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PRIMARY RESEARCH PAPER

# Outbreaks, coexistence, and life cycle of jellyfish species in relation to abiotic and biological factors along a South American coast

C. Resgalla Jr. · L. Petri · B. G. Teodoro da Silva · R. T. Brilha · S. A. Araújo · T. C. M. Almeida

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**Abstract** *Olindias sambaquiensis* and *Rhacostoma atlanticum* are the most abundant species of macro-hydromedusae on the southern coast of Brazil; the first is associated with outbreaks of stings in bathers during the summer, and the second with interference in fishing. Due to their direct relationship with human activities, their life cycles were investigated, using laboratory cultivation and study of their cohorts in the field, as well as the patterns of abundance in light of the abiotic and biotic factors of the study area. The coexistence of the two species is possible due to differences in their life cycles, duration of the polyp phase, and the formation of well-defined cohorts. Variations in abundance of the species from one year to another cannot be explained by abiotic variables alone, such as seawater temperature, but may also be associated with the balance between these and other biotic forces, such as local production and, possibly, effects of competition between species. However, on a monthly scale, the aggregations of *O. sambaquiensis* in southern Brazil appear to be associated with the lowest frequency of north quadrant winds, which could, in addition to promoting resurgence processes, lead to dispersion of the organisms off the coast.

**Keywords** Reproductive cycle · Cohorts · Aggregations · Wind patterns

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C. Resgalla Jr. (✉) · L. Petri · B. G. T. da Silva · S. A. Araújo · T. C. M. Almeida
School of Sea, Science and Technology, University of Vale do Itajaí (UNIVALI), Rua Uruguai, 458, Itajaí, Santa Catarina 88302-909, Brazil
e-mail: cresgalla@univali.br

R. T. Brilha
Military Fire Brigade of the state of Santa Catarina, Itajaí, Brazil

## Introduction

Studies on jellyfish and their interference in human activities have gained ground in recent years, due to a supposed increase in populations in different parts of the world (Purcell et al., 2007; Doyle et al., 2013). These interferences include problems associated with fishing yield, with repercussions on the reduction of stocks of commercial interest, as well as problems associated with fishing gear (Richardson et al., 2009). On the other hand, the increase in jellyfish populations has also driven the trade of these animals in countries where there is no tradition of their capture (Brotz et al., 2016). Similarly, recent studies have pointed out that jellyfish abundance peaks respond to decadal oscillations (Condon et al., 2013) and do not always respond to interference from human activity such as overfishing or global warming (Pitt et al., 2018), or that at least, this correlation is difficult to confirm. In terms of ecology, other studies have shown that fishing activities can deplete zooplanktivorous fish, which are direct competitors of jellyfish, and together with their high growth rates, cause large-scale ecosystem changes (Purcell et al., 2007), favoring their dominance in the environment (Palomares & Pauly, 2009). The occurrence of jellyfish outbreaks in coastal regions has also had repercussions on public health related to stings among bathers, requiring increasing investments to isolate recreational bathing areas (Bailey et al., 2003).

In Brazil, recent studies on interference by jellyfish in human activities have drawn attention to the occurrence of fishery landings, indicating high temporal variability in terms of occurrence of species and abundance of catch (Schroeder et al., 2014; Rutkowski et al., 2018). Likewise, in the southern region of Brazil, studies on outbreaks of stings among summer bathers have gained importance due to their widespread coverage in the regional and national media (Resgalla et al., 2005, 2011).

The species of jellyfish associated with these events are the hydromedusae *Rhacostoma atlanticum* L. Agassiz, 1850, which is frequently observed in continental shelf fishery catches (Rutkowski et al., 2018), and *Olindias sambaquiensis* Müller, 1861, which also occurs in fishery landings but is mainly associated with stings among bathers on the beaches of southern Brazil and Argentina (Mianzan & Zamponi, 1988; Resgalla et al., 2011; Brendel et al., 2017). These are the two most frequent and abundant species on the coast of the state of Santa Catarina (De Barba et al., 2016) and were highlighted by Mianzan & Guerrero (2000), occurring in high biomasses on the southern coast of Brazil since the 1990s. *Rhacostoma atlanticum* occurs in an area from Colombia to Argentina, while *O. sambaquiensis* is more restricted to Brazil and Argentina (Oliveira et al., 2016).

Despite the abundance of these hydromedusae, and the facts associated with them, little has been studied or added to our knowledge of the species. The biological characteristics and the conditions of oceanographic and biological productivities in the area could explain the possible relationships between their occurrences and their interference on human activities. As emphasized by Doyle et al. (2013), Imazu (2008), and Mills (2001), the importance of jellyfish in the trophic webs lies precisely in their outbreaks, which show high potential for interference in the coastal ecosystems, such as the carbon cycle associated with prey/predator and competition in trophic relationships. Therefore, the objective of this work was to present a compilation of 5-year information based on studies on the partial life cycle (medusa stage) of *R. atlanticum* and *O. sambaquiensis* obtained in the laboratory and in the field, their occurrence in the fishery, and the incidence of stings in beach regions. It is hoped that this information will further understanding of the existence of temporal patterns that may be related to the biotic, climatic and oceanographic conditions in the southern region of Brazil.

## Materials and methods

According to Graham et al. (2003) there are many problems associated with megaplankton sampling, from the type of sampler used to the area of coverage to the frequency of sampling. Considering the limitations of determining the occurrences of these organisms in the samples, this work condenses 5 years of information from bottom trawl sampling, as well as compiled data on the occurrences of these organisms in industrial fishing, and of the occurrence of stings among bathers during the summer months, in the south of Brazil. The main objectives of this compilation are to fill in the gaps in the occurrence statistics, and to make the information as robust as possible for the interpretation of the data.

### Study area

Santa Catarina lies between two other states that form the South region of Brazil. It has a coastline of 531 km, with approximately 200 beaches. It also has the largest fishing port in Brazil, which is located on the Itajaí-Açu River. The state is bounded to the north (25°57′41″S) by the state of Paraná, with 98 km of coastline, and to the south (29°23′55″S) by the state of Rio Grande do Sul, with 623 km of coastline (Fig. 1).

### Sampling

Medusae samples were obtained over a period 60 months, from February 2012 to January 2017, as by-catch of the artisanal shrimp fishing off the north coast of Santa Carina. The sampling area comprised

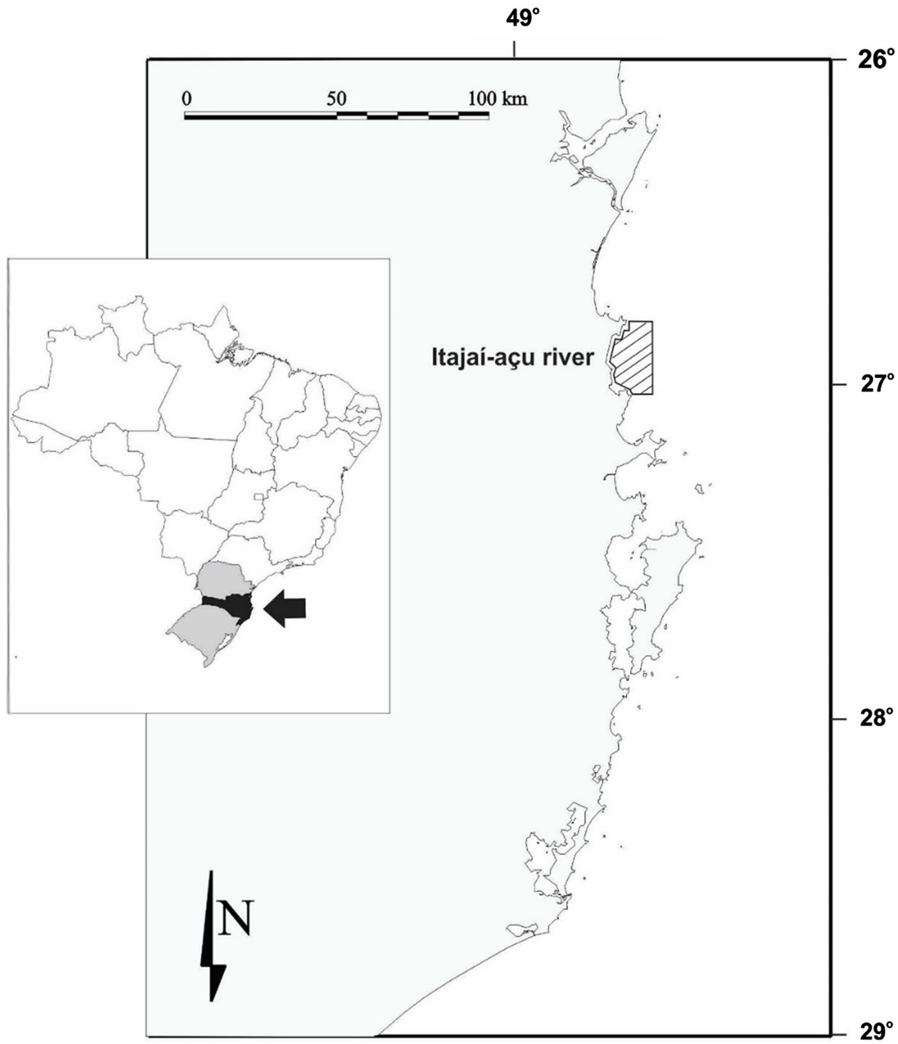


**Fig. 1** Location of the South region of Brazil (the three states in gray) and the state of Santa Catarina (in black) and surrounding area of the coastal region, the mouth of the river Itajaí-Açu (shaded area)

the area from the mouth of the Itajaí-Açu River to the isobaths of 20 m, within 25 km off the coast (26°45′ to 27°00′S) (Fig. 1). The trawls were performed from a motorized boat using nets with a mesh size of 50 mm between opposite knots in the main body and 30 mm at the end of the net. The length of the nets was 14 m and the opening was 5 m. The animals obtained were kept in buckets containing sea water until they could be transported to the laboratory.

For this work, only *Olindias sambaquiensis* and *Rhacostoma atlanticum* were used, as these are the two most frequent and abundant species recorded in sampling off the northern coast of Santa Catarina. For information on the community of macromedusae in the study area, see the reference work of De Barba et al. (2016).

In the laboratory, the animals were kept overnight in an aquarium with filtered seawater to release spermatozoa and ovules. After this period, the jellyfish were weighed (wet), measured individually, and frozen for biochemical analyses of proteins, lipids, and carbohydrates that were presented by De Barba et al. (2016).

## Density estimates and cohort analysis

The jellyfish catch data obtained in the fishing net hauls were standardized by the number of organisms per 10 min of trawl time (the time normally used in trawls to prevent damage to the organisms) and used as a measure of abundance for comparison between species. During this trawl time, using a double drag, 7770 $m^3$ of water was filtered through the nets. Biometric data (diameter) were used to determine the frequency distribution of size classes and the modes (highest frequency class) in each sample period, and thus estimate the cohorts throughout the year by the union of their modes. To avoid gaps in the absence of occurrence of the species, the means of 5 years of sampling were estimated, to evaluate the population dynamics of *R. atlanticum* and *O. sambaquiensis*. Diameter/length and weight (wet) ratios were determined for the species, in order to present estimates of comparative biomass between species.

### Culture

The eggs released by the animals kept overnight in the aquariums were removed and concentrated in a 20 µm mesh, distributed in 50 ml crystallizing dishes with filtered seawater. The eggs were incubated at 23°C, with salinity between 30 and 32, in the dark, and monitored for observation of the planula larvae and fixation of polyps. The water in the crystallizing dishes was not renewed while the planula larvae were developing, and was then renewed every 48 h after the appearance of the polyps.

Development was monitored daily, recording any cultivation changes. Once the polyps had appeared, they were fed with New Life Spectrum® micro-flaked industrial feed, crushed, newly hatched nauplius and decapsulated *Artemia* sp cyst (Jarms et al., 2002). Observations and photographic records were made in each stage of development, noting the morphological changes in the animals.

### Fishery landing data

Information on the occurrence of jellyfish in industrial fishing was conducted as part of a daily industrial fishery monitoring program (GEP—Fisheries Study Group of the University of Vale do Itajaí) in the fishing ports of Itajaí and Navegantes, on the north coast of Santa Catarina, which together make up the main industrial fishing center in the South of Brazil. Data were gathered between February 2013 and October 2016, through interviews with boat captains during the landing of trawl fishing vessels operating off the coasts of the Southeast and South Brazil. For the interviews, data were initially collected about the trip they had just returned from, including information about the presence or absence of jellyfish and identification of the jellyfish with the help of a visual guide developed in a previous study by Schroeder et al. (2014). For this study, only the interviews with boat captains using the bottom trawling mode were used, since this fishing gear has the highest occurrences of jellyfish, according to Schroeder et al. (2014) and Rutkowski et al. (2018).

### Data on stings involving jellyfish (Fire Brigade—Lifeguards)

For Santa Catarina, interviews were carried out with the lifeguards on the organism responsible for causing stings, based on a form presented by Resgalla et al. (2005). Using this information, it was possible to delimit the occurrence of the species along 531 km of coastline, with a concentration of information for the northern (7th Battalion), central (1st Battalion) and southern coasts (4th Battalion) of the state.

Records of jellyfish sting and the number of drownings prevented (indirect estimate of the number of tourists per season) for the 2012/2013 and 2016/2017 seasons were obtained from the database stored in the central digital directory of Military Fire Brigade [*Corpo de Bombeiros Militar*] of the state of Santa Catarina. These records were generated from data surveys of stings occurrences recorded by beach lifeguards during the period of summer operations, which begins in October and runs until March of the following year.

### Obtaining environmental data

For the annual and seasonal compositions between 2012 and 2016, treatment Sea Surface Temperature (SST) data and Chlorophyll data for the study area (25° 27′30″, 29° 42′30″S, and 47°47′30″48° 37′30″W) were obtained from the OceanColor Website of NASA (https://oceancolor.gsfc.nasa.gov/cgi/l3), and the readings were taken by the software SeaDAS (https://seadas.gsfc.nasa.gov/), also from NASA. SST data, also obtained from the NASA website, were also obtained for the southern part of the state (27°57′30″, 29°12′30″S and 47°57′30″; 48°37′30″W) relating to the area of resurgence, and the Fire Brigade area with the highest recorded incidence of jellyfish stings in the state.

Daily records of wind speed and direction were obtained from the National Institute of Meteorology

(INMET) database (http://www.inmet.gov.br/portal/) for the Urussanga station (28°31′57″S and 49°18′54″W and Altitude 48.17 m), for the period December to February of 2016/2017, which corresponds to the summer season in this region. These data were restricted to the southern part of the state (4th Battalion), the site of the highest occurrence of jellyfish stings involving and bathers.

### Data analysis

The correlation analysis between the diameter and weight of the species of hydromedusae were carried out to compare the differences in growth strategies.

Correlation analyses between the number of stings and chlorophyll, sea surface temperatures in summer and winter for the entire coast of Santa Catarina and for the resurgence area in the south of the state in the summer were performed according to Zar (2010) to test for the existence of interannual patterns that might explain the possible differences observed between years of large and small occurrences of jellyfish stings.

The Chi-square test for independent samples was performed according to Siegel (1975) for comparisons of wind frequency, to confirm whether there were any wind patterns that might explain the daily periods of incidence of jellyfish stings on the beaches.

## Results

### Variations of densities and cohort analysis of *O. sambaquiensis* and *R. atlanticum*

*Olindias sambaquiensis* was the most abundant hydromedusa species in bottom trawls on the North coast of Santa Catarina, presenting an overall average of 8.1 indiv. 10 min. trawl$^{-1}$ with peaks in late autumn and early winter (maximum of 21.6 indiv. 10 min trawl$^{-1}$) and late spring (maximum of 23.4 indiv. 10 min trawl$^{-1}$) (Fig. 2A). These peaks were associated with abrupt changes in water temperature (reduction in autumn and increase in spring, with variation from 3.2 to 3.5°C in a period of 1 month) (Fig. 2B) and an increase of animals of smaller size classes (Fig. 2C), indicating periods of recruitment of juveniles to the adult population. Due to the occurrence of larger individuals followed by density peaks of juveniles (small organisms) it is suggested that this species presents two cohorts throughout the year, but the data also indicated smaller recruitment, a smaller number of new animals outside the two main cohorts, and low longevity of adults (4 to 6 months) due to limited periods of occurrence of larger organisms.

Comparatively, *R. atlanticum* presented lower densities (average of 3.5 indiv. 10 min trawl$^{-1}$) and high densities in the summer and autumn (maximum of 18.9 indiv. 10 min trawl$^{-1}$) (Fig. 3A). It presented two well-defined cohorts during the year, with recruitment of juveniles to the adult population in late spring and autumn (Fig. 3B, C), also associated with water temperature variations. The cohort analysis suggested well-defined reproductive periods and longer longevity of the animals (from 6 to 7 months) compared to *O. sambaquiensis*.

In terms of biomass, the two species of hydromedusae showed biometrics (diameter and wet weight) within the same range (Fig. 4). *Olindias sambaquiensis* showed records of larger specimens and larger mass. However, for those larger than 40 mm in diameter, there are two trends, one of greater weight corresponding to animals with developed gonads, and one of lesser weight with animals without the development of gonads, according to Chiaverano et al. (2004). Despite the larger sizes recorded for *O. sambaquiensis*, *R. atlanticum* presented a double mass ratio for the same diameter. For example, jellyfish of *O. sambaquiensis* of 6 cm in diameter have an estimated wet weight of 13.7 g, while those of *R. atlanticum* have a wet weight of 27.9 g.

### Cultivation

Polyps and juvenile medusae of the *O. sambaquiensis* were obtained only in a single opportunity, in February 2016, during maintenance of eggs at the weekend. Thus, from the incubation of the eggs on Friday until Monday, i.e., for a period of 72 h, the appearance of polyps and juvenile medusae was observed, and these were kept for 24 days for jellyfish and 49 days for laboratory polyps. Morphologically, the polyps presented in the form of colonial hydroids, with different stages of development, small and sessile, coming from a single hydrorhiza, with distal tentacles, without apparent mouth and hypostome, and no perisarcal thecae (Fig. 5). The presence or absence of a mouth and gastric cavity should be confirmed in future studies. From the most developed hydroid with a

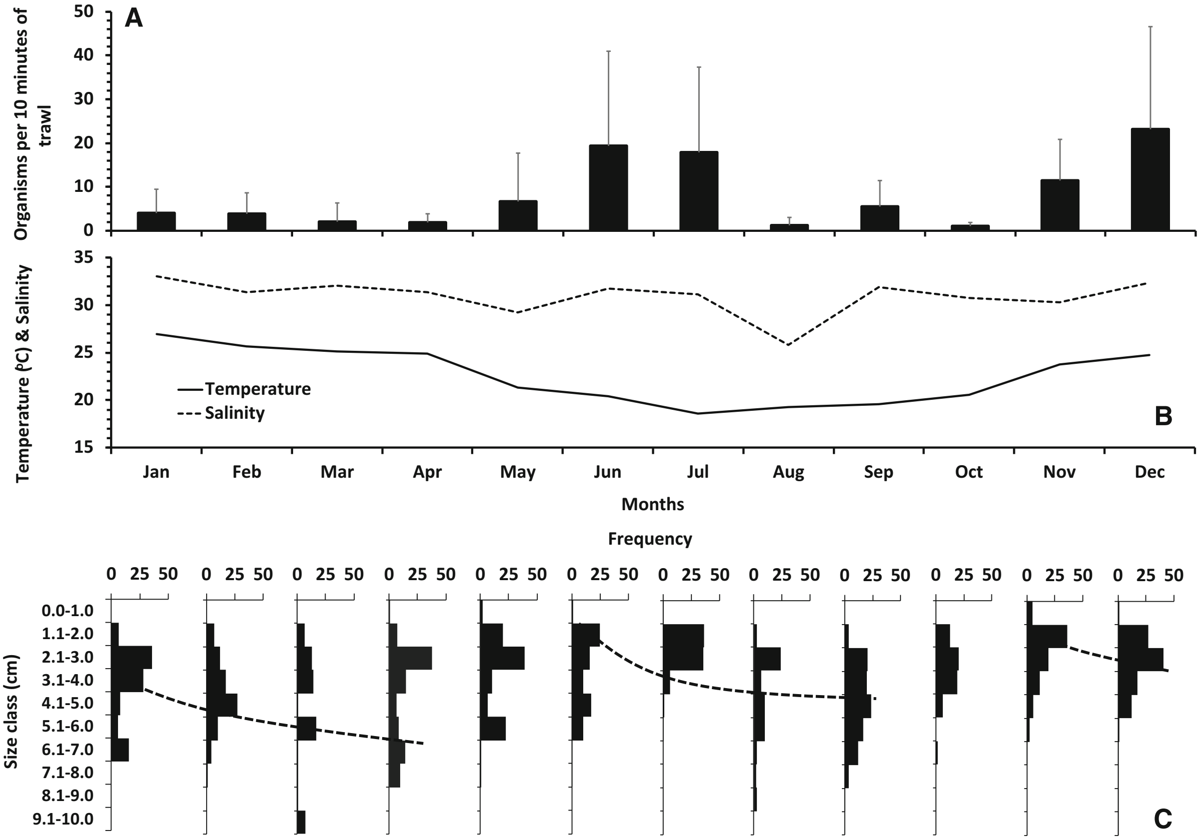


**Fig. 2** Average temperature (°C) and salinity of the surface water (**A**), average (bar) and standard deviation (line) of number of organisms per 10 min of trawl (**B**) and average frequency distribution of size classes (cm) (**C**) from February 2012 to January 2017 for *O. sambaquiensis* on the North coast of Santa Catarina (South of Brazil)

medusa bud originate the juvenile medusa with eight tentacles.

The cultivations in early stages of development of *R. atlanticum* were more frequent and had varying degrees of success. Twenty-four hours after incubation of the eggs, free-swimming planula larvae were observed in the crystallizing dishes, which remained in this state for 7 to 15 days before undergoing metamorphosis to form a campanulinid hydroid; stolonal; with delicate, tubular, elongated, radially symmetrical hydrotheca, operculum; hydranth contractile with a basal intertentacular membrane, and 15 moniliform tentacles when completely extended (Fig. 6). After 9 to 10 days and with abundant feeding, the hydroids released the first juvenile medusa, with two bulbous tentacles, by budding. The jellyfish were kept for 30 days, until they had four tentacles with bulbs, and the polyps were kept for 60 days. Regression of the polyp (loss of tentacles) was observed on two occasions, returning to the form of a primary polyp, with new formation of tentacles.

The planula larvae, the tentacles of the polyps, and the juvenile medusa for *R. atlanticum* and *O. sambaquiensis* were within the same size range (Table 1).

## Fishing

The interviews obtained from the boat captains of trawlers operating on the south and southeast coast of Brazil were used as a secondary source of data on the greatest abundance of jellyfish during the study period. The results of these interviews indicated a frequent incidence of jellyfish in the catches (from 32 to 55% of the trawls), but with a decreasing incidence over the years of the study (Fig. 7), showing the lowest occurrences in 2015 and 2016. Despite this, *R. atlanticum* has always been the dominant species (from 53 to 81%) compared to *O. sambaquiensis* and

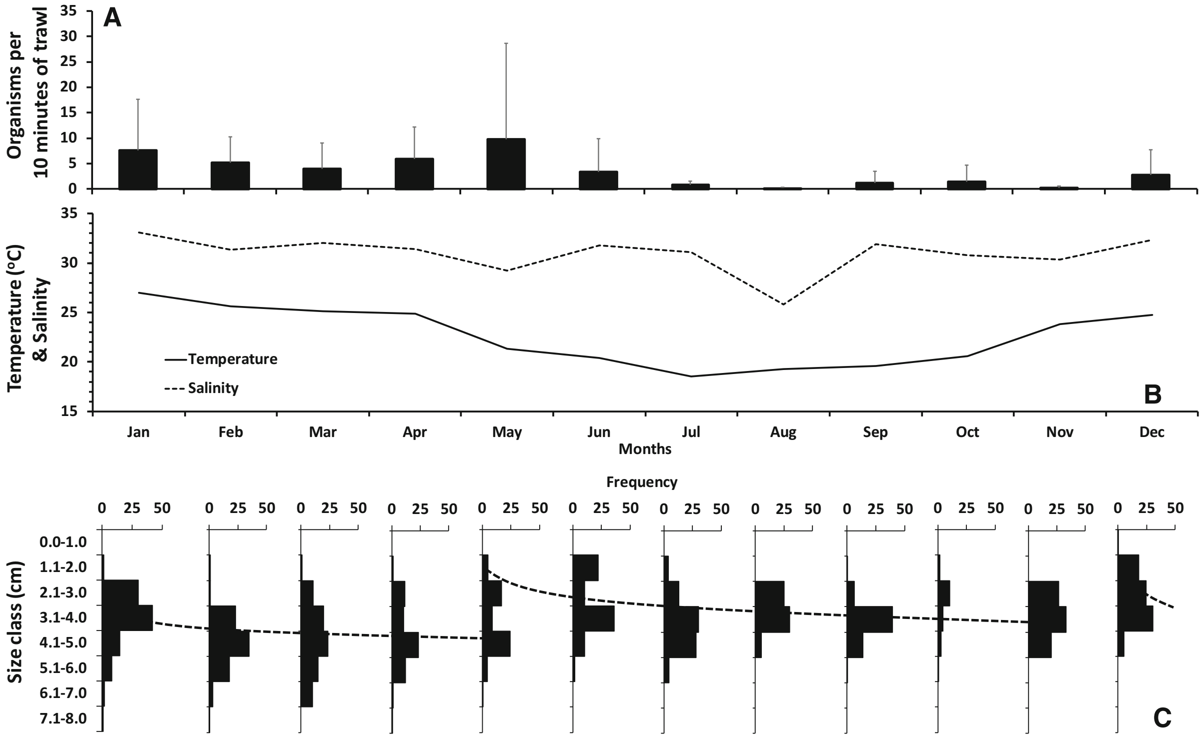


**Fig. 3** Average temperature (°C) and salinity of the surface water (**A**), average (bar) and standard deviation (line) for number of organisms per 10 min of trawl (**B**), and average frequency distribution of size classes (cm) (**C**) from February 2012 to January 2017 for *R. atlanticum* on the North coast of Santa Catarina (South of Brazil)

other representatives of the Scyphozoa and Cubozoa species. These points were highlighted in the studies of Schroeder et al. (2014) and Rutkowski et al. (2018), used as sources of data for this work.

## Stings

Based on the interviews conducted with the lifeguards of the beaches during the 5 years of summer seasons (December to March), with occurrences of outbreaks of stings among bathers, and stranding of jellyfish on the beaches (*arribadas*), *O. sambaquiensis* was the species responsible for the majority of cases of stings on the southern coast of Brazil (Fig. 8). In the south of the state (4th Battalion) in particular, the number of stings caused by jellyfish accounts for more than 65% of all cases in the entire state of Santa Catarina. *Physalia physalis* (Linnaeus, 1758) (Portuguese man o'war) and *Chrysaora lactea* Eschscholtz, 1829 are sporadic and occur in a more localized way. *Rhacostoma atlanticum* does not exhibit long tentacles or strong enough toxins in its nematocysts to be considered a stinging species. In addition, strandings of this species on the beaches are not frequent, therefore it is considered a species with more coastal occurrence.

For injuries caused by jellyfish during the summer seasons, the summers of 2014/2015, 2015/2016 and 2016/2017 had the highest numbers of incidences (above 60,000 cases), even though the number of tourists was practically constant over the last 5 years of study (number of drownings prevented) (Fig. 9A). Seasons with and without occurrences of jellyfish sting outbreaks did not present any clear pattern in terms of sea surface temperature (Pearson's $r = 0.611$ for summer and 0.254 for winter), or biological production that could be correlated with phytoplankton biomass ($r = 0.411$). However, there are trends in years preceding summers with outbreaks of the stings be characterized, in part, by less severe winters, such as those of 2014 and 2015 (Fig. 9B), whereas in 2016, chlorophyll (and possibly phytoplankton biomass) was high (Fig. 9C).

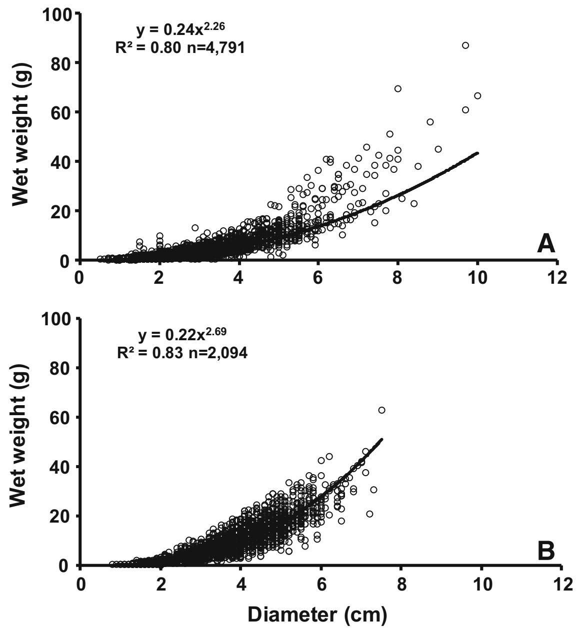


**Fig. 4** Relationship between diameter (cm) and mass (grams) for *Olindias sambaquiensis* (**A**) and *Rhacostoma atlanticum* (**B**), where $R^2$ is the coefficient of determination and n is the number of organisms measured

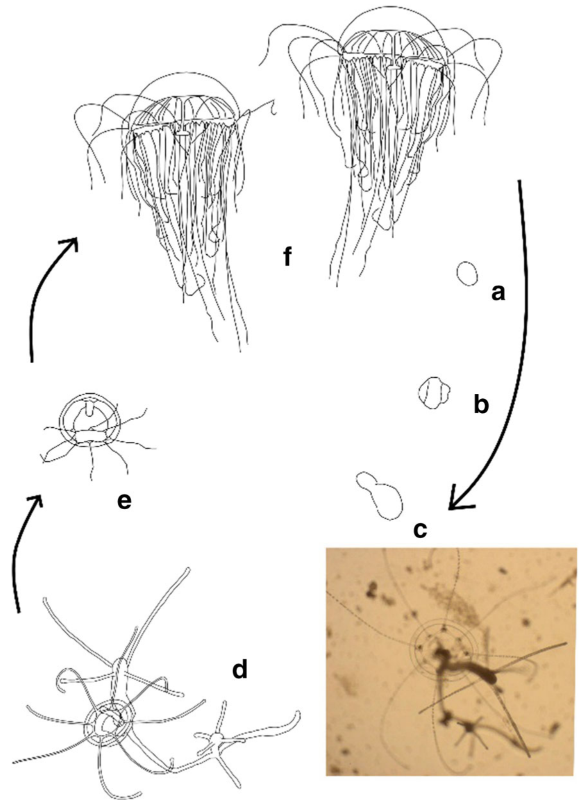


**Fig. 5** Life cycle of *Olindias sambaquiensis*, with planula larva (**a**), differentiated planula larva (**b**), primary polyp (**c**), developed polyp (**d**), juvenile medusa with 8 tentacles (**e**), and adults (**f**). Time from the egg to the juvenile medusa is 72 h. From the juvenile medusa to recruitment of the population (size class less than 1.0 cm), it is not known. Photo of the developed polyp and budding of a juvenile medusa. In particular, a primary polyp in the same hydrorhiza

Particularly toward the south of the state (4th Battalion), and as already registered by the local fire brigade, summers with warmer waters show a higher incidence of jellyfish stings. This observation is partially confirmed by the sea surface temperature in the region (Fig. 10), which presented a Pearson correlation coefficient of the 0.876 ($P = 0.515$) with the number of stings.

Within the daily shift schedule of summer seasons, however, it has been observed that there is a tendency for higher numbers of stings involving bathers to occur after the weekends (information obtained from interviews with the fire brigade) and in periods with lesser incidence of northerly winds and/or higher incidence of southerly winds, as in the case of the 2016/2017 season (Fig. 11) ($\chi^2$, $P = 0.073$). In terms of speed, the south and northerly winds varied within the same range, with an average of 1.39 m $s^{-1}$ for southerly winds and 1.34 m $s^{-1}$ for northerly winds, with no clear pattern between years with and without outbreaks.

## Discussion

From the late 1990s onward, Mianzan & Guerrero (2000) highlighted high biomasses of the *O. sambaquiensis* and the *R. atlanticum* on the southern coast of Brazil, while Rutkowski et al. (2018) highlighted the dominance of these hydrozoans as by-catch of industrial fishing in the southeast and south regions during the same period. These facts, associated with the dominance, and frequency of these species observed by De Barba et al. (2016) on the northern coast of Santa Catarina, reveal their ecological importance in the planktonic community due to their position in the food chain, and they may exert a strong pressure of competition with species of planktivorous fish (Rutkowski et al., 2018). Also, *O. sambaquiensis*,

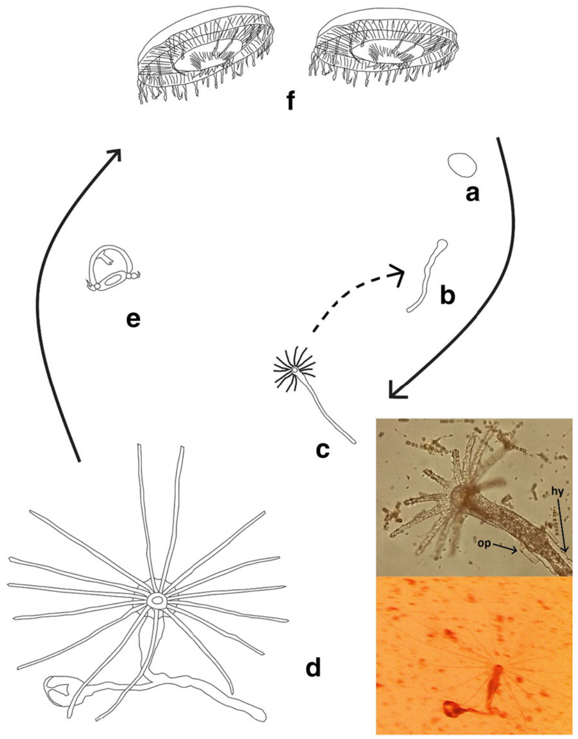


Fig. 6 Life cycle of *Rhacostoma atlanticum*, with planula larva (**a**), primary stolon (**b**), primary polyp that may regress to the stolon (**c**), developed polyp with bud (**d**), juvenile medusa with 2 tentacles (**e**), and adults (**f**). Time from the planula larva to the polyp is 7 to 15 days, and that from the polyp to the juvenile medusa is 9 to 10 days. From the juvenile medusa to the recruitment of the population (size class smaller than 1.0 cm) it is not known. Photo with detail of the polyp and budding of the juvenile medusa, where, *hy* hydrotheca and *op* operculum

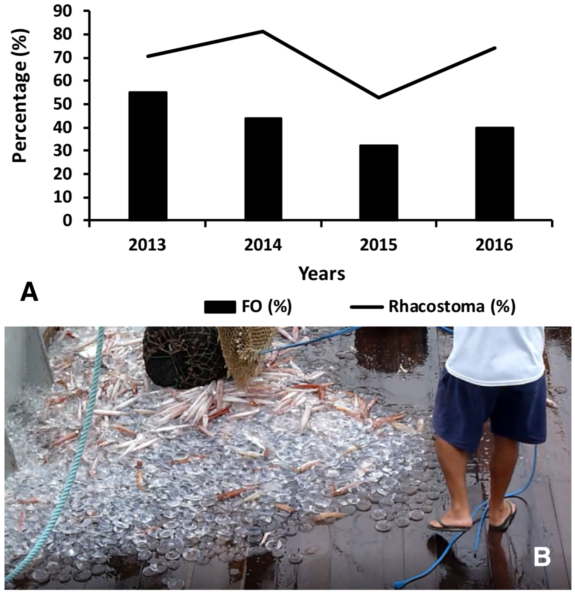


**Fig. 7** **A** Frequency of occurrence (FO, %) of jellyfish in the fishery and frequency of occurrence of *Rhacostoma atlanticum* (%) for the years from 2013 to 2016 according to interviews with trawler boat captains operating in the South and Southeast coasts of Brazil. **B** Photo of scientific on-board observer on the occurrence of *Rhacostoma atlanticum* in a mid-water trawl for the capture of squid (*Loligo plei*)

is known to cause stings problems in bathers on the main beaches of southern Brazil (Resgalla et al., 2005, 2011).

While these species are prominent in the pelagic system, there have been few studies on the ecology of these jellyfish in recent years that could be applied to occurrences in fishing and in stings with bathers on the beaches of the South of Brazil.

There have been few studies on the population dynamics of hydromedusae. In particular, Chiaverano et al. (2004) described *O. sambaquiensis*, for the coast of Argentina, with the presence of only one cohort per year, limited to the period between spring and autumn, and found at temperatures above 15°C for the meduzoid phase. For the southern coast of Brazil, two cohorts are suggested in this study that have increases

**Table 1** Comparison between planula larvae size (mean and standard deviation, $n = 11$), polyp tentacles, juvenile medusa (μm), and observed development time of *Olindias sambaquiensis* and *Rhacostoma atlanticum*

| | *Olindias sambaquiensis* | *Rhacostoma atlanticum* |
|---|---|---|
| Planula larvae | 110 ± 21 length | 140 ± 17 length |
| Polyp tentacles | 520 length | 620 length |
| Juvenile medusa | 360 width | 670 width |
| | 460 height | 570 height |
| Time to larvae settling | < 72 h | 7 to 15 days |
| Time to budding of primary medusa | < 72 h | 16 to 25 days |

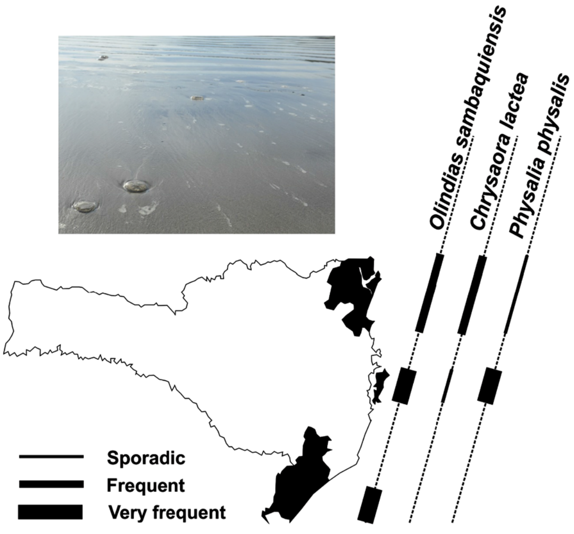


**Fig. 8** Frequency of the main species involved in stings of bathers on the coast of Santa Catarina, based on interviews with lifeguards on 5 years of summer seasons (2012–2017). The black areas on the map indicate the regions of the coast under the 7th Battalion (North), the 1st Battalion (center) and the 4th Battalion (South) of the Fire Brigade of the state of Santa Catarina. Photo of occurrence of *O. sambaquiensis* in beach ("arribada"), taken by the local media (Rafaela Martins, DC)

in polyp production outside the density peaks. This higher reproductive rate is considered to be due to higher environmental temperatures (annual average of surface water of 22.7°C, a minimum recorded temperature of 17.2°C), and availability of food all year round (Resgalla et al., 2008), factors that can stimulate the development of jellyfish gonads (Ishii & Bamstedt, 1998). The existence of two trends between diameter and mass of *O. sambaquiensis*, associated with the presence of gonads, also suggests a continual entry of recruits into the adult population.

Temperature may also favor the existence of two cohorts for *R. atlanticum*, and its greater longevity suggests that energy expenditures are used for growth due to the high diameter-to-weight ratio. This could explain the well-defined characteristics of the cohorts and of the more uniform diameter-to-mass ratio. At the same time, these bioecological characteristics make the species more vulnerable to large interannual variations, and more dependent on the existence of adults in the population, as suggested by Mills (2001) for strong collection pressure of *Aequorea vitoria* (Murbach & Shearer, 1902) (hydromedusa of the same *Rhacostoma* family), which suffered a reduction in density and biomass on the coast of the state of Washington (USA).

The description of the first stages of development of hydromedusae of the Olindiidae and Aequoreidae families is rare and is practically nonexistent for the species *Olindias sambaquiensis* and *Rhacostoma atlanticum*. The polyps obtained from *Olindias sambaquiensis* were distinct from those obtained from *Olindias phosphorica* (sensu Delle Chiaje, 1841), which is characterized by a small, solitary hydrant with no tentacles and a distal mouth (Bouillon et al., 2004, 2006) and *Olindias formosus* (Goto, 1903), which has a hydrant with tentacles and a mouth (Patry et al., 2014). The first description presented by Zamponi & Facal (1987) of *O. sambaquiensis* highlights the formation of the primary polyp without tentacles in 120 h (Fig. 5c), probably originating from eggs without sufficient reserves for complete and similar development to that frequently observed in this work, in the various attempts to cultivate the species.

For *Rhacostoma atlanticum*, the hydroid description of the *Aequorea* family is consistent with that reported by Bouillon et al. (2004, 2006), i.e., delicate hydrotheca with operculum. The bud gives rise to a typical juvenile medusa with two tentacles evolving to four tentacles with bulbs.

These biological characteristics among the species suggest differentiated reproductive strategies that result in greater abundance of *O. sambaquiensis* in the environment in relation to *R. atlanticum*. With greater energy expenditure in the gonads and a faster reproductive cycle, planula larvae and polyps of short duration, and continuous reproduction, the chances of success are favored until the adult stage for *O. sambaquiensis*. It appears that *R. atlanticum* is more susceptible to disruption of the life cycle by environmental changes, with more defined cohorts, a longer life cycle, and a more defined phenology. Despite these differences, temporal variations of abundance imposed by high density cohorts observed at the end of spring are common for both species. Peaks of zooplankton density were observed in the late winter and early spring by Resgalla et al. (2008) for the coastal region adjacent to the mouth of the Itajaí-Açu River that could support the formation of summer cohorts for both species.

However, there are some gaps in the knowledge that still need to be filled, but that are difficult to cover because the small size of these animals means that it is

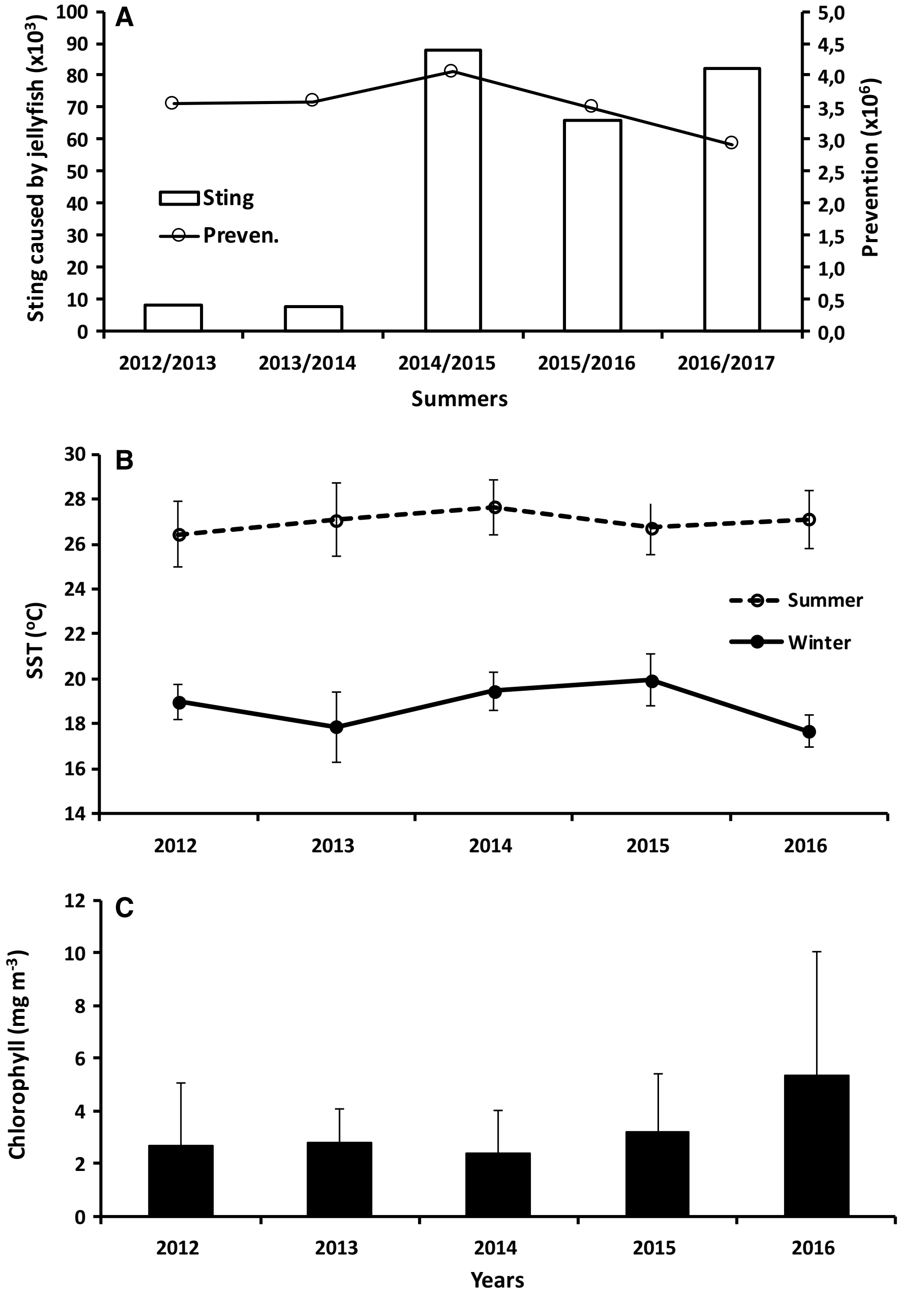


**Fig. 9** **A** Number of lesions caused by jellyfish (Stings) and number of drownings prevented, by season, and for the whole of the state of Santa Catarina; **B** Average (point) and standard deviation (line) of the sea surface temperature (SST) for the coast of the state for summer and winter of each year of the study; **C** Average (bar) and standard deviation (line) of the chlorophyll values (mg $m^{-3}$) per year for the coast of the state

not possible to study the presence of polyps in their environment, the site of recruitment, their feeding habits, or their demersal behavior, as suggested by Chiaverano (2001) and Rutkowski et al. (2018).

In any case, there is evidence of a differentiation in the distribution of the species, more on the inner shelf for *R. atlanticum*, due to its occurrences in industrial fishing, and closer to the coast for *O. sambaquiensis*,

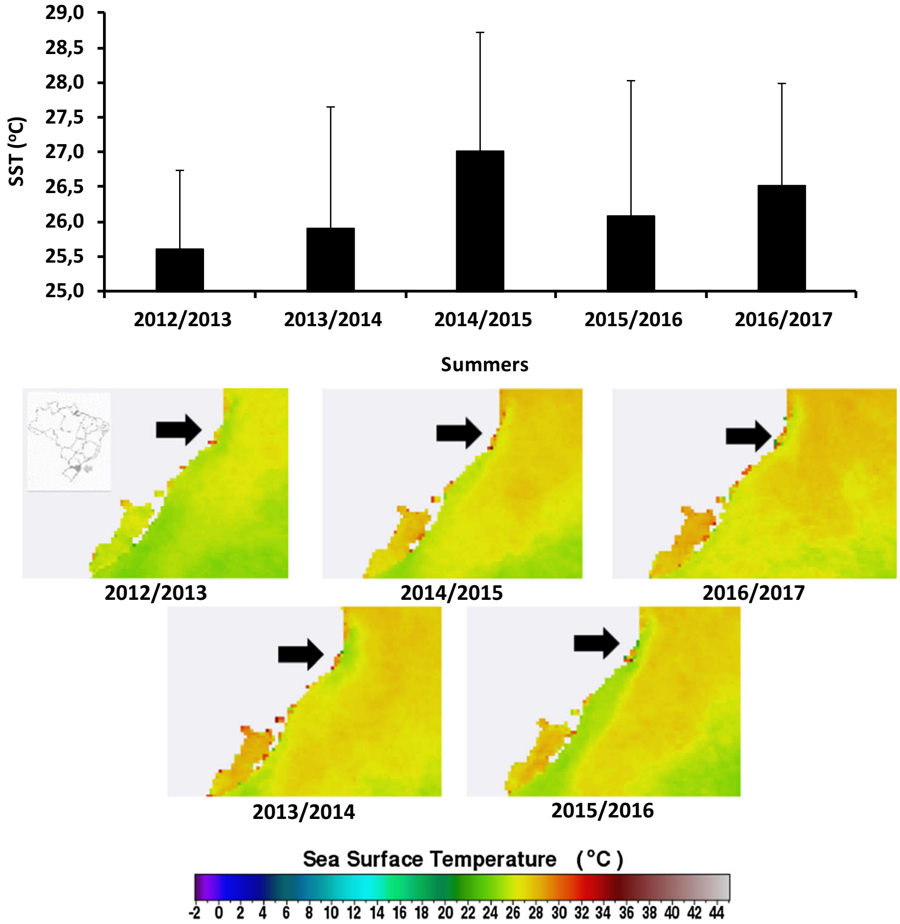


**Fig. 10** Satellite images from NASA's OceanColor Web (https://oceancolor.gsfc.nasa.gov/cgi/l3) in summer composition between 2012 and 2016 and the average (bar) and standard deviation (line) for temperature for each period obtained by reading the software SeaDAS (https://seadas.gsfc.nasa.gov/) also from NASA, for the south of the state (27°57′30″; 29°12′30″S and 47°57′30″; 48°37′30″W)

due to its association with bather sting incidents. This spatial differentiation between the two species was also observed by Mianzan & Guerrero (2000), and may be associated with swimming capacity or demersal behavior, as highlighted by Rutkowski et al. (2018). This differentiation in patterns of distribution may also be a strategy to reduce competition between species, as suggested by Sparks et al. (2001) for *Aequorea aequorea* (Forsskål, 1775) (closer to the shelf) and *Chrysaora hysoscella* (Linnaeus, 1767) (closer to the coast) on the coast of Africa. Even though there is differentiated distribution among species, just as there are trophic differences between them, one possibility is competition for food throughout the development of the organism.

In terms of the dynamics of the water masses, the South of Brazilian is characterized by the flow of current (Tropical Water) in the north–south direction during the summer months, whereas during the winter months, the coastal branch of the Malvinas current (a mixture of water from the Rio de la Plata River and sub Antarctic waters) flows in the reverse direction (Piola et al., 2005). For the special case of the coast of the state of Santa Catarina, in its northern portion, there are continental contributions without seasonality, whereas in the south portion, in the summer, the northerly winds favor the resurgence process in the southern region of Santa Marta Grande (Carvalho et al., 1998; Resgalla, 2011).

Based on what is known about hydrographic dynamics, it can be hypothesized that the area of

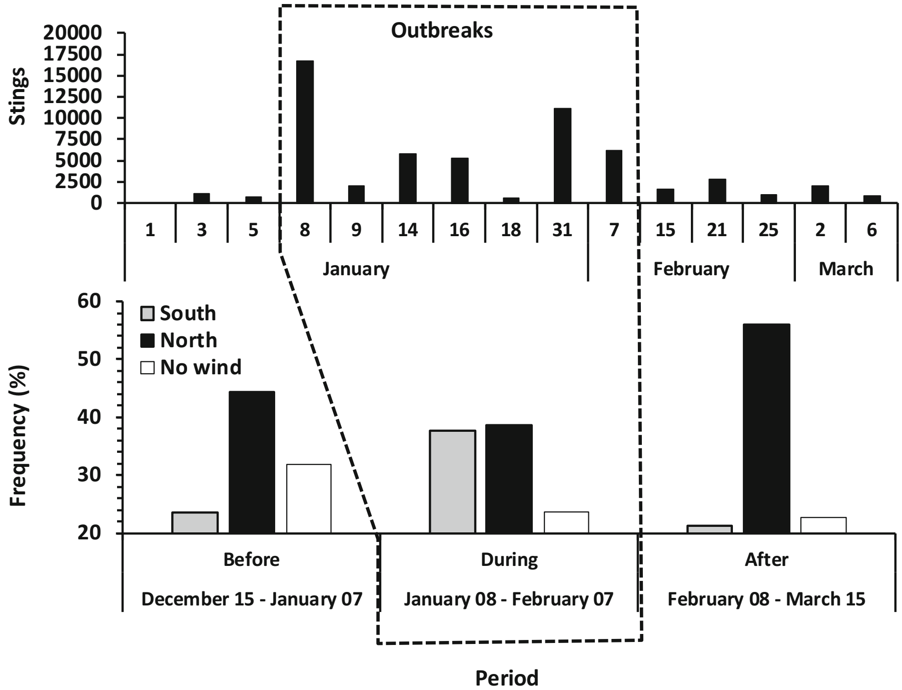


**Fig. 11** Daily records of stings with jellyfish for the summer seasons of 2017 and frequency of occurrence of southerly and northerly winds in periods before, during, and after the outbreaks of stings. Marginal difference for wind frequency, according to the $\chi^2$ test (4, 0.05) = 0.073

reproduction and development of the polyp stage could take place in the north region, where the influence of the continental contributions, particulate material that would serve as substrate for the fixation and nutrient enrichment in the coastal zone by continental inputs (Resgalla, 2011). In addition, the flow of the currents would favor the movement of the animals to the south of the state, where records of stings by *Olindias* are greater compared to other coastal areas of the state.

In this context, the high incidence of the *O. sambaquiensis* recorded for the summers of 2014/2015, 2015/2016, and 2016/2017 may have been influenced by two event scales on the Santa Catarina coast. One such event is on an annual scale, with a greater abundance of the animals on the coast in response to long-term processes, such as climate, food, and the relationship between species. Not all of these factors are clear and easy to measure and interpret. For example, although it has not been statistically confirmed, summer seasons with higher incidences of stings were partially preceded by less rigorous winters (2014 and 2015), which may have favored the survival and reproduction of polyps (Prieto et al., 2010). Also, these seasons also partially exhibited high phytoplankton biomass (2016), which would have triggered secondary production and availability of food which, in turn, could (1) sustain the two species of hydromedusae, decreasing the competition between them, and/or (2) favor the high abundances of *O. sambaquiensis* in that summer, due to the lower abundance of *R. atlanticum* recorded in the fishery.

Nevertheless, variations in the abundance of the species of hydromedusae in the southern region of Brazil involve a joint response to abiotic and biotic forces, which may still be considered unpredictable, and not well understood, as has already been highlighted by other studies in other parts of the world (Arai, 1992). In addition, the samples collected in the north coast of the state, and presented in this study, responded in the same way to the abundance of summers with and without outbreaks of stings, and even showed alternating dominance between *O. sambaquiensis* and *R. atlanticum*. Despite these trends, monitoring medium- to long-term data is still necessary for a correct diagnosis of the causes of these variations in abundance.

A second process, with a shorter temporal scale (days or weeks), is that associated with aggregations of *O. sambaquiensis* on the southern beaches of the state. Once there is an abundance of jellyfish in the shelf, these could be transported and could aggregate along the shoreline, causing the stings recorded for the seasons from 2015 to 2017. This phenomenon has already been well studied on the coast of Argentina, initially by Mianzan & Zamponi (1988) and Chiaverano (2001) and more recently by Brendel et al. (2017). According to these authors, the aggregations of *O. sambaquiensis* are associated with northerly winds, which causes the animals to drift from the shore from the bottom, where they concentrate. On our coast, in addition to the higher presence of humans on the beaches at weekends, northerly winds are inversely associated with aggregations, and the higher the incidence of southerly winds, the higher the occurrence of stings (Resgalla et al., 2005, 2011). This pattern may be associated with processes of water convergence in relation to the shelf, provided by the southerly winds, which accumulate the animals in the beach region, while the northerly winds promote divergence and consequently, resurgence processes and a decrease in water temperature, as well as transporting the animals off the shelf. This pattern, which is distinct from that observed in Blanca Bay in Argentina, can be explained by the distinct orientation of the coast (W–E for Blanca Bay in Argentina and NE–SW for southern Brazil), differences in depth, and incidence of the waves in each region.

## Conclusions

The coexistence of two species of macrohydromedusae in southern Brazil may be possible due to differences in the reproductive cycle, with energy expenditure in the gonads, a short polyp stage, and continuous reproduction observed for *O. sambaquiensis* compared to a more deterministic phenology with well-defined cohorts over the year and greater longevity, as in *R. atlanticum*.

The variation in abundance of the species over the years cannot be explained by abiotic variables alone, such as temperature, but may also be associated with a balance between these and other biotic forces, such as local production and the effects of competition between species. These biotic forces may induce differences in spatial distributions, with *R. atlanticum* occurring in more open water on the shelf and *O. sambaquiensis* occurring in the nearshore zone, where it is associated with incidents of stings among bathers in the South of Brazil.

Finally, the aggregations of *O. sambaquiensis* in the South of Brazil seem to be associated with a lower incidence of northerly winds, which could cause dispersion of organisms outside of the nearshore zone, unlike the southerly winds, which promote the convergence of waters toward the coast.

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