Journal of Shellfish Research, Vol. 29, No. 2, 423–428, 2010.

REPRODUCTIVE SEASONALITY AND OVIPOSITION INDUCTION IN *TROPHON GEVERSIANUS* (GASTROPODA: MURICIDAE) FROM GOLFO NUEVO, ARGENTINA

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ABSTRACT The reproductive biology of a population of the edible muricid *Trophon geversianus* inhabiting an intertidal rocky shore in Golfo Nuevo (Chubut, Argentina) was studied regarding the seasonality of oviposition and oviposition induction under laboratory conditions. Sex ratio in the population differed from 1:1 (female biased). The mean shell length was 22 mm for males and 24 mm for females, although the females presented significantly larger maximum sizes. No external sexual dimorphism was evident, whereas the female snails differed internally by the presence of the albumin and capsule gland and by gonad color. Although the population under study inhabits an area with marine traffic and a concentration of 1.9 ng Sn/g, it did not present signs of imposex, in contrast with other sympatric species. *T. geversianus* presented a marked reproductive seasonality during the study period. Oviposition started in May and concluded in November, when hatching of crawling embryos was registered up to January. This seasonality coincided with changes in water surface temperature, ambient temperature, and photoperiod. Reproductive activities were registered when the environmental stress was minimum. In the aquarium, each female laid an average of 12 egg capsules (range, 6–26) per oviposition event, and needed a total of 25 h (range,12–57 h) to complete attachment of a single egg capsule. Data presented here could be useful for culture of the species.

KEY WORDS: rocky shores, reproductive seasonality, imposex, oviposition, egg capsules, gastropod, *Trophon*

INTRODUCTION

Small-scale fisheries, and specifically the benthic invertebrate fisheries, have played an important role in the development of new fishery management principles and tools. Within them, marine gastropods represent about 2% of the world mollusc catches (Leiva & Castilla 2002). Reproductive biology provides valuable information for fisheries and, in particular, the reproductive cycle is a basic component of analysis of population dynamics in gastropods (Underwood 1979), facilitating the development of fishery policies or culture plans of species with commercial interest.

The Muricidae is an economically important family of predatory marine gastropods (Benkendorff et al. 2004). Many species are relatively large and harvested commercially as a source of food (Gallardo 1973, González & Gallardo 1999). There are several published studies on the reproductive biology of Muricidae species, among them are *Thais emarginata* (Le Boeuf 1971), *Concholepas concholepas* (Ramorino 1975, Castilla & Cancino 1976, Garrido & Gallardo 1993), *Chorus giganteus* (Gallardo 1981), *Oecenebra erinacea* (Hawkins & Hutchinson 1988), *Thais clavigera* and *Morula musiva* (Tong 1988), *Thais haemastoma canaliculata* (Roller & Stickle 1989), *Trophon geversianus* (Santana 1998), *Plicopurpura pansa* (Naegel & Gómez del Prado-Rosas 2004), *Thais* (*Stramonita*) *chocolata* (Romero et al. 2004), and *Coronium coronatum* (Pastorino et al. 2007). This family presents several species with commercial relevance involved in regional fisheries all over the world. The biology, ecology, and fishery of the muricid *C. concholepas* (''loco'') have been intensively investigated in Chile (previous citations and Castilla 1974, Castilla 1988, Di Salvo 1988, Gallardo 1994, Lara & Montes 1989).

Gastropod catches in Chile include at least 20 different species, several of which belong to the families Muricidae and Fissurellidae (Leiva & Castilla 2002). During the past two decades, exportation of *C. concholepas* has generated revenues for Chile of more than US$390 million (SERNAPESCA 1999). Other muricid species extracted commercially in Chile are *T. chocolata*, *C. giganteus*, *T. geversianus*, and *Xantochorus cassidiformis* (Leiva & Castilla 2002).

Historical analysis reveals that benthic shellfish populations in Latin America are becoming increasingly limited, catch has begun to drop, and stocks are fully to heavily exploited, overexploited, or depleted (Castilla & Defeo 2001). The ''nonloco'' gastropod fisheries were subject to few regulation measures (e.g., minimum catch sizes and closure during reproductive seasons) despite their sustained decline in catches since 1990 (Leiva & Castilla 2002).

The Muricidae are an important component of marine communities around the world, with more than 1,150 species grouped in 8 subfamilies (Vokes 1996). Particularly, the subfamily Trophoninae is one of the most conspicuous groups of marine gastropods living currently around the southern tip of South America (Pastorino 2005). Within this group, *T. geversianus* (Pallas, 1774) has the widest geographical range of the genus; it is distributed from Buenos Aires province to Burdwood Bank in the southwestern Atlantic, Tierra del Fuego and Malvinas islands, and along the southeast Pacific coast from 42°S to 56°S between Isla Grande of Chiloé and the Cabo de Hornos (Castellanos & Landoni 1993, Pastorino 2005, Griffin & Pastorino 2005). The species' total shell length measures up to 100 mm and is extremely variable in shape (Pastorino 2005). It is gonochoric with internal fertilization and direct embryonic development, with the presence of nurse eggs in the egg capsule as supplementary food (Penchaszadeh 1976). The species has a low reproductive potential with slow and long-lived growth. In Chile, it can achieve a commercial size (60 mm) between 3 y

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old and 4 y old (González et al. 2007), and is one of the commercially harvested benthic species. No information is available on its biological productivity (Andrade et al. 2009), but previous research presents substantial knowledge about their reproductive biology, ecology, and culture (Guzmán et al. 1997, Chávez & Medina 1998, Santana & Cañete 2001, Andrade 2006, González et al. 2007). In Argentina, previous studies have focused on its taxonomy and anatomy (Pastorino 2005), and egg capsules and development (Zaixso 1973, Penchaszadeh 1976). Nevertheless, the reproductive biology of *T. geversianus* from Patagonian waters has been poorly studied to date. Although it is not yet a locally commercially harvested species, it is a potential resource for artisanal fisheries. This article notes the importance of studying its reproductive biology before its fishery develops.

The current work was carried out in the intertidal of Punta Cuevas, Golfo Nuevo (Chubut, Argentina), where previous studies proved the occurrence of imposex in gastropods of the family Volutidae (Bigatti & Penchaszadeh 2005) and nassarids, with concentrations of 1.9 ± 1.17 ng Sn/g (Bigatti et al. 2009). The imposex phenomenon (female gastropods with masculine organs) has specifically been related to the exposure of the trisubstituted organotin compounds tributyltin (TBT) and triphenyltin that has been widely used as antifouling agents. Currently, it has been documented in more than 200 gastropods species (Shi et al. 2005).

In this article we describe the reproductive seasonality of *T. geversianus* and its relationship with environmental parameters (temperature and photoperiod), imposex studies, and experiments to induce oviposition under controlled conditions with culture implications.

MATERIALS AND METHODS

Sampling

Sampling and observations were performed monthly from August 2007 to May 2009, during low tide, on the rocky intertidal of Punta Cuevas, Golfo Nuevo (Chubut, Argentina) (42°46′ 37″S, 64°59′51″W; Fig. 1). The tidal regime in Golfo Nuevo is semidiurnal, with mean amplitudes of 4.7 m and 2.9 m (Villaverde et al. 1974).

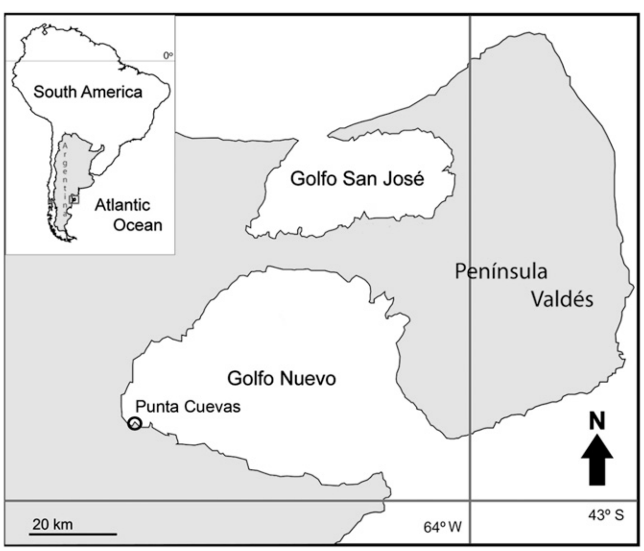

Figure 1. Sampling location at Punta Cuevas in Golfo Nuevo, Argentina.

A total of 250 individuals (representing all sizes) were randomly collected. The total shell length (SL) was measured to the nearest 0.1 mm using calipers. SL was compared between sexes with Student's *t*-test. After shell removal, sex was determined according to the presence of accessory glands in females (capsule and albumin gland), and the gonad color (yellow for the females and orange to red for the males). The sex ratio was determined and compared with 1:1 with a chi-square test. All tests and statistical analyses were done with Statistica 7.0 statistics software package (StatSoft, Inc., Tulsa, OK).

To study the imposex phenomenon, we estimated the percentage of "imposexed" females ($n = 172$) and the relative penis length index following Gibbs and Bryan (1994).

Reproductive Seasonality

The "data Lab" from Centro Nacional Patagónico–CONICET provided monthly data for air temperature (mean, minimum, and maximum values) and wind speed (mean and maximum values). The mean water surface temperature was obtained by a thermometer of continuous registration, and the photoperiod was obtained from Servicio de Hidrografía Naval Argentino (2009). In the field, we registered the occurrence of the following reproductive activities: mating, oviposition and hatching, and the finding of the snails in the intertidal (frequency of snails above the bivalve community). All activities were related to the environmental variables based on qualitative observation. A total of 80 egg capsules were collected from the intertidal and the total length, capsular body length and width, and plug (capsule opening) diameter was measured in the laboratory (Fig. 2) with a 0.1-mm precision caliper.

Laboratory Oviposition Induction

Thirty individuals were collected in Punta Cuevas (19 females and 11 males) and moved to aquaria with a temperature range of 12–14°C and circulating seawater. Initially, the snails were acclimatized for 2 wk using a photoperiod of 15 h light/9 h dark, corresponding to the summer in the southern hemisphere. Later, this photoperiod was decreased to winter conditions (9 h light/15 h dark), reducing half an hour each week. In the aquaria, the snails were fed *ad libitum* with mussel (*Brachydontes rodriguezii, Perumytilus purpuratus, Mytilus edulis,* and *Aulacomya atra*) collected from the intertidal. The aquaria were visited every day to register all new oviposition events. The time taken to attach an egg capsule, the number of egg capsules laid by a female, and the number of females laying egg capsules were registered.

RESULTS

Sampling

The area was exposed to high maximum wind values of up to 88 km/h and mean air temperature varied between 7°C in August (austral winter) and 22°C in January (austral summer), although it was very variable among days. The maximum air temperature registered was 37°C (in January), with a minimum of –9°C in August (Fig. 3). The mean water surface temperature ranged from 9.7°C in August to 19.6°C in February (Fig. 3).

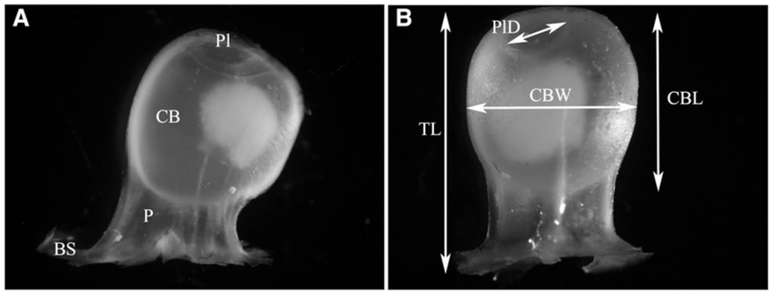

Figure 2. (A, B) Egg capsule (mean total length, 6.6 ± 1.1 mm) general aspect (A) and morphometric parameters (B). BS, basal sheet; CB, capsular body; CBL, capsular body length; CBW, capsular body width; P, peduncle; Pl, plug; PlD, plug diameter; TL, total length.

The photoperiod varied between 9 h light in June and 16 h light in January (Fig. 3).

Total shell length of males ($n = 78$) varied from 12–28 mm (22.01 ± 2.94 mm; mean ± SD), whereas females ($n = 172$) ranged from 18–33 mm (24.85 ± 2.62 mm). On average, the females had significantly larger size ($n = 250$; $t = 7.61$, $P < 0.0001$). Females always showed conspicuous capsule and albumin glands, and its gonads were yellow. Males had a prominent penis and its gonad color was orange to red. The sex ratio was significantly different from 1:1 ($n = 250$; df = 248, $P < 0.0001$); 31.3% were male and 68.7% were female. None of the 172 collected females presented penis or vas deferens. Therefore, the percentage of imposex and the relative penis length index were null.

Reproductive Seasonality

The oviposition consisted of a row of egg capsules attached to hard substrates. The egg capsules (total length, 6.6 ± 1.1 mm; mean ± SD) were formed by a capsular body (capsular body length, 5.6 ± 0.9 mm; capsular body width, 5.3 ± 0.8 mm) with two sides, one more convex than the other, and a peduncle that maintained them erect ending in a basal sheet and attached to the substrate. A plug (plug diameter, 1.9 ± 0.2 mm) was present at the top of their more convex face (Fig. 2). Externally, the egg capsules had a whitish color immediately after attachment to substrate and the wall turned dark yellow as development advanced.

Mating in the field was observed from late March (when the ambient and water temperatures began to decrease; Fig. 3) until October (Table 1). During mating, the male (always smaller) was situated over the female, extending its penis around the shell and into the female's mantle cavity. The mating frequency increased between June and August (Table 1). The first egg capsules were observed usually attached to the bottom in shelters, resembling intertidal crevices, at the beginning of May with an oviposition peak between July and September (when the water temperature had lower values; Fig. 3). In October, when the water temperature began to increase slightly, a decline in the frequency of females laying egg capsules was registered, stopping in November (Fig. 3). Hatching began in September, evidenced by egg capsules with their plug opened, and was maximal between November and December (Table 1). In January, very few hatching egg capsules were observed. The snails that commonly were above the bivalve community were registered within the mussel bed during the months of higher temperature and photoperiod (Table 1; Fig. 3). Predation on intertidal bivalves was observed all year round; moreover, it was the only observable activity in the population in summer (January and February).

During summer, the presence of egg capsules with atypical coloration (pink) and collapsed wall aspects was observed. Under stereoscopic examination those egg capsules presented a diffuse intracapsular content, with no visible eggs or embryos (unviable egg capsules).

Laboratory Oviposition Induction

No females ($n = 19$) laid egg capsules during the first 3 wk under the initial conditions (15 h light/9 h dark, 12–14°C). Only when the photoperiod decreased to 13 h light/11 h dark (5 wk after beginning the experiment) did we observe a female depositing

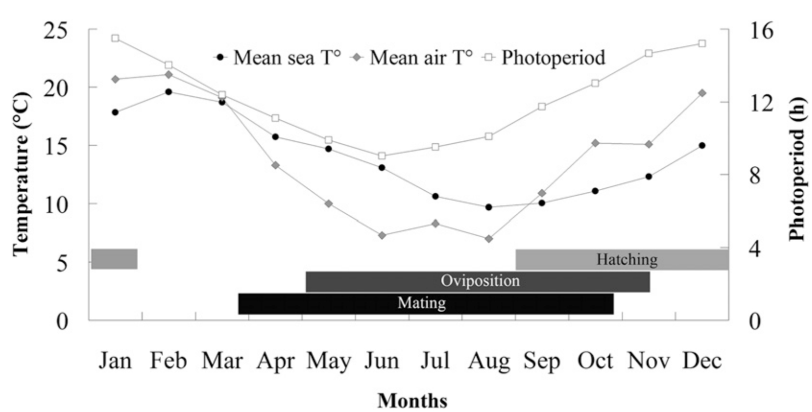

Figure 3. Mean sea temperature, mean air temperature, and photoperiod (August 2007 to May 2009). Horizontal bars show mating, oviposition, and hatching periods.

TABLE 1.

***Trophon geversianus* reproductive and behavioral events observed in the field throughout the study period.**

Months	Mating	Oviposition	Hatching	Feeding	Exposition*
Jan	No	No	+	++	+
Feb	No	No	No	++	+
Mar	+	No	No	+	++
Apr	+	No	No	+	++
May	++	+	No	+	++
Jun	+++	++	No	+	+++
Jul	+++	+++	No	+	+++
Aug	+++	+++	No	+	+++
Sep	++	+++	+	+	+++
Oct	+	++	++	+	+++
Nov	No	+	+++	+	+++
Dec	No	No	+++	+	++

* Snails observed over the bivalve bed.
+, low frequency; ++, medium frequency; +++, high frequency.

the first egg capsule. Seven weeks after beginning the experiment, the number of spawning females increased up to 16 at a 12-h light/12-h dark photoperiod, corresponding to the autumn and spring in the southern hemisphere. Those females deposited the egg capsules mainly on the vertical glass aquarium surface. Each female attached an average of 12.5 ± 6 egg capsules (n = 16) in rows, ranging from 6–26 egg capsules. The average time to attach 1 egg capsule was 25.6 ± 10.9 h (n = 16; range, 12–57 h). The egg capsules of different females were deposited in irregular groups in close proximity, and it was difficult to recognize which one came from which female. Individuals in aquaria were fed the same way as in the field, preying on the offered mussels by boring the prey valve.

DISCUSSION

The individual sizes of *T. geversianus* from Punta Cuevas (42°46′37″S, 64°59′51″W) were smaller (males, 12–28 mm; females, 18–33 mm) than those observed by Santana (1998) in the Straits of Magellan (52°30′S, 70°51′W; southernmost distribution area of *T. geversianus*), where the registered range was from 33–69 mm (without differing among sexes). Individuals used for this study showed no evident external sexual dimorphism. Nevertheless, the males were significantly smaller than females (evident when mating).

Although the level of TBT contamination in the area of Punta Cuevas (during our study period) found by Bigatti et al. (2009) was 1.9 ± 1.17 ng Sn/g, female adult individuals of *T. geversianus* did not present signs of imposex. In contrast, the Nassariidae *Buccinanops globulosus* that inhabits the sandy bottom intertidal at Punta Cuevas presented 100% imposex. Near the study site, in a commercial port (approximately 4 km from Punta Cuevas), *T. geversianus* inhabits subtidal mixed bottoms, where Bigatti et al. (2009) registered 7.69% imposex with concentrations of 1.7 ng Sn/g. Thus, *T. geversianus* could be used as a bio-indicator of high concentrations of TBT, as reported by Bigatti et al. (2009). This may result from the fact that individuals live attached to rocks, avoiding direct contact with the soft bottoms (Cumplido 2009), where most of the TBT is concentrated (up to 9 mo in the water column) (Gibbs & Bryan 1994).

Reproductive Seasonality

The population of *T. geversianus* studied in Punta Cuevas showed a defined reproductive cycle throughout the year. Females began to lay the egg capsules in May, and increased in frequency while the temperature (water and ambient) fell, with a maximum between July and September, and then decreased until stopping in November. Santana (1998) observed that population spawning in the Straits of Magellan began in October and finished in March (toward the end of the southern summer). Zaixso (1973) studied a population from Puerto Deseado (47°44′S, 65°53′W; Santa Cruz, Argentina) and reported that spawning was observed during January and February. The author also noted that the egg capsules had embryos inside, suggesting that oviposition began in December and continued until February. This difference in the period of oviposition may be related to latitudinal changes of climate parameters.

In our study, female oviposition behavior coincided with observations by Zaixso (1973) and Santana (1998), although egg capsule size recorded by those authors was larger than that registered at Punta Cuevas (mean, 6.6 mm). Those from the Straits of Magellan had an average total length of 13.8 mm, whereas those from Puerto Deseado had an average total length of 11.8 mm. According to these studies, egg capsule size may increase toward higher latitudes, although this hypothesis should be proved by monitoring the egg capsules along the Patagonian coast.

Both temperature and photoperiod played an important role regulating oviposition (Himmelman 1999). According to Himmelman (1999), experimental studies showed that photoperiod determines the precise moment at which many species release their gametes or larvae. Many gastropods species have been reported to be induced to release gametes by temperature switches as the main factor (Fretter & Graham 1994, Giese & Pearse 1974). In the case of *T. geversianus,* it was noted that oviposition in the field increased corresponding to an increase in the quantity of light hours from its lowest value in June. Temperature ranged from 9–15°C, coinciding with the range of temperature observed in the Straits of Magellan by Santana (1998). Apparently, both factors contribute to stimulate reproduction in *T. geversianus*. Studies carried out in the same gulf on the volutid snail *Odontocymbiola magellanica* (Gmelin, 1791) indicate the highest peak in reproductive activities from July to early December, probably related to an increase in the photoperiod (Bigatti et al. 2008).

Most of the intertidal rocky shores are subjected daily to aerial exposure, presenting problems of desiccation and extreme temperatures for inhabiting organisms (Bertness 1999). When environmental stress was maximum at the studied site (January to early March) with high dehydration and temperature changes, the reproductive activity of *T. geversianus* was null. Intertidal organisms avoid high summer temperatures and the associated fluctuations with some of the same mechanisms they use to minimize water loss. Many of them live in refuges such as crevices, tide pools, or algal canopies, thereby minimizing exposure to high temperatures (Bertness 1999). During the summer, the snails were always found inside tide pools or within mussel beds. This behavior may be related to protection against environmental stress. Individuals were exposed to a large amplitude of temperature in the water and air throughout the year as a result of the semidiurnal tides (temperature change of 46°C between

minimum and maximum values). This reveals high plasticity of the intertidal population of *T. geversianus*, supporting high environmental stress that could be modeling its reproductive behavior. The reproductive seasonality of subtidal populations of this species at Golfo Nuevo, under more stable environmental conditions, may probably present a different pattern. Rawlings (1999) stated that egg capsules spawned intertidally are well adapted to protect embryos from desiccation, and then one would predict such capsules to be more resistant to water loss than subtidal capsules.

Developing embryos in intertidal encapsulation are potentially exposed to stress factors (e.g., desiccation, osmotic stress, temperature stress, and exposure to benthic predators) that they would avoid by being planktonic (Spight 1975, Pechenik 1983). The unviable egg capsules of *T. geversianus* found with a hazy appearance and pink color inside are coincident with observations of *Nucella crassilabrum* egg capsules, in which embryos killed by physical stresses were identified by their pink color (Gallardo 1979).

Laboratory Oviposition Induction

This is the first report in Argentina detailing the oviposition of *T. geversianus* under laboratory conditions. At a constant temperature (12–14°C), oviposition occurred when the photoperiod decreased to 13 h light or less. The production of egg coverings by neogastropods represents a substantial energetic investment relative to free spawning gastropods with no form of parental care (Rawlings 1999). A female *T. geversianus* needed 1 day, on average, to lay an egg capsule. Considering the number of egg capsules laid per female (3–26 egg capsules), it would take a month to complete oviposition, implying a large energy investment in reproductive activity. Previous studies culturing Muricidae in Chile for the species *C. concholepas* and *C. giganteus* evidenced experimental problems, mainly with regard to larval feeding development and metamorphosis (Di Salvo 1988, González & Gallardo 1999). These studies proved that the free larval phase is the most critical stage of the reproductive cycle, and this limits the production of juveniles in captivity (Leiva et al. 1998), aspects that *T. geversianus* do not present because of their development modality (Santana & Cañete 2001). Our results indicates that *T. geversianus* show high potential for muricid culture because it is a very plastic species and reproduces easily in captivity, is easy to maintain, and can be fed normally as in their natural environment. Moreover, oviposition conditions can be easily forced in aquaria by manipulating photoperiod.

Further exhaustive studies on the embryonic development and population dynamics of this species are necessary to propose fisheries management of this potential commercial target for fisheries in Argentina. Some aspects that should be studied are stocks, gonadal cycle, size and age at sexual maturity, and minimum size catch. For species of commercial value, knowledge of larval development, including the food source used by the embryos and larvae, is valuable in the development of seed production (Ilano et al. 2004). Vulnerability of animals to overexploitation depends upon their reproductive behavior and mating systems (Vincent & Sadovy 1998). The absence of a planktonic phase of *T. geversianus* limits its ability to disperse, which, together with its low productivity—4 hatchlings per egg capsule (Cumplido 2009)—makes this species potentially vulnerable to overfishing. The results obtained in this work could be useful to existing fisheries of *T. geversianus,* which should avoid the capture of the species during its reproductive season.

ACKNOWLEDGMENTS

This research was supported in part by PICTR 01869, PIP 0051, PICT 0323, Proyecto de Investigación del Ministerio de Educación de la Provincia de Chubut. All research work including sampling and experiments comply with current Argentinean laws. M. C. thanks Natalia Dreiling and Lic. Verónica Savoya for their comments and for providing pertinent literature. M. C. dedicates this work to Dr. Martín Cumplido.

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