from the Falkland Islands (despite of being a secondary homonym of *Z. chilensis*) (Last & Gledhill 2007). Possible mismatch between Argentinian specimens may be related to the species’ geographical distribution polymorphism (Leible et al. 1990).

Recently, Jeong & Lee (2014) provided what was ostensibly a description of the complete mitochondrial genome of *Z. chilensis*. The structure of the mitogenome is similar to those of other skates, with 16,909 base-pairs (bp) in length and comprising 13 protein-coding regions, 22 tRNA genes, 2 rRNA genes and 2 non-coding areas.
However, Vargas-Caro et al. (2014) compared the mitochondrial genome of *Z. chilensis* by Jeong & Lee (2014) with one from Chilean waters and found 97.4% similarity (instead of close to 100% as might be expected). As the tissue sample used by Jeong & Lee (2014) was taken from a raw fillet in a Korean restaurant (without examination of the specimen), the 2.6% of difference may indicate the presence of two separate stocks of *Z. chilensis* in South America, or two different species. The uncertainties highlight the need for caution when using genetic resources without a taxonomic reference or voucher specimens (Vargas-Caro et al. 2014).

### Parasites

Parasites have been widely used as biological ‘tags’ to provide information for fisheries management on the movements and population discreteness of their fish hosts (Lester 1990, Moser 1991, Williams et al. 1992, MacKenzie 2002). Basically, a fish can become infected by a parasite only when it is within the endemic area of that parasite. The more parasites with different endemic areas that can be used as biological ‘tags’, the better the information that will be obtained about the past movements of fish populations and, hence, about the stock structure (MacKenzie & Abaunza 2013). Parasite load studies have particular value in deep waters, where standard tagging and recapture methods can be difficult (Mosquera et al. 2003). The use of parasites as an auxiliary tool is well documented for teleost fishes; however there is little information for chondrichthyans (Moore 2001). Approximately 20 parasites have been described to generic or species level from specimens of *Z. chilensis* (*n* = 12) and *D. trachyderma* (*n* = 8) and these have been summarized in Table 3 and 4 respectively.

### Table 3. Parasites reported to infect the yellownose skate *Zearaja chilensis*.

| Species Reference |
|-------------------|
| **Platyhelminthes: Cestoda** |
| Order Tetraphyllidea; Family Onchobothridae |
| *Acanthobothrium annapinkiensis* Carvajal & Goldstein (1971) |
| Order Tetraphyllidea; Family Phyllobothriidae |
| *Ehrenboothrium magalosoma* Carvajal & Dailey (1975), Leible et al. (1990) |
| *Ehrenboothrium multiloculatum* Carvajal & Dailey (1975), Carvajal et al. (1985), Leible et al. (1990) |
| *Ehrenboothrium williamsi* Leible et al. (1990) |
| *Phyllobothrium sp.* Leible et al. (1990) |
| Order Trypanorhyncha; Family Grillotiidae |
| *Grillotia dollfusi* Carvajal & Goldstein (1971), Leible et al. (1990) |
| **Platyhelminthes: Trematoda** |
| Order Plagiocotida; Family Azinyidae |
| *Ondistomum cestoides* Threlfall & Carvajal (1986), Abursto et al. (2008) |
| **Phylum Nematoda: Rhabditida** |
| Order Ascaridida; Family Anisakidae |
| *Anisakis sp.* Fernández & Villalba (1985) |
| *Pseudoterranova sp.* |
| Order Spirurida; Family Physalopteridae |
| *Proleptus Carvajali* Fernández & Villalba (1985) |
| **Arthropoda: Maxillopoda** |
| Order Cyclopoida; Family Chondracanthidae |
| *Acanthochondrites sp.* Fernández & Villalba (1985) |

### Table 4. Parasites reported to infect the roughskin skate *Dipturus trachyderma*.

| Species Reference |
|-------------------|
| **Platyhelminthes: Cestoda** |
| Order Trypanorhyncha; Family Tentacularidae |
| *Myxobothrium beveridgei* Knoff et al. (2002, 2004) |
| Order Trypanorhyncha; Family Lacinosthrydinae |
| *Paragrillotia sp.* Leible et al. (1990) |
| Order Tetraphyllidea; Family Phyllobothriidae |
| *Phyllobothrium c.f. lactuca* Leible et al. (1990) |
| **Platyhelminthes: Trematoda** |
| Order Plagiocotida; Family Azinyidae |
| *Ondistomum volviferum* Knoff et al. (2001 b), Kohn et al. (2007) |
| **Nematoda: Rhabditida** |
| Order Ascaridida; Family Anisakidae |
| *Anisakis sp.* |
| *Contracaecum sp.* Knoff et al. (2001 a) |
| *Raphidascaris sp.* |
| **Acanthocephala: Palacanthocephala** |
| Order Echinorhynchida; Family Rhadinorhynchidae |
| *Gorgorhynchus sp.* Knoff et al. (2001 b), Saritos et al. (2008) |
Sites of infection are mostly the stomach and the spiral valve, but mouth and gills are also documented (Villalba & Fernández 1985).

Conclusions

For the first time, available information concerning *Zearaja chilensis* and *Dipturus trachyderma* has been reviewed in a single assessment. Conservation is the act of guarding and protecting biodiversity, and involves management, but defining a taxonomic entity is the first step for conservation. Here we provide taxonomic clarity, and collate all relevant information with regard to the biology, ecology and fisheries that impact these species.

The yellownose skate *Z. chilensis* and the roughskin skate *D. trachyderma* require particular attention to mitigate the chance of population collapse in South American waters. Population decline and symptoms of fishing collapse have already been documented for *Z. chilensis* and current research has provided strong evidence that longnose skates have a high potential risk of near-future extinction. Given the growing concern for longnose skate populations, there is a strong ongoing need for science to help improve community understanding and the conservation management of the species to ensure their long-term sustainability. In this review we have highlighted the knowledge gaps that need to be addressed in order to better understand the biology and ecology of the species and the key threatening processes.

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Conflicts of interest

We declare no conflict of interest regarding the results published in this article.

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Una revisión sobre las rayas de hocico largo *Zearaja chilensis* y *Dipturus trachyderma* (Rajiformes: Rajidae)

**Resumen.** Las rayas de nariz larga tienen una alta vulnerabilidad intrínseca entre los peces, debido a su gran tamaño corporal, bajas tasas de crecimiento y relativamente baja fecundidad; por otra parte, el hecho de ser blanco de explotación pesquera coloca a su población bajo una presión considerable. Las rayas de nariz larga se encuentran alrededor del mundo en aguas costeras subtropicales y templadas. Aunque se han registrado a lo largo de 150 años en Suramérica, los críticos vacíos de información que aún persisten comprometen la capacidad de determinar el estatus de estas especies. Con base en una revisión de 185 publicaciones, se realizó una síntesis comparativa de la biología y ecología de dos de las especies de elasmobranquios comerciales de aguas suramericanas: la raya volantín (*Zearaja chilensis*) y la raya espinosa (*Dipturus trachyderma*). Se examinaron y compararon su taxonomía, distribución, hábitos alimenticios, reproducción, crecimiento, longevidad y explotación pesquera. El número de estudios publicados sobre ambas especies se ha incrementado considerablemente desde 2000 y especialmente después de 2005, aunque algunos tópicos de investigación permanecen poco entendidos. Considerando la similitud morfológica externa de las rayas de nariz larga, especialmente en sus estadios juveniles, y que su nicho potencial se superpone tanto en profundidad como en latitud, se recomienda determinar su estacionalidad reproductiva, con el fin de asegurar su sostenibilidad en el largo plazo.

**Palabras clave:** biología de la conservación; pesquería; raya volantín; Suramérica; raya espinosa

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Uma revisão das raias longnose *Zearaja chilensis* e *Dipturus trachyderma* (Rajiformes: Rajidae)

**Resumo.** Raias longnose podem ter uma elevada vulnerabilidade intrínseca entre os peixes, devido ao seu grande tamanho de corpo, taxas lentas de crescimento e fecundidade relativamente baixa, e sua exploração como espécies alvo de pesca coloca suas populações sob considerável pressão. São encontradas ao redor do mundo em águas costeiras subtropicais e temperadas. Embora raias longnose hajam sido registradas por mais de 150 anos na América do Sul, a capacidade de avaliar o status dessas espécies ainda é comprometida por lacunas críticas de conhecimento. Com base em uma revisão de 185 publicações, uma síntese comparativa da biologia e ecologia foi realizada uma síntese comparativa da biologia e ecologia de duas espécies de elasmobrânquios comerciais de águas sul-americanas, a raya nariz-amarelo (*Zearaja chilensis*) e a raia pele-áspera (*Dipturus trachyderma*); com vistas a analisar e comparar a sua taxonomia, distribuição, pesca, hábitos alimentar, reprodução, crescimento e longevidade. Houve um aumento acentuado no número de estudos publicados para ambas as espécies desde 2000, e especialmente depois de 2005, embora alguns tópicos de investigação permaneçam pouco compreendidos. Considerando as similaridades morfológicas exteriores das raias longnose, especialmente quando jovens, e a potencial sobreposição de nichos ocupados tanto em relação a profundidade quanto a latitude, recomenda-se que a sazonalidade reprodutiva seja avaliada para assegurar a sua sustentabilidade em longo prazo.

**Palavras-chave:** biologia da conservação; pesca; raya pele-áspera; América do Sul; raya nariz-amarelo