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Reproduction and population structure of the salp *Iasis zonaria* (Pallas, 1774) in the southwestern Atlantic Ocean (34°30' to 39°30'S) during three successive winters (1999–2001)

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The salp *Iasis zonaria* is often found over the Argentine continental shelf of the southwestern Atlantic Ocean and, occasionally, its high densities dominate over other groups of zooplankton. Therefore, a better understanding of the basic aspects of its life history is essential for understanding the mechanisms underlying bloom formation. In this study, *I. zonaria* was collected during the austral winters of 1999, 2000 and 2001. Additional data were obtained from this area from May to November 1978. The most widespread distribution and largest catches occurred in 1999 (≈ 55 100 ind. 10 m⁻²). Densities decreased markedly in 2000 and the species was virtually absent in 2001. The growth of the solitary stage blastogenetic stolon and formation of several blocks of aggregate buds are described. Eight development stages were characterized and it is estimated that each solitary can produce at least four blocks and a total of ≈ 420 aggregates. The average number of buds per block increases from the older (first formed) to the youngest. The total number of buds (y) was related to solitary length (x) as: $y = 4.94 x - 134.57$. Four developmental stages were described for aggregate individuals. Based on monthly samples collected in

1978, the estimated lifespan of aggregate individuals varies between 11 and 14 months.

KEYWORDS: population structure; salp reproduction; salps; south Atlantic Ocean; zooplankton

INTRODUCTION

Salps are holoplanktonic tunicates widely distributed throughout the world's oceans. They are capable of ingesting food particles from $<2\ \mu\text{m}$ to 1 mm with high efficiency (e.g. Kremer and Madin, 1992), significantly contributing through their fecal pellets to the vertical flux of materials and carbon to deeper waters (e.g. Caron *et al.*, 1989; Phillips *et al.*, 2009). Typically, salps are found at low densities but, at times, they form dense swarms which dominate over other zooplankton taxa. Swarm development of several species (e.g. *Salpa thompsoni*, *Thalia democratica*, *S. aspera* and *S. fusiformis*) has been described in various locations (e.g. Wiebe *et al.*, 1979; Loeb *et al.*, 1997; Madin *et al.*, 2006; Daponte *et al.*, 2011). The swarms are formed presumably in response to favorable conditions and result from the rapid growth (e.g. Heron and Benham, 1985), efficient filter feeding (e.g. Madin and Kremer, 1995) and a life cycle that involves a highly productive asexual reproductive stage.

During swarming events, ecosystem functioning is altered mainly due to modification of the epipelagic food web (Landry and Calbet, 2004), mediated by decreased organic matter available to higher trophic levels (e.g. Daponte *et al.*, 2011) and enhanced export flux of organic matter to the deep layers (e.g. Fortier *et al.*, 1994). The complex life history of salps involves an alternation between the solitary (oozooids) and aggregate (blastozooids) generations. Oozooids reproduce asexually by budding producing blastozooids that reproduce sexually; it is asexual reproduction that is responsible for explosive population increases. In this context, it is essential to know which species are capable of producing swarms and to better understand the reproductive mechanisms underlying swarm formation. Aggregate stage formation by the solitaries varies between species, and is either by budding of a blastogenic stolon that continuously forms buds of aggregates or by the stolon forming blocks of buds which contain a variable number of equally sized aggregates. Except for *S. thompsoni* and *S. gerlachei* (Foxton, 1966; Casareto and Nemoto, 1986; Daponte *et al.*, 2001), *S. fusiformis* (Braconnot *et al.*, 1988), *Thalia democratica* (Braconnot, 1963; Heron, 1972a,b; Deibel, 1982; Heron and Benham, 1984, 1985; Tsuda and Nemoto, 1992; Daponte *et al.*, 1996) and *Cyclosalpa bakeri* (Madin and

Purcell, 1992), there are no estimates of the minimum number of blocks and of buds per block that can cause massive population increases. The species under consideration, *Iasis zonaria*, appears to be capable of swarm formation. It has been occasionally found in high densities at the Bay of Bengal (Nagabhushanam, 1960), off of South Africa (Pakhomov *et al.*, 1994) and in some areas over the Argentinian Continental Shelf (Mianzan *et al.*, 2001; Daponte *et al.*, 2011). This is an oceanic, cosmopolitan and eurythermal species (van Soest, 1975). However, despite its wide distribution, many aspects of the basic biology and ecology of *I. zonaria* remain unknown. The literature has mainly focused on its abundance and spatio-temporal distribution in some areas (Nagabhushanam, 1960; Esnal *et al.*, 1983; Casareto, 1988), but information about reproduction of the solitaries and aggregate stages and population structure remains scarce. Korotneff (Korotneff, 1896) described the stages of development of the embryo of a variety of salp species including *I. zonaria*, Johnson (Johnson, 1910) provided a brief description of the growing stolon and Esnal *et al.* (Esnal *et al.*, 1987) published a preliminary study on reproductive aspects of the oozoid and blastozooid generations. Since *I. zonaria* is frequently found over the continental shelf of the south-west Atlantic (Esnal and Daponte, 1999), and occasionally occurs in high densities here, a detailed knowledge of the reproductive mechanisms underlying swarm formation is important. The objectives of this study were (i) to analyze the morphology of stolon development, (ii) estimate the number of blocks and buds per block that it can produce, (iii) analyze the minimum number of solitaries that may produce the aggregates, (iv) define developmental stages for aggregates and solitaries in order to analyze the changes that occur in populations under high and low density conditions, and (v) estimate the generation time of *Iasis zonaria* in the south-west Atlantic.

METHOD

Iasis zonaria was collected over the Argentinian continental shelf from $34^{\circ}30'$ to $39^{\circ}30'S$ during surveys conducted in austral winters of 1999 (41 samples, 5–13 June), 2000 (46 samples, 20–31 July) and 2001 (40 samples, 30 June

to 10 July) aboard the RV Holmberg and Oca Balda (Fig. 1a). Additional data were obtained from 241 ichthyoplankton samples collected from 32 to 46°S by the RV Walter Herwig and Shinkai Maru from May (31 samples), June (46 samples), July (34 samples), September (41 samples), October (45 samples) and November (44 samples) 1978, no sampling was performed in the area during August (Fig. 1b).

The waters here reflect interactions between continental run off and open ocean waters of the subantarctic Malvinas and subtropical Brazil Currents. In the middle continental shelf, cold fresh Subantarctic Shelf Waters (SASW), derived from Patagonia, dominate south of

~33°S while warm salty Subtropical Shelf Waters (STSW), derived from the Brazil Current, extend north of this (Piola *et al.*, 2000). The open ocean circulation is dominated by opposing flows of the Brazil and the Malvinas currents that meet at 36°S, forming the Brazil/Malvinas Confluence. The boundary between SASW and STSW forms the Subtropical Shelf Front (STSF); this is located near the 50 m isobath at 32°S and extends southwards towards the shelf break near 36°S. The major source of coastal run off here is the Rio de la Plata, which drains the second largest watershed in South America, and discharges an average of $22\,000\text{--}30\,000\text{ m}^3\text{ s}^{-1}$. This oceanographic system is characterized by strong vertical stratification with freshwater flowing seaward at the surface and denser shelf water flowing coastward along the bottom.

Oceanographic sampling in the winters 1999, 2000 and 2001 was carried out along eight transects, T1 to T8, oriented perpendicularly to the major water masses, from the 50 m isobath to 200 m isobath (shelf break). Oceanographic data were obtained with a Seabird 19 Conductivity/Temperature/Depth profiler, calibrated with salinity measurements made with a Guildline salinometer. Each transect comprised from three to eight stations (Fig. 1a), some located beyond the continental slope. Plankton samples were collected with a Nacskhai net, mouth diameter 20 cm, fitted with a 400 μm mesh net, equipped with a Hydro-bios flowmeter and towed obliquely from 5 m above the bottom to the surface at a speed of 3.5 knots. The filtered volume varied between 20 and 385 m^3 . Entire samples were preserved in a 2% buffered formaldehyde seawater solution.

For each sample, all the solitary and aggregate individuals of *Iasis zonaria* were sorted out and enumerated from samples ≤ 100 individuals. Subsamples ($\frac{1}{2}$ or $\frac{1}{4}$) were taken for larger catches. Abundance is expressed as number of individuals per 10 m^2 . Total length from the oral to the atrial siphon of each specimen was measured to the nearest millimeter. Length–frequency distributions are based on the number of measured individuals and 1 mm length categories, which ranged from 19 to 81 mm for solitaires and from 3 to 42 mm for aggregates, were considered.

Stolon growth for solitaires (Fig. 2a and b) was examined by considering the number of blocks present, the number of buds per block and the length of aggregates located in the central area of each block (all the aggregates of a block are considered to be identical in size).

In addition to the size of free aggregates (Fig. 2c), data included the number of oocytes present in the ovary, degree of development of the ovarian sacs (OS: oocyte surrounded by follicular cells), presence of embryos larger than 1 cm and presence of placental remnants or

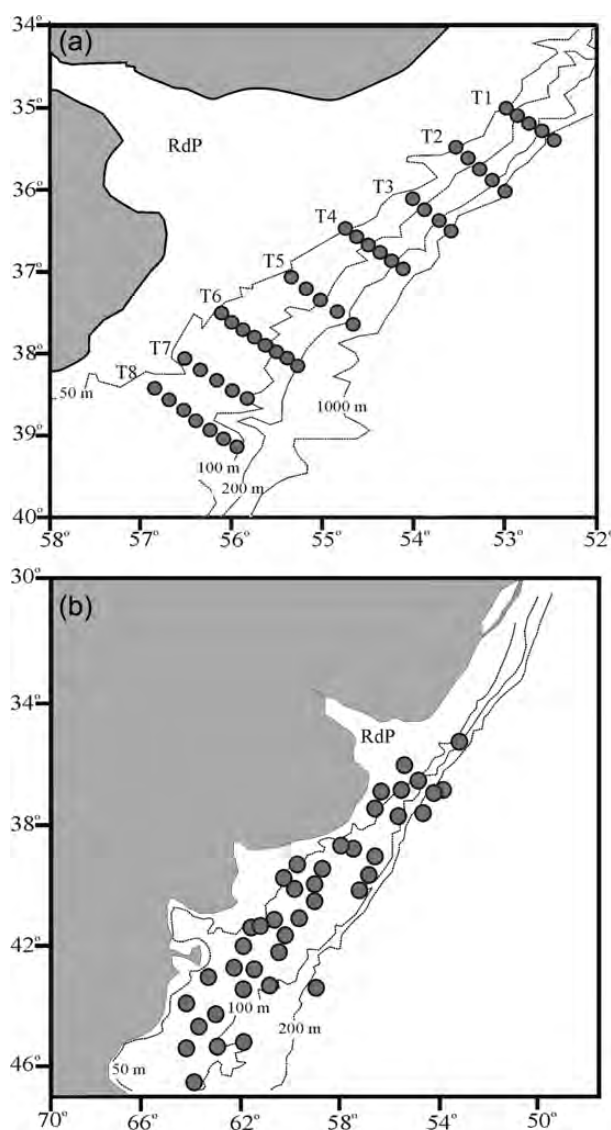


Fig. 1. Sampling stations. (a) In the austral winters of 1999, 2000 and 2001, (b) from May to November 1978. RdP, Rio de la Plata; T1 to T8, transects 1 to 8.

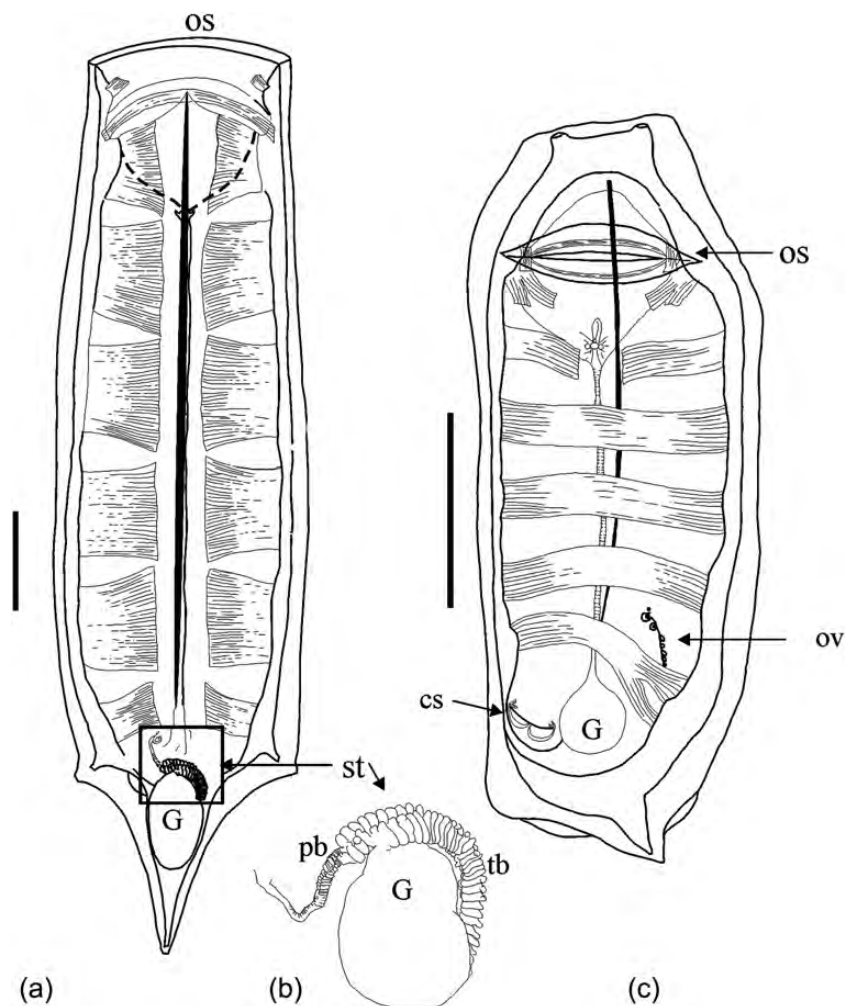


Fig. 2. *Iasis zonaria* (Pallas, 1774). (a) Solitary individual (oozooid) ventral view, (b) solon detail with two blocks of aggregates, (c) aggregate individual (blastozooid) dorsal view. Scale: 5 mm. cs, cloacal siphon; G, gut; os, oral siphon; ov, ovary; pb, proximal block; st, stolon; tb, terminal block.

placental scar indicating that at least one embryo was released.

All these characteristics were used to establish developmental stages for the solitaries and aggregates.

With these resulting data we determined:

- average number of blocks produced by solitaries;
- average number of buds per block in solitaries;
- the most abundant stage and their length for solitaries;
- the offspring to parent ratio, estimated from the ratio of the aggregate generation to their solitary parents (considering only solitary stages with a scar indicating the release of at least one block of aggregates);
- the aggregate to solitary ratio, based on the proportions for all stages of the free swimming aggregate generation and all stages of the solitary generation;

- ratio of immature solitaries to mature solitaries;
- number of solitaries present and the percentage of solitaries with abnormalities.

Solitaries that did not show block formation in the stolon or that showed only one block were considered “immature”. Those with more than one block and/or a scar were considered “mature”. Aggregates with one or two fully developed solitaries or a placental scar were considered as “mature aggregates”. The maturity criteria were established following Heron and Benham (Heron and Benham, 1985).

The length distribution for aggregates obtained during monthly surveys from May to November 1978 aboard the vessels Walter Herwig and Shinkai Maru were used to estimate the lifespan of the aggregate. In this case, oceanographic sampling was carried out from 35 to 46°S

and from the 40 m isobath to the shelf break (200 m isobath). Plankton samples were collected with a Bongo net, mouth diameter 30 cm, fitted with a 330 μm mesh net.

Iasis zonaria average density in the area (including the stations without salps) was calculated as number of individuals per 10 m².

The Kruskal–Wallis test was used in different comparisons associated with Dunn's multiple comparison test, with a significance level of $P < 0.05$. They were used to compare the length between each solitary developmental stage for 1999 and 2000, and each aggregate developmental stage for 1999. Also it was employed to compare the mean numbers of buds/block.

Two-way ANOVA (factors: year and developmental stage) was used to compare the average length-developmental stage in 1999 and 2000, $P < 0.0001$.

The correlation and linear regression between the size of solitary individuals and the total number of buds present in the stolon were determined.

RESULTS

Environmental characteristics and general aspects of the distribution

In winter 1999, water column temperature and salinity ranged between 8.0–13.0°C and 32.4–34.2, respectively. SASW was detected across the middle shelf, STSW was observed in the offshore waters of T1 and T2 and low salinity water from the Rio de la Plata were found along the coast. In 2000, temperature ranged between 7.5 and 10.5°C and salinity between 33.9 and 34.7. SASW was detected over the middle and external shelf and STSW in deeper waters of T 1. Temperature across the entire shelf was the lowest among the three winters, averaging 1.13°C and 1.64 less than 1999 and 2001, respectively. In 2001, temperature and salinity varied from 9.0 to 19.6°C and 29.7 to 39.5, respectively. The influence of STSW was detected further south than in other years, extending over the external sector of T 1 to T 3. The influence of Rio de la Plata water was detected in the coastal portion of T 1. More detailed oceanographic information can be found in Daponte *et al.* (Daponte *et al.*, 2011).

Iasis zonaria was present at >80% of stations during winter 1999, 51% of stations in 2000 and > 7% in 2001. It was widely distributed over the entire area during winter 1999, with largest catches ($\approx 55\ 100$ ind. 10 m⁻²) nearest the mouth of the Rio de la Plata.

Densities were markedly decreased in 2000, with the largest catch of 1887 ind. 10 m⁻² at an offshore station of T 1. In 2001, the largest catch comprised 95 ind. 10 m⁻² and its presence was restricted to three stations located in the middle shelf, two of which were at T1 in the northern

area (Fig. 3a and b). Average density was 2188.6 ind. m⁻² (± 8224.5) in 1999, 65.2 ind. m⁻² (± 276.9) in 2000 and 2.4 ind. m⁻² (± 14.4) in 2001.

In 1999, aggregates and solitaries co-occurred at >86%, while in 2000 they co-occurred at 50% of stations. In 1999, 128 solitary individuals were captured, while in 2000 and 2001 only 28 and 5 solitary individuals were collected, respectively. Aggregates numerically dominated the catches in 1999 (3034 individuals) and 2000 (239 individuals), and in 2001 only solitaries were captured. Solitary and aggregate length–frequency distributions varied among the three winters (Fig. 4a and b). In 1999, solitary length ranged from 25 to 81 mm with the majority of individuals (57%) in the range of 50–65 mm. Aggregate length frequencies were 3–40 mm, $\pm 75\%$ of which were 5–10 mm. In 2000, solitary lengths were evenly distributed between 27 and 80 mm and aggregates ranged from 4 to 42 mm with 65.6% between 15 and 30 mm. In 2001, the few solitaries collected ranged from 55 to 81 mm; as noted above, no aggregates were obtained.

Developmental stages

Solitaries: development of the blastogenetic stolon

In 1999, the youngest specimens showed cell accumulation in the midventral line between the posterior part of the endostyle and the anterior part of the tightly looped gut. These cells proliferated and gave rise to a tube-like stolon (Fig. 2a and 5a). As it developed, the stolon extended into the posterior region, first curling in a ventral position (Fig. 5b) and then around the gut (Fig. 5c). As it grew, the stolon began to segment, forming in this way a single row of aggregates. Subsequently, these aggregates were re-arranged as a double row that extends from a “deployment point” (Brooks, 1893; Johnson, 1910), producing a single aggregate's block consisting of individuals with the same age and size (Fig. 5c). With continued development, additional blocks of younger aggregates were formed on the stolon. The fully developed stolon (Fig. 5d) had three blocks extending from the deployment point, the terminal two of which were fully differentiated. Between the terminal and medial block and the medial and proximal block, we observed regions with a malformed block (Fig. 5e). Johnson (Johnson, 1910) called this an “intermediate piece” in her description of the stolon of other species, but since she did not observe it in *I. zonaria* she considered it non-existent.

As the stolon grew, it tunneled through the tunic and when the terminal block was ready to be released, it separated from the medial block at the intermediate piece and exited through an aperture formed in the tunic at

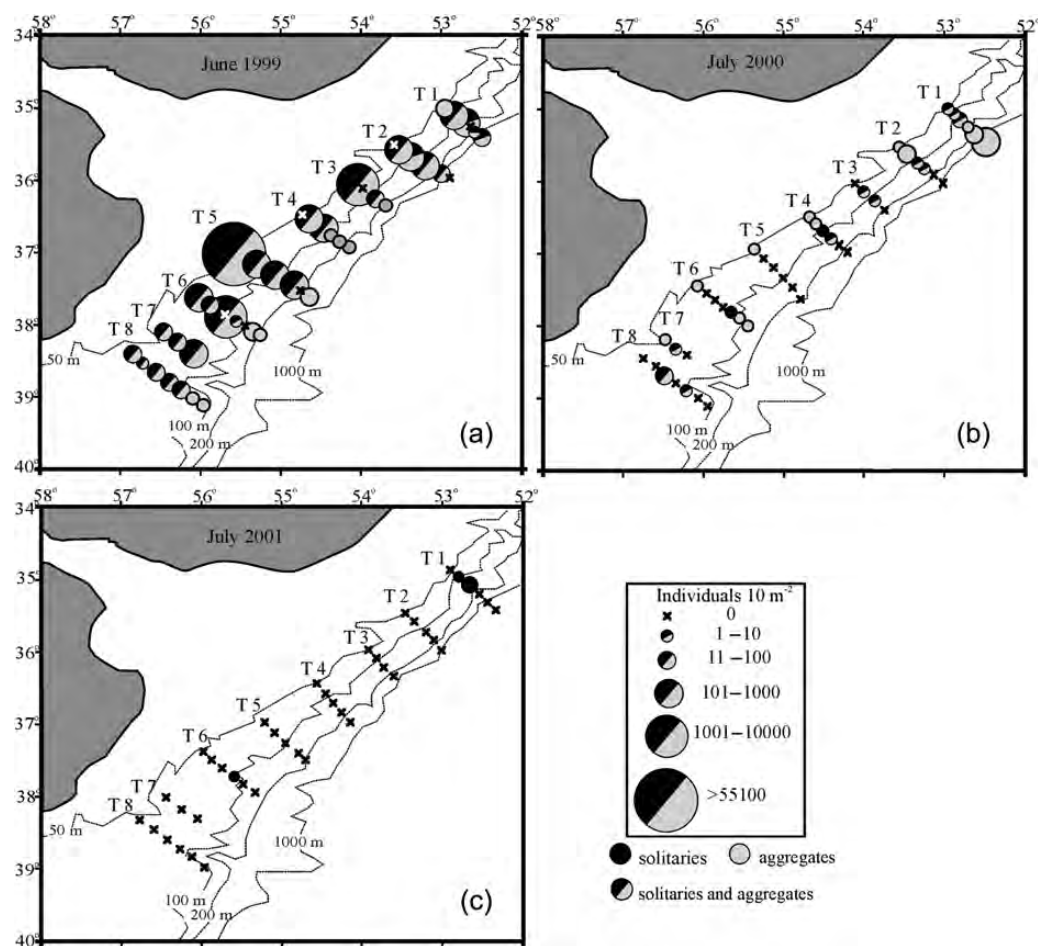


Fig. 3. Distribution and abundance (ind. 10 m⁻²) of solitary and aggregate individuals of *Iasis zonaria*. (a) June 1999, (b) July 2000 and (c) July 2001. T 1–T 8, transects 1–8.

the right ventrolateral region. Once the block was released, the aperture closed and its location was indicated by a scar in the tunic (Fig. 5f). The presence of this scar and remnants of the intermediate piece at the stolon's terminal end indicate the release of at least one block of aggregates.

Based on these observations, solitary reproductive categories were defined according to the following developmental stages:

- (1) un-segmented stolon, remnants of embryonic tissues (eleoblast and placenta), the gut looks transparent (empty gut);
- (2) segmented stolon, aggregates located in a single row, no eleoblast or placenta;
- (3) segmented stolon, aggregates located in a double row forming a single block;
- (4) two blocks of aggregates formed;
- (5) three blocks of aggregates formed;

- (6) two blocks of aggregates formed, the last one with remnants of the intermediate piece, scar present in the tunic;
- (7) three blocks of aggregates formed, the last one with remnants of the intermediate piece, scar present in the tunic.

Senile: large size, scar present in the tunic, stolon without aggregates or with malformed aggregates.

Stages 5 and 6 were assigned considering solitary length in addition to the number of buds/blocks.

Based on our observations, the average number of buds per block increases from the oldest/terminal block to the youngest/proximal block (Fig. 6). Analysis of mean differences between the number of buds in the different blocks by the Kruskal–Wallis test yielded significant differences between the numbers of buds on the proximal and medial blocks ($P < 0.05$) as well as between the proximal and terminal blocks ($P < 0.05$). Although the

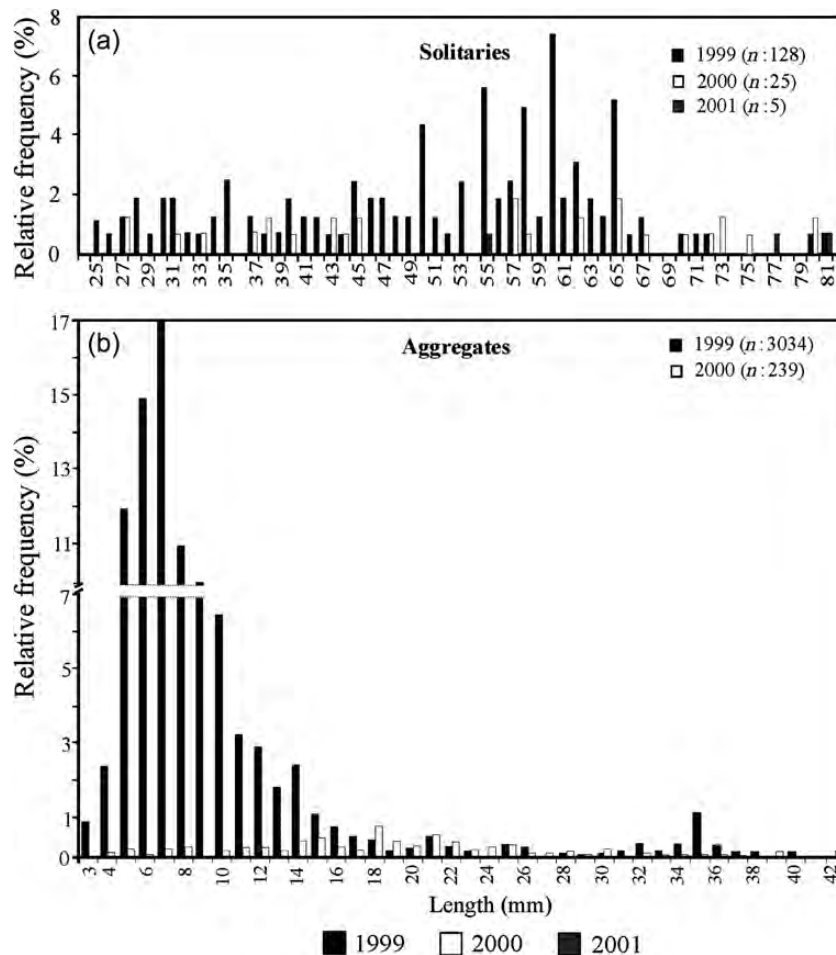


Fig. 4. Length distribution of (a) solitaries and (b) aggregates of *Iasis zonaria* in 1999, 2000 and 2001.

medial block contained more buds than the terminal block, the difference was not significant.

The length of the aggregates within each block was approximately the same but the average length of each block differed, being larger in the oldest block. For example, in the stolon of stage 4 solitary individuals (three blocks, no scar), the terminal block reached 3.28 ± 0.28 mm, the medial 0.83 ± 0.19 mm and the proximal 0.42 ± 0.15 mm (Fig. 6), this value being the average diameter of the stolon at the beginning of segmentation.

The total number of buds was positively correlated with solitary length between 42 and 82 mm ($n = 86$, $\alpha = 0.05$) following $y = 4.94x - 134.57$ ($r^2 = 0.58$) where y is the total number of buds and x the solitary length (Fig. 7).

The stolon development study established that *Iasis zonaria* could produce during its entire life at least four blocks of aggregates. Based on the maximum average of aggregates per block (see in Fig. 6: 78.6, 95.9, 120.9 and 126), each stolon potentially could produce ≈ 420 buds.

In July 2000, 75% of solitaries showed the development described in 1999, but the remaining individuals had abnormalities. One of these was a fully developed block at the proximal end of the stolon with a great number of undeveloped aggregates of different sizes at the terminal end and an amorphous mass within the tunnel. In a few cases (less than 1%), there were malformed stolons with only two to six easily identifiable aggregates and the rest abortive (Fig. 8), or a decrease in the stolon diameter towards the terminal end with no bud formation at all. The few solitaries collected in 2001, were in stage 4 (with normal stolon), 5 (some with abnormal stolon) and senile.

Aggregates: embryo development

The ovary (Fig. 2c), located on the cloacal cavity wall, showed a variable number of OS that ranged from 3 to 9 in 1999 and 3 to 10 in 2000, with an overall average of 6 OS/ovary. Once fertilized, varying degrees of OS development could be seen (Fig. 9a). When the solitary

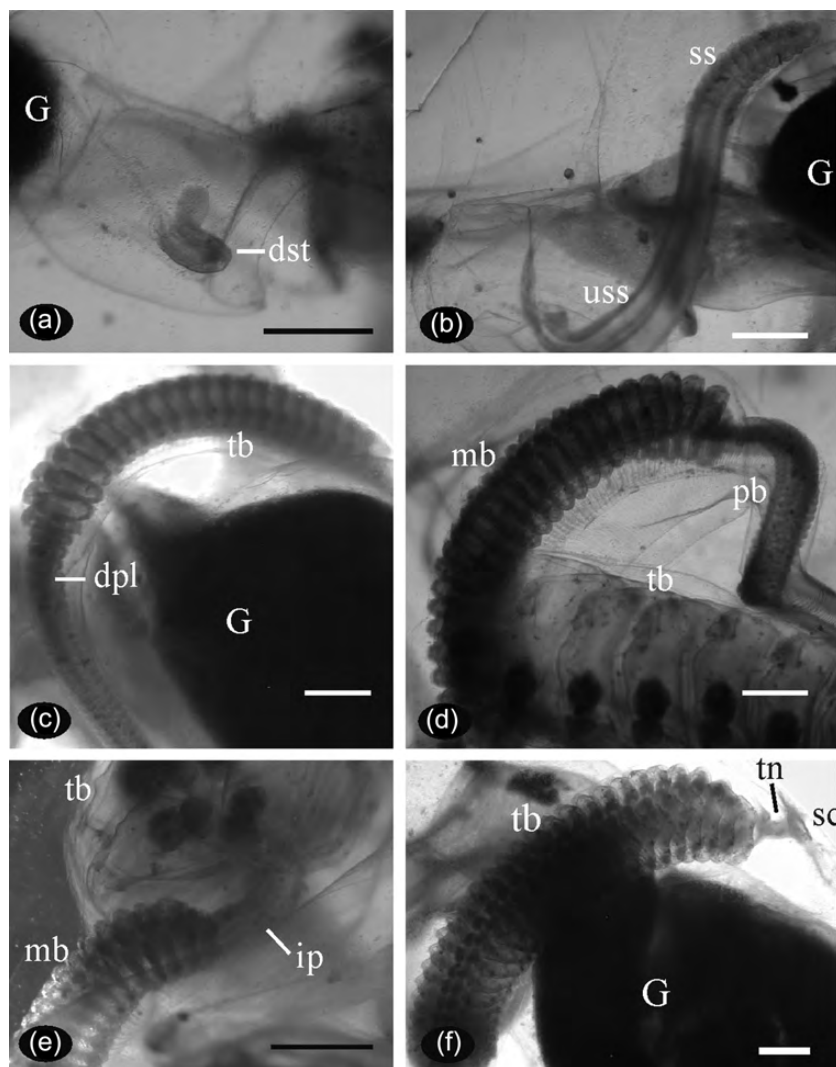


Fig. 5. Stolon development morphology for *Iasis zonaria* (a) beginning of stolon development, (b) beginning of segmentation and deployment, (c) formation of the first block, (d) fully developed stolon, (e) intermediate piece, (f) tunnel and scar in the tunic. Scale: 1.6 mm. dpl, deployment point; dst, developing stolon; G, gut; ip, intermediate piece; mb, medial block; pb, proximal block; sc, scar; ss, segmented stolon; st, stolon; tb, terminal block; tn, tunnel; uss, unsegmented stolon.

embryo was fully developed, it was released, leaving a visible scar as a result of placental detachment. The mature aggregates had one or two fully developed solitaires (Fig. 9b) or a placental scar in some cases, a portion of placenta remained attached, similar to the “spent” stage of Foxton (Foxton, 1966).

Aggregates were grouped according to the following stages of development (Fig. 10):

- (A) OS spherical with no sign of embryo development;
- (B) 60% of OS in different degrees of development;
- (C) at least 1 embryo > 10 mm in length;
- (D) with placental scar or placental remnants, indicating that at least one embryo had been released.

We grouped some aggregates with abnormal development (no embryos present or disrupted embryo development) as “X” stages according to Chiba *et al.* (Chiba *et al.*, 1999).

In 1999 aggregates, ≥ 30 mm had a placental scar but in 2000 the placental scar was observed only in individuals > 32 mm. The length of embryos inside the aggregates ranged between 10 and 25 mm, the maximum length corresponding to that at which individuals are released. The smaller length individuals that were found in samples appeared to have been expelled prematurely during capture, therefore individuals < 25 mm were not considered in the solitary length–frequency distribution

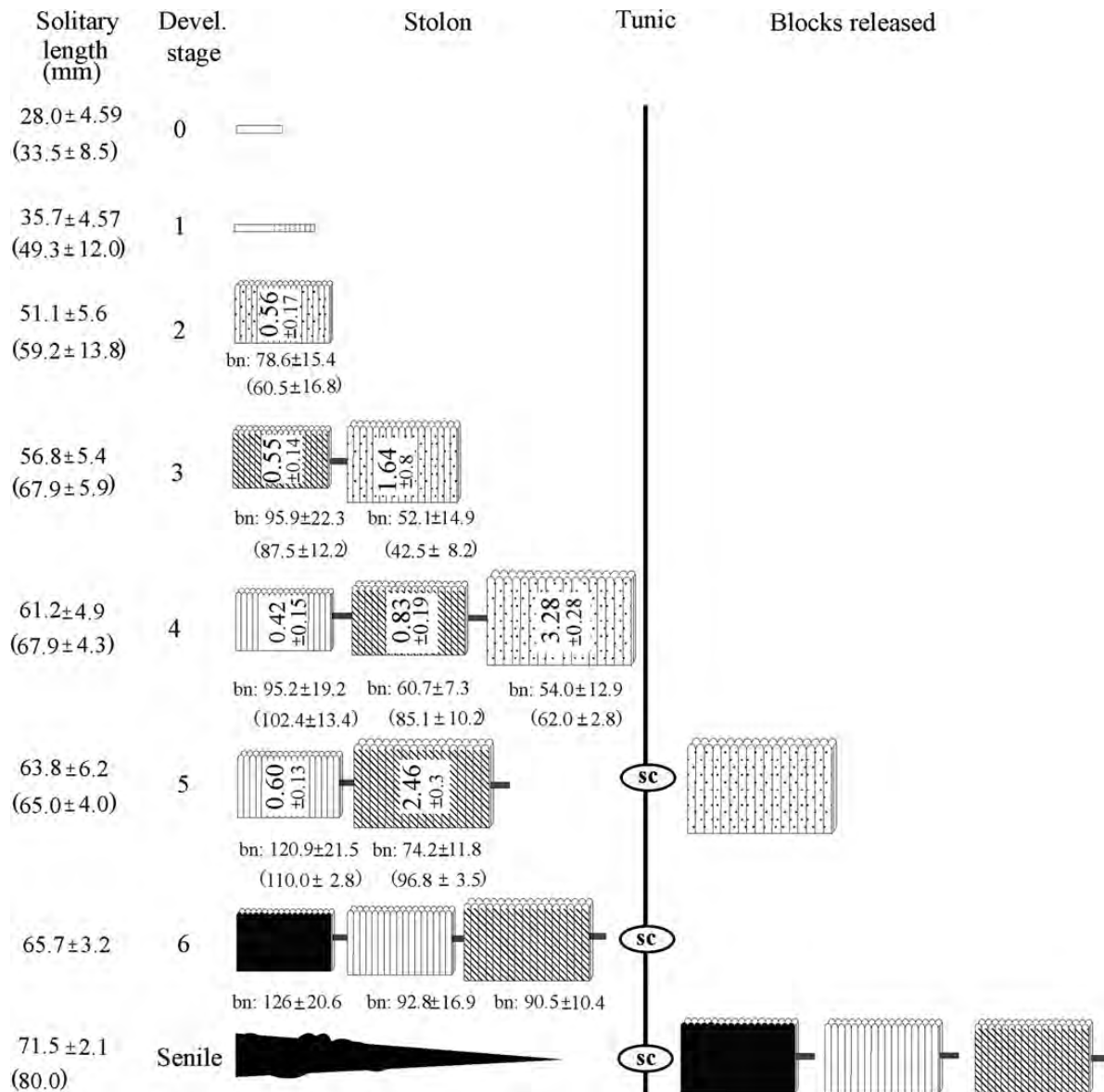


Fig. 6. Schematic representation of stolon development for *Iasis zonaria* showing the formation of blocks. Solitary length values express the average length (mm) of individuals in each stage. 0 to Senile: development stages. The values within the blocks represent the average length of aggregates for each block. bn, average number of buds/block; sc, scar. The values without parentheses correspond to 1999 and within parentheses to 2000.

(Fig. 4a). Only in 2000 did we observe large aggregates corresponding to the X stage.

Analysis of the size-class distribution of developmental stages

Solitaires

The frequency of developmental stages (0 to Senile) differed each year (Fig. 11a). In 1999 stages from 0 to Senile were found, with stages 2 and 3 being the most abundant. In 2000, when solitary stage abundance was only 25% of that observed the year before, we found no stage 6

individuals and stage 5 was slightly more common than other stages. The few solitaires collected in 2001 were in stages 4, 5 and 6. The immature to mature solitaires' ratio varied within the two winters with sufficient material: ≈ 1 in 1999 and ≈ 0.6 in 2000 and in 2001 (Table I). Figure 12a and b shows the average length increase in successive solitary maturity stages during 1999 and 2000. The average length increase during development from stage 0 to Senile was 5.9 mm in 1999 and 7.8 mm in 2000; however, length increase is only statistically significant for stages 1, 2 and 5 (two-way ANOVA, $P < 0.0001$, Table II).

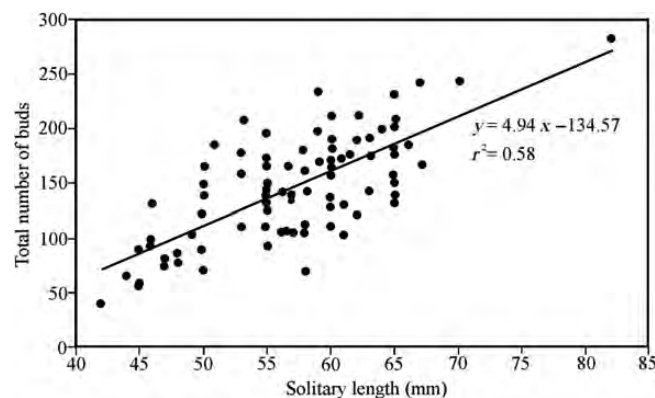


Fig. 7. Correlation between the total number of buds and solitary lengths for *Iasis zonaria* in 1999.

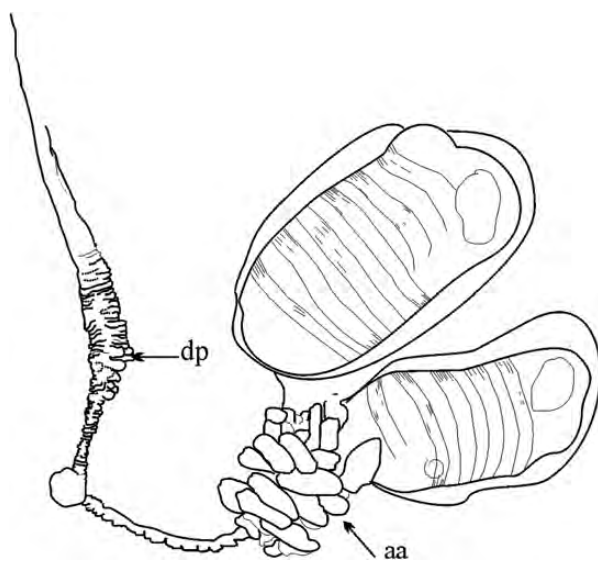


Fig. 8. General view of a malformed stolon of *Iasis zonaria*. From the deployment point (dp), a region can be observed with abortive aggregates (aa) and two fully developed aggregates at the end.

Aggregates

Greatest abundance (Table I) and frequency of aggregates occurred in 1999 (Fig. 11b). All five stages of development (A–D) were found, with stage A (without evidence of fertilization) being the most frequent. Aggregate abundance in 2000 was <15% that in 1999 and stage B (>60% with developing OS) was most frequent. No aggregates were collected in 2001.

As observed for solitaries, the average length of aggregate developmental stages in 1999 increased from the youngest to most mature (Fig. 12c and d). Length differences between stages were significant (Kruskal–Wallis, $P < 0.0001$) except between C and D.

Abundance relationships between aggregates and solitaries and between the solitary stages as well as the average number of blocks and buds are presented in

Table I. The winter of 1999 was characterized by a large number of salps overall, and abundance of the solitary stage was five times higher than in 2000. The average number of buds/blocks in the stolon was 50% higher, but the average number of blocks was $\approx 18\%$ lower than the following year. The ratio between free aggregates and scarred solitaries decreased by 50% and the ratio between free aggregates and total solitaries decreased by 65% in 2000. Moreover, in 2000, the proportion of solitaries with stolon malformations reached 40%.

Reanalysis of the data from Esnal *et al.* (Esnal *et al.*, 1987) from the samples collected in 1978 yielded information on monthly changes of solitary maturity stages (Fig. 13) and the aggregate length distribution (Fig. 14) across this 6-month fall–winter–spring period. In Table III, the sampling effort is shown: number of stations with salps, density ranges for stations with salps and the aggregate/solitary ratio for each month.

Regarding solitary individuals, it was observed that only in June it was possible to find all development stages (from 0 to Senile), mature stages being (3–Senile) more abundant than immature ones. In July, the highest values corresponded to stage 1 (young oozoid with an unsegmented stolon) and stage 4 (mature oozoid with three blocks of buds in the stolon). During September, stage 4 was the most abundant one and no recently liberated oozoids (stage 0) nor senile individuals were observed. In October, although the number of individuals was larger than the month before, no stage 0 nor Senile individuals were found either. During November, the number of individuals decreased and only stages 2, 4 and 6 were observed.

In the case of aggregates, the number of individuals per size varied among the months sampled. In May (Fig. 14a), specimens >12 mm were found and three different modal groups could be identified: 20, 24 and 31 mm. The last one mainly corresponded to stages C (aggregates with a fully developed embryo), while the

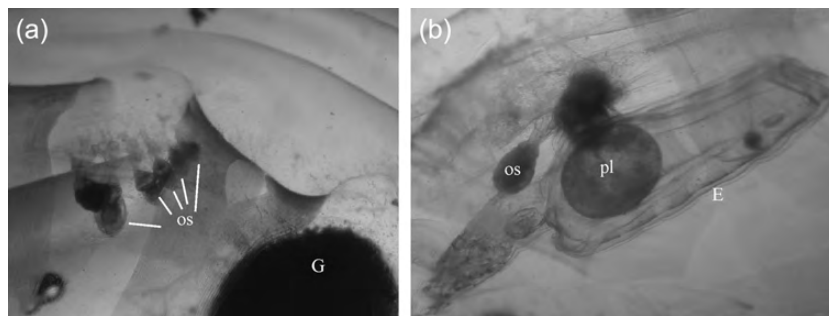


Fig. 9. Development of OS for *Iasis zonaria*. (a) Five OS at different stages of development, (b) fully developed embryo and an ovarian sac in development. E, embryo; G, gut; pl, placenta; os, ovarian sac.

other two groups mostly corresponded to stage B. In June (Fig. 14b), the lengths varied between 4 and 47 mm and showed two strong modal peaks between 7 (stage A) and 11 mm (mostly stage A) and modest modal peaks between 20 and 41 mm, corresponding the 20–23 mm group to stage B and the 38–47 mm group to stages C and D. In July (Fig. 14c), the number of individuals decreased along the whole length range. The highest peaks were at the 10 mm (stage A), followed by some lower peaks at 14 mm (stage A), 25 mm (mostly stage B) and 30–50 mm (stages C and D). In August, no sampling was performed. The highest abundance was observed in September, the beginning of the austral spring (Fig. 14d). Lengths varied between 3 and 36 mm with several modal peaks at 3 mm (stage A), 9–10 mm (stage A) and 12 mm (mostly stage A). The abundance decreased towards larger sizes. In October (Fig. 14e), the length distribution varied between 4 and 39 mm. Small sizes were abundant, showing a peak at 7 mm (stage A) and smaller peaks at 11 mm (stage A), 14 mm (stages A and B), 25 mm (stage B) and 28–30 mm (stages B and C). The largest size found was 39 mm and corresponded to stage D. In November (Fig. 14f), there was a significant decrease in abundance. The highest values were registered at 10 mm (mostly stage A), 15 mm (stages A and B), 22–25 mm (stages B and C) and 34–35 mm (stage D).

Considering the spring months, from September to November, in which most of the lengths were present and comparing the shift of the largest peaks among these months (assuming these peaks correspond to the same group of individuals), several results can be extracted. In September, the largest frequency corresponds to the 3 mm specimens belonging to developmental stage A (immature). In October, the most frequent size was in the range of 7 mm, and some aggregates showed signs of ovarian sac development. In November, the highest peak was shifted to 10 mm. It can therefore be observed that between September and November the length of immature aggregates increased by 7 mm. When considering the September 9 mm size group, this reached 11 mm in

October and 15 mm in November (6 mm increase). Overall, the average increase in 2 months would be ≈ 6.5 mm. If we assume 3 mm as the initial size of an aggregate in September, it would require ≈ 11 months to achieve the length of 40 mm observed in spring or ≈ 14 months to achieve the 50 mm size that was observed in winter.

Growth rate estimates could not be performed on the solitaries due to the small number of specimens.

DISCUSSION

The presence of *Iasis zonaria* during the three winters analyzed was highly variable. The salps were widely distributed and very abundant in 1999, but their numbers were markedly decreased in 2000 and almost non-existent in 2001. Although the hydrographic conditions in 2001 were much different, with a broader range of temperature and salinity than the previous 2 years, it is difficult to interpret how this might have influenced salp abundance. Daponte *et al.* (Daponte *et al.*, 2011) could not find significant correlations between *I. zonaria* abundance and salinity and/or temperature during the sampled periods. The oceanographic studies in the area point out that the mean current direction over the central platform is N-NE (Rivas, 1997; Piola *et al.*, 2000). Moreover, the STSE, located between 32 and 36°S, is also present as a result of the meeting of two different water masses (STSW and SASW) with an off-shore direction along this front (Piola *et al.*, 2000). This water circulation, together with the simultaneous presence of mature solitary individuals and young aggregates, suggests that the population increase is mainly due to *in situ* reproduction and not to advection.

Rapid population increases of salps primarily result from asexual reproduction by solitary individuals through their production of many offspring via stolon budding. Aggregate production potential varies among salp species. The total number of aggregates (≈ 420) *Iasis zonaria* solitaries can produce is smaller than that of *Salpa*

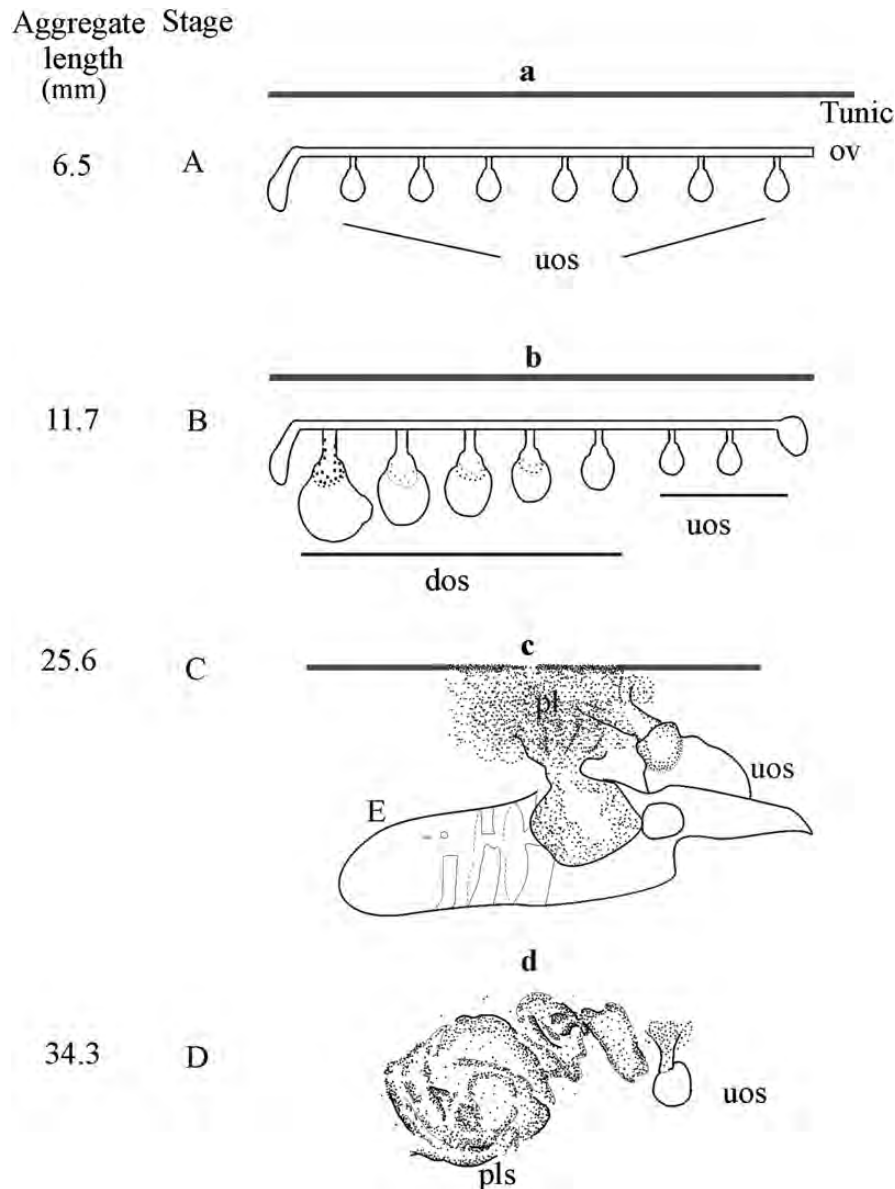


Fig. 10. Schematic representation of developmental stages for *Iasis zonaria*. (a) No signs of ovarian development, (b) OS at different stages of development, (c) ovary with a developing embryo and a fully developed embryo, (d) placental scar. dos, developing ovarian sac; E, embryo; ov, oviduct with undeveloped OS (uos); pls, placental scar. (a, b, c) lateral view, (d) dorsal view. A–B–C–D: development stages. The values express the average length of the individuals in each stage in 1999.

thompsoni (≈ 800), another large species that proliferates in Antarctic and sub-Antarctic waters (Foxton, 1966; Casareto and Nemoto 1986; Casareto, 1988; Daponte *et al.*, 2001). However, this production potential is greater than that of other oceanic species such as *Salpa fusiformis* (93–179; Braconnot *et al.*, 1988) or *Cyclosalpa bakeri* (≈ 170 ; Madin and Purcell, 1992) as well as small neritic species *Thalia democratica* (32–112; Braconnot, 1963).

Regarding stolon morphology, the fully developed stolon of *Iasis zonaria* has three blocks of buds beginning

from the deployment point (the point where the stolon passes from a single to a double row of buds). However, in *Thalia democratica*, as in the genus *Salpa*, only two blocks are found. The region called the “intermediate piece” characterized by the presence of abortive buds that mark the boundary between successive blocks of buds is also observed in the genus *Salpa* but not in the genus *Thalia* (Daponte *et al.*, 1996). An increased number of buds for successive blocks were also described for *Salpa thompsoni* (Foxton, 1966; Casareto and Nemoto, 1986; Casareto,

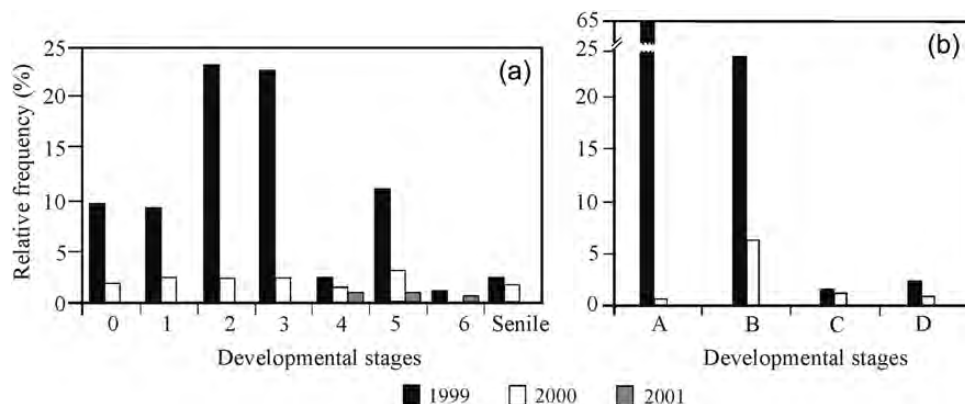


Fig. 11. Frequency relative to total catch (all years) for each development stage of *Iasis zonaria* solitaries (a) and aggregates (b) during the austral winter (June 1999, July 2000 and 2001).

Table I: Demographic data for Iasis zonaria populations within the Argentinian shelf survey area during 1999, 2000 and 2001 along the sampled area

	1999	2000	2001
Total stations/stations with salps	46/37, 80.4%	46/28, 60.86%	44/3, 6.81%
Mean density (ind. 10 m^{-2}) including stations without salps	2188.6 (± 8224.5)	65.2 (± 276.9)	2.4 (± 14.4)
Density range for stations with salps (ind. 10 m^{-2})	55 110–14.4	1877.5–1.7	94.9–9.7
Total solitaries	128	28	5
Total aggregates	3034	239	0
Average number of blocks in solitaries	1.9 (± 0.57) ($n = 86$)	2.3 (± 0.58) ($n = 18$)	–
Average number buds/block	41 (± 14.6) ($n = 86$)	27.5 (± 12.9) ($n = 18$)	–
Free aggregates/solitaries with scar	126:1	16:1	–
Free aggregates/total solitaries	27:1	9.56:1	–
Immature solitaries: mature solitaries	0.9	0.6	–
More abundant stage of solitaries:	2–3	5	–
Abnormal solitaries	–	40%	90%

1988; Daponte *et al.*, 2001) and members of the “*Thalia democratica* species group” (Daponte *et al.*, 1996).

As for sexual reproduction, unlike the aggregates of most species which have only a single ovarian sac, *I. zonaria* can have between 2 and 11 OS but further development of the oocytes only produces one to two fully developed embryos. Similar observations have been made for *I. magalhanica*, whereby the ovary can form numerous OS, but eventually produces only two fully formed embryos (Daponte and Esnal, 1994).

Comparing *I. zonaria* population structure over the three successive winters and the dominance of young aggregates and the abundance of newly born and immature solitaries (ratio immature: mature ≈ 1 , Table I) suggests that the population was actively reproducing sexually and asexually. Probably, the fully developed solitary stages (3–Senile) were responsible for the high number of aggregates. Accordingly, the young solitary stages 0–2, which probably reached mature stages 5–Senile in 2000, were responsible for producing the new aggregates between the two winters. The large stage

spent aggregates (34.3 mm) may represent survivors from the 1999 reproductive season and would therefore be the source of the young solitaries found the following winter. In 1999, the difference between the estimated number of aggregates that a solitary can produce (≈ 420) and the ratio between the number of aggregates and the number of solitaries with a scar (32:1; Table I) could be a predictor of mortality. Similarly, Foxton (Foxton, 1966) suggested that extensive mortality of *Salpa thompsoni* solitaries could be predicted by observing the mismatch between the number of developing embryos inside aggregates and the small number of total solitaries in the water column. The high abundance of *I. zonaria* in the survey area during winter 1999, along with the free aggregates:total solitaries and immature:mature solitaries ratios, also indicate that the population was actively reproducing sexually and asexually.

Although *I. zonaria* was widely distributed across the survey area in 2000, its abundance was reduced to 20% when compared with the previous winter. The low percentages of mature aggregates (C and D) and newly born

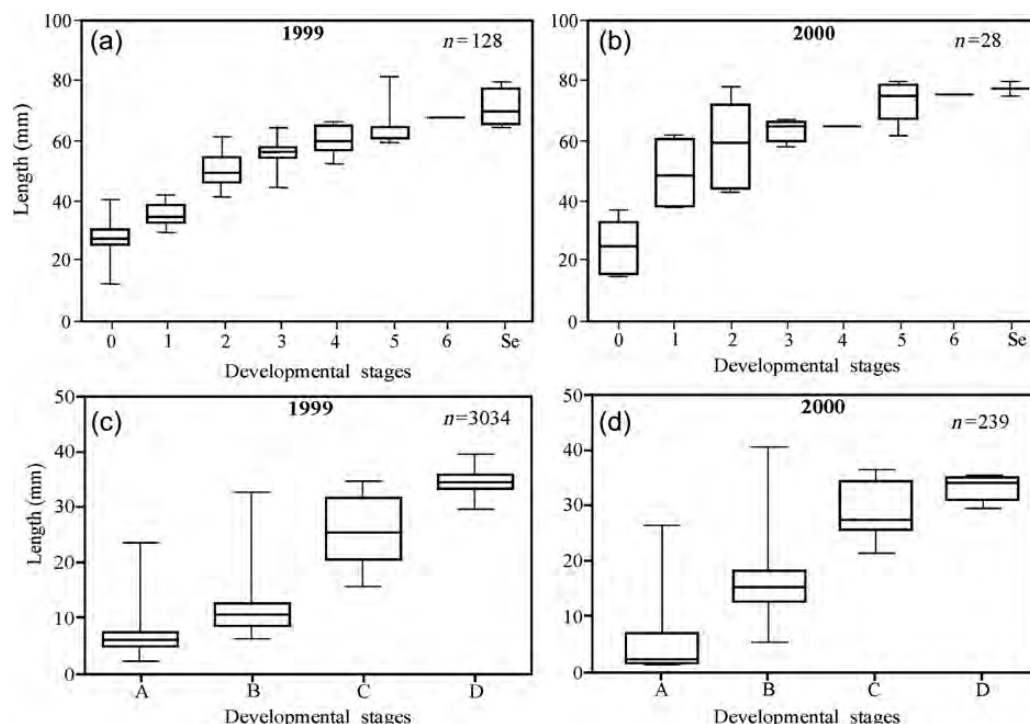


Fig. 12. Average length for the different stages of development of solitaries (a and b) and aggregates (c and d) of *Iasis zonaria* in 1999 and 2000. The short horizontal lines show minimum and maximum values. The box is defined by values of lower and upper quartiles with median shown as a line across the box.

Table II: Dunn's multiple comparison for the length of the different stages of development of solitary individuals of Iasis zonaria in 1999 and 2000

Year	Developmental stages combinations		
1999	0 versus 2		
	0 versus 3	1 versus 3	
	0 versus 4	1 versus 4	
	0 versus 5	1 versus 5	2 versus 5
	0 versus Senile	1 versus Senile	2 versus Senile
2000	0 versus 5		
	0 versus Senile		

Combinations that varied significantly ($P < 0.05$) are shown.
0–Senile = developmental stages.

solitaries suggest a decrease in sexual reproduction. The larger abundance of solitary individuals at more advanced maturity stages and nearing the end of reproductive capacity (stages 5–Senile) also indicates a reduction in asexual reproduction. In addition to this, the increased incidence of malformed stolons and aggregates that show poorly developed embryos, arrested development or failed fertilization, would explain the marked decrease in abundance. When salps are in low abundance,

the chance that sperm released by male aggregates may reach the unfertilized oocytes is greatly reduced, such a situation in 2000 could result in the extremely low numbers of salps observed in 2001. No juvenile solitaries were observed then, but the very large solitaries present were capable of asexual reproduction. Given favorable environmental conditions (e.g. nutrient rich water promoting appropriate phytoplankton levels) this “seed” population, composed of stages with the capability to release large number of aggregates, may initiate a new population explosion. Heron and Benham (Heron and Benham, 1984) described the population structure of an “overwintering” population of *T. democratica* that is similar to what we observed in 2001 for *I. zonaria*, where solitaries were apparently awaiting for favorable conditions to initiate the aggregates’ chain release.

Demographic differences observed among the three winters also reflect environmental differences. These include the number of buds/block that was larger in 1999 (Table I) and the average length of the different stages of solitaries and aggregates that was higher in 2000. These observations are in accordance with decreasing water temperatures caused by the increased influence of cold Malvinas Current water farther north along the shelf in 2000 (Daponte *et al.*, 2011). Decreased temperatures possibly caused solitaries to grow more

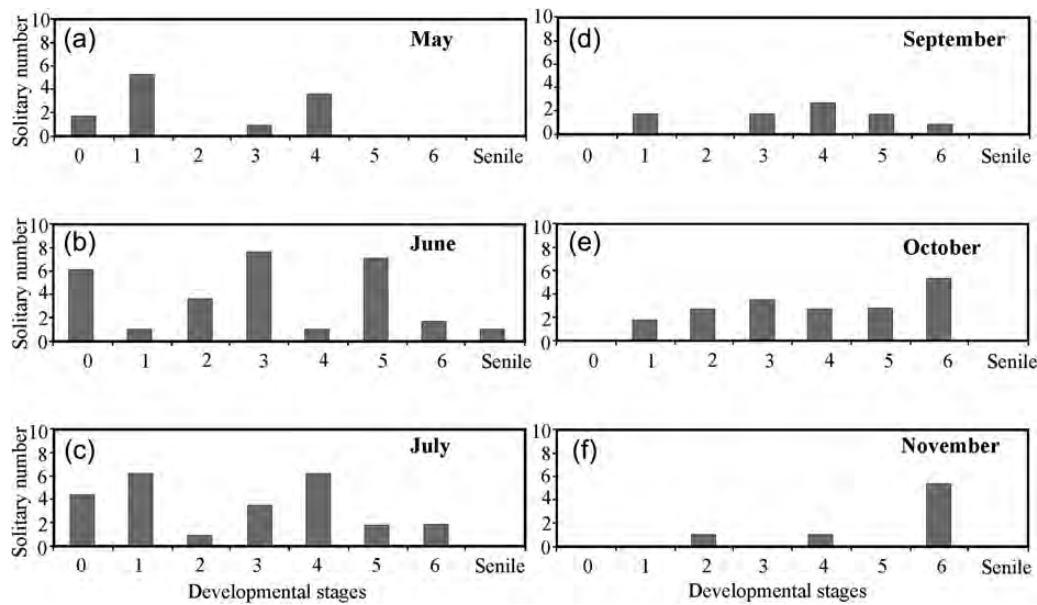


Fig. 13. Total number of individuals for each month for the different developmental stages of *Iasis zonaria* solitaires from May to November (a–f) 1978.

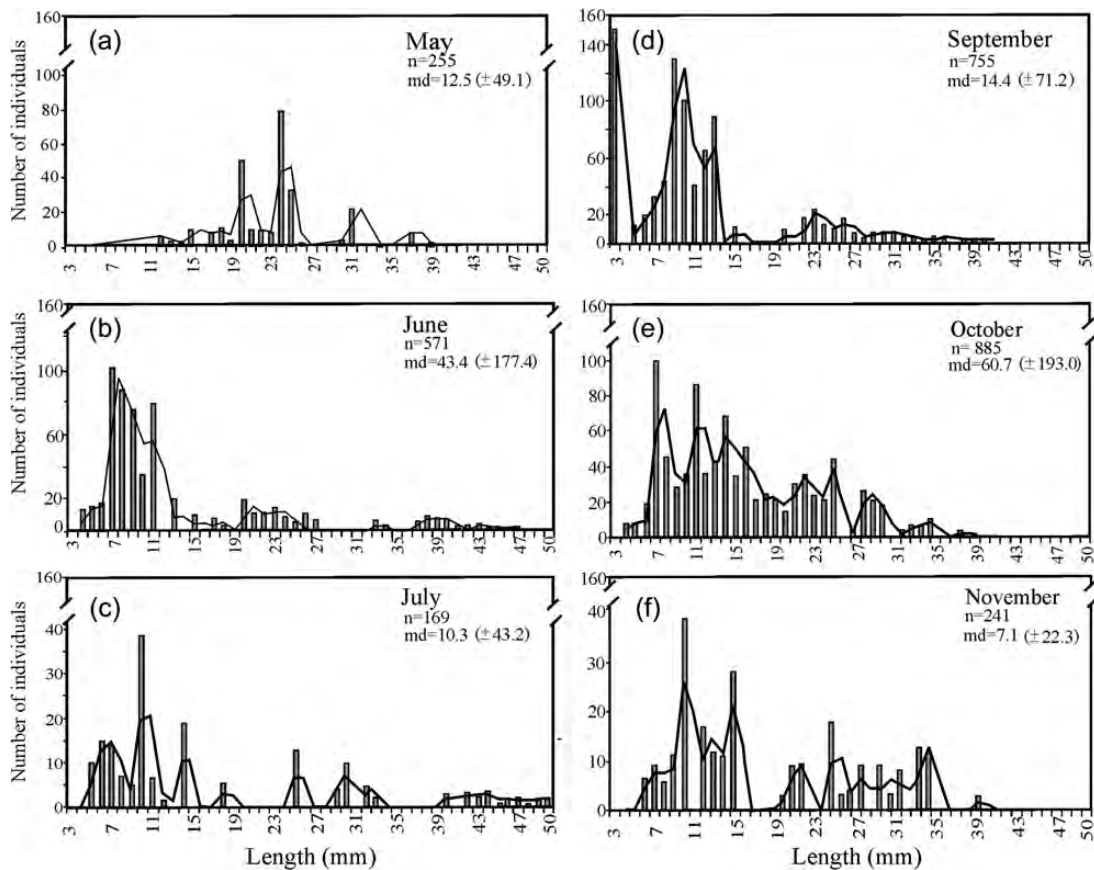


Fig. 14. Length distribution of *Iasis zonaria* aggregates from May to November (a–f) 1978. md: mean density (ind. 10^{-3}).

Table III: Data collected from the monthly surveys (May to November 1978) aboard the vessels *Walter Herwig* and *Shinkai Maru* from 32°S to 46°S

	May	June	July	August	September	October	November
Total stations/st with salps	31/6	46/16	34/12	0	41/4	45/18	44/9
Mean density (ind. 10 m ⁻²)	12.5 (± 49.1)	43.4 (± 177.4)	10.3 (± 43.3)	–	14.4 (± 71.2)	60.7 (± 193.0)	7.1 (± 22.31)
Density for stations with salps	254–2.73	1260–1.5	264.4–18.5	–	455.9–331	865.25–433	101–4.6
Aggr. /Sol.	32.41	17.91	7.82	–	81.5	64.47	84.25

Mean density: including stations without salps. Aggr. /Sol. ratio between free aggregates in the water column and all solitary developmental stages.

slowly but to attain larger sizes. Decreased temperature and larger sizes could explain increased bud production by the few mature solitaries (stages 4–5; Fig. 6) and malformations of younger solitaries in 2000.

Taking into account the developmental stages for solitary individuals from May to November 1978, it may be suggested that despite the lack of data for August, mature oozoids (4 to Senile) present in June and July were responsible for the production of the young aggregates found in September (Figs 13 and 14). Besides, the larger aggregates (stages C and D) are probably responsible for producing the young oozoids (0, 1 and 2) observed from May to July. The aggregate:solitary ratio shows a larger number of aggregate individuals in spring, coinciding with the higher abundance of phytoplankton in the area (Carreto *et al.*, 1995). Although it is generally agreed that salps avoid both high chlorophyll conditions and high particulate concentration, Fortier *et al.* (Fortier *et al.*, 1994) hypothesized that the grazing of a swarm of salps could control phytoplankton density to a level at which their feeding apparatus would not clog.

Based on the analysis of the increments in aggregate length during spring 1978, a growth rate of ~3.5 mm was estimated; this results in an estimation of the aggregates' lifespan from chain release to solitary production of between 11 and 14 months.

This result is probably not accurate due to the fact that only a conventional sampling method was used; as no replicate tows were performed at any single station, this could lead to a distorted view of the actual size frequency of the field population, creating false modal peaks. However, the result is not very different to that calculated by Loeb and Santora (Loeb and Santora, 2011) for *S. thompsoni*, another large oceanic species. In that case, a maximum lifespan of ~7 months was observed for aggregates and from ~7.5 to 15 months for solitary individuals, suggesting a maximum total generation time of ~2 years. It should be noted that as *I. zonaria* inhabits warmer waters, it is possible that the generation time is overestimated as a result of the sampling limitations mentioned above. Therefore, further studies will be necessary to refine these estimations. The values for both *I. zonaria* and *S. thompsoni* are considerably higher than the ones

calculated by Madin and Purcell (Madin and Purcell, 1992) in field studies of *Cyclosalpa bakeri* solitaries (30 days) and by Braconnot (Braconnot, 1963) and Deibel (Deibel, 1982) in laboratory cultures of *Thalia democratica* for the total generation time (average 21 days). These differences are not surprising, especially in the case of *T. democratica*, a small warm-water species where one would naturally expect the intrinsic growth rates to be quite different.

Deibel and Lowen (Deibel and Lowen, 2012) analyzed the response of life-history traits to environmental conditions in pelagic tunicates. These traits are related to life-time fitness that was assumed as the maximum intrinsic rate of natural increase: $r_{\max} = \ln b/T$ where b is the life-time egg production and T the development time from fertilization to spawning. As pelagic tunicates are semelparous, T is the generation time. Most salp species produce only a single egg per aggregate or, if more eggs are produced as in the case of *I. zonaria*, only two of them fully develop. Therefore, the number of aggregate buds produced by each solitary individual is the only reproductive life-history trait with the plasticity to respond to environmental conditions and upon which natural selection can act. Accordingly, in the case of salps, it makes sense to determine the r_{\max} value based on the number of buds and the lifespan of solitary individuals. If equivalent lifespans are supposed for *I. zonaria* aggregates and solitaries, this would also result in a total generation time of almost 2 years as in *S. thompsoni*. When applied to the r_{\max} calculation, it results in very small values even if the lifespan of the solitary individual is considered as T . In other words, $r_{\max} = \ln 420/330\text{d}$ (11 months) = 0.02 day⁻¹ for *I. zonaria* and 0.03 day⁻¹ for *S. thompsoni*, considering in the latter case $b = 800$ according to Daponte *et al.* (Daponte *et al.*, 2001) and $T = 7.5$ months (225 days) according to Loeb and Santora (Loeb and Santora, 2011). Therefore, the r_{\max} value does not adequately reflect the extraordinary ability of these species to form blooms.

Unfortunately, due to the scarce available information for *I. zonaria* solitaries, it is not possible to get a real estimation of its lifespan. Moreover, it is not possible to determine how long it takes to increase their number 400 times nor what environmental conditions are required

for this. Further studies are required in order to be able to predict bloom production on the Argentine shelf.

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