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REPRODUCTION AND RECRUITMENT PATTERNS OF THE SURF CLAM *DONAX SERRA* (BIVALVIA, DONACIDAE) ON TWO NAMIBIAN SANDY BEACHES

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Reproduction and recruitment of the surf clam *Donax serra* on two Namibian beaches were studied over a period of two years. Histological examination of the gonads indicated a discontinous annual reproductive cycle, related to monthly mean sea surface temperature. The spawning season lasted from August/September to February, but juveniles (2–6 mm anterior-posterior shell length) were only present for three months in the intertidal zone. The condition index indicates that the species spawns during autumn and summer, but histological validation is needed. The period when juveniles are abundant is decoupled from the spawning period and therefore cannot be predicted clearly, even if the spawning period is known. Starvation, hydrodynamic processes, chemical parameters and different release times during the spawning period are thought to cause the differences in settlement time and recruitment strength between locations.

Key words: condition index, *Donax serra*, histology, Namibia, recruitment, reproduction, sandy beach ecology

Fuelled by upwelling, the Benguela ecosystem off Namibia is one of the most productive marine systems in the world (Jarman and Carter 1981, Schulz 1982). The macrozoobenthos of the intertidal and shallow subtidal of large exposed Namibian sandy beaches is typically dominated by the surf clam *Donax serra* (Röding, 1798, McLachlan 1985, 1986, Donn and Cockcroft 1989, McLachlan *et al.* 1996), but despite its abundance, many aspects of its population dynamics in Namibia are unknown.

The reproductive biology of *D. serra* elsewhere in southern Africa is documented in other studies, but it is summarized here. Sexual differentiation occurs at a mean length of 44 mm in the Eastern Cape (McLachlan and Hanekom 1979) and 48 mm on the South African west coast (De Villiers 1975). Sexes can only be distinguished histologically (De Villiers 1975). The exact duration of the meroplanktonic larval phase is not known exactly and is therefore subject to some speculation. Whereas Lastra (1994) speculated on a value of 1–2 weeks, Birkett and Cook (1987) estimated 3–4 months, both for South African west coast populations. Early post-larval *D. serra* settle subtidally after metamorphosis and subsequently migrate to the upper intertidal (Donn 1987, Lastra and McLachlan 1996). The factors that promote settlement and habitat selection are unknown, but grain size is significantly correlated with the abundance of recruits (Lastra and McLachlan 1996). At the time of settlement, spat are approximately 1–1.5 mm shell length and resemble adults closely (Lastra 1994).

In this paper, information is given on the reproductive biology of *D. serra* populations that inhabit two Namibian sandy beaches subject to different levels of exposure to wave action. Gametogenic activity and recruitment are compared.

MATERIAL AND METHODS

Research area and sampling

The study was carried out at two Namibian sandy beaches (Fig. 1), Langstrand (22°47´S, 14°33´E) and Paaltjies IV (22°59´S, 14°24´E). According to McLachlan's (1980) rating scale for exposure, Paaltjies IV can be characterized as very exposed and reflective and Langstrand as exposed and of an intermediate type, being partly recessed behind the sand peninsula known as Pelican Point (Fig. 1). The area is subject to subequal semidiurnal tides with a maximum tide range of 2 m; spring tides average 1.4 m and neap tides 0.7 m. Sea surface temperature (SST) varies between 11°C in winter and 23°C in summer. A summary of the main abiotic features of the two beaches is given by McLachlan (1985).

A total of 50 adult *D. serra* (>54 mm) was collected at monthly intervals (Langstrand, February 1998 to November 1999; Paaltjies IV, January 1998 to

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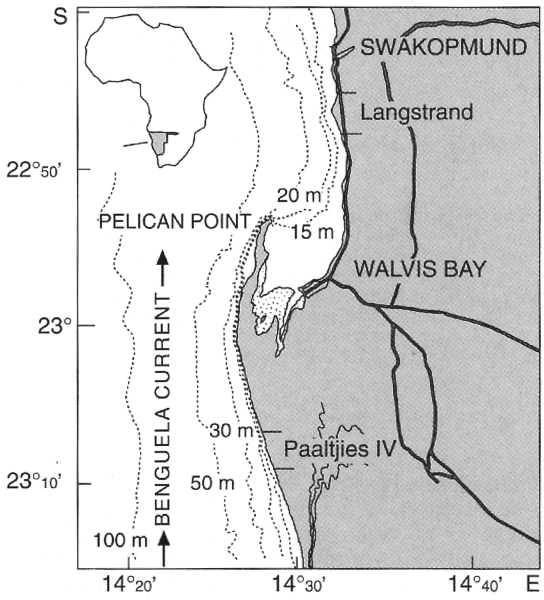

Fig. 1: Map showing the sampling sites Langstrand and Paaltjies IV and the nearby location in Swakopmund where sea surface temperature measurements were taken

December 1999). Between sites, sampling time was moved two weeks between full (at Langstrand) and new moon (at Paaltjies IV). Surf clams were dug out by hand in the surf zone at random sampling sites during low tide. No more than three clams were dug out from the same site. In addition, recruits (here defined as clams ranging from 2 to 6 mm shell length) were sampled quantitatively at a series of stations (2 m intervals) along a transect transverse to the shoreline. At each station, three replicates of a 0.16 m^2 sample were excavated to 35 cm depth using a stirring box and the sand sieved on a 1-mm screen. All clams were taken to the laboratory immediately for further investigation. A subsample of 20 adult individuals was preserved in buffered formalin for histological sectioning.

Gametogenic cycle

Tissue samples (Fig. 2) of formalin-preserved adult *D. serra* were embedded in paraplast wax. Histological sections (1–3 µm, GIEMSA stained) were produced according to standard methods (Romeis 1989). Gonads (458 from Langstrand and 456 from Paaltjies IV) were classified into four stages of development (cytolysed, inactive, active, spawning) by microscopic examination, based on the description of De Villiers (1975). The stages are summarized below.

In the *cytolysed stage*, reproductive material appears completely degenerated, and alveoli are very small and wide apart. Phagocytic cells are present in massive numbers. Before gametogenesis at the *inactive stage*, the reproductive material is typically scant and intersected by broad, continuous transverse muscular fascicles. Alveoli are well formed, small, sometimes separated and usually filled with follicle cells. After spawning the quantity of reproductive material in inactive forms varies. Alveoli appear loosely arranged, scattered with a prominent portion of transverse muscular fascicles. Phagocytes are common. At the *active stage*, germ cells are in various stages of development and fill the alveoli. Alveoli are large and their walls are always complete and close together. There are few or no phagocytes or follicle cells. *Spawning stage* animals show clear signs of a recent loss of gametes. The reproductive material varies in quantity, but it is fairly abundant. The alveolar pattern is disturbed, walls are broken and alveoli appear flattened.

Condition index and recruitment

Seasonal variation in the weight of the total visceral mass was used to track changes in gonad weight by calculating a condition index (*CI*). Total wet weight was recorded to the nearest 0.1 mg immediately after collection and drying on absorbent paper. Thereafter, valves, mantle, siphons, and retractor and adductor muscles (Fig. 2) were removed. The wet weight of the resulting standard compact unit, consisting of the visceral mass and foot, was recorded. The *CI* was calculated according to the equation of De Villiers (1975), namely $CI = 100W_v/(W_t - W_v)$, where W_v is the wet weight of the visceral mass (including the foot) and W_t is the total wet weight.

Recruits in the sampling transect were counted and measured (anterior-posterior shell length) at each sampling date on both beaches.

RESULTS

Monthly mean SST displayed seasonality, with values highest in January/February and lowest between May and October. The mean annual range was 5.6°C (Fig.

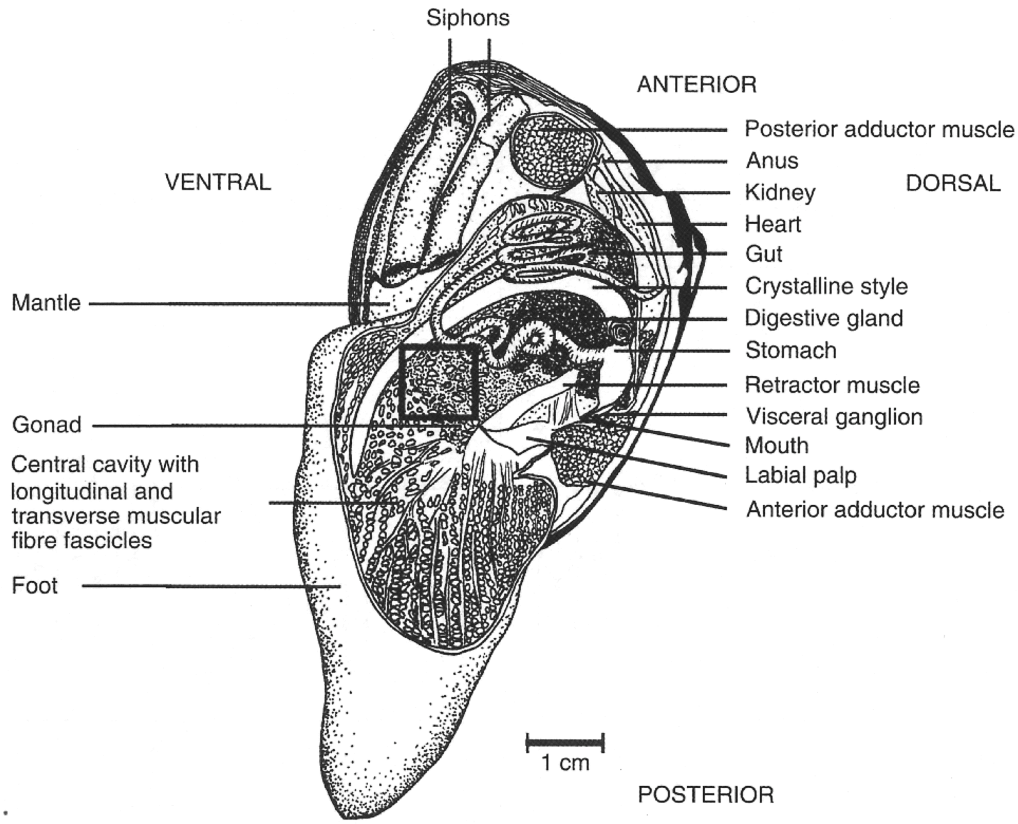

Fig. 2: Anatomy of *Donax serra*. The square shows the location of the tissue sample used for histological examination

3a, e). The morphology of *D. serra* was assessed macroscopically to define the region in which most of the gonad was located; thereafter, tissue samples were taken (Fig. 2). The percentage of mature *D. serra* gonads (both sexes) in each gonad stage is shown in Figure 4. Sex ratios did not deviate significantly from unity (Langstrand, 225 males and 220 females, $\chi^2 = 0.086$, $df = 1$, $p > 0.01$; Paaltjies IV: 220 males and 235 females, $\chi^2 = 0.43$, $df = 1$, $p > 0.01$). No case of hermaphroditism was found at either beach. The gonads of both populations were mature in summer and inactive during autumn and early winter, without the intervention of a typical cytolysed state (Fig. 4).

The gametogenic cycle at Langstrand (Fig. 3b) was correlated with the mean *CI*, which decreased significantly three times (Fig. 3c): from June to August 1998 (ANOVA, $p < 0.05$), from October 1998 to January 1999 (ANOVA, $p < 0.05$) and from July to September 1999 (ANOVA, $p < 0.05$). In between and thereafter, *CI* increased significantly (January–February 1999, ANOVA, $p < 0.05$; September–November 1999, ANOVA, $p < 0.05$). The settling period of recruits did not exceed three months: December 1997, September–October 1998, March–May 1999 and September–November 1999 (Fig. 3d).

The gametogenic cycle at Paaltjies IV had a similar seasonal pattern (Fig. 3b), except that the six-month spawning period started a month earlier. *CI* decreased from March to June 1998 (ANOVA, $p < 0.05$), increased from July to September (ANOVA, $p < 0.05$), then decreased a second time between October 1998 and early 1999 (October–January, ANOVA, $p < 0.05$). No adult *D. serra* were collected at Paaltjies IV during March or April 1999. Recruits were abundant at

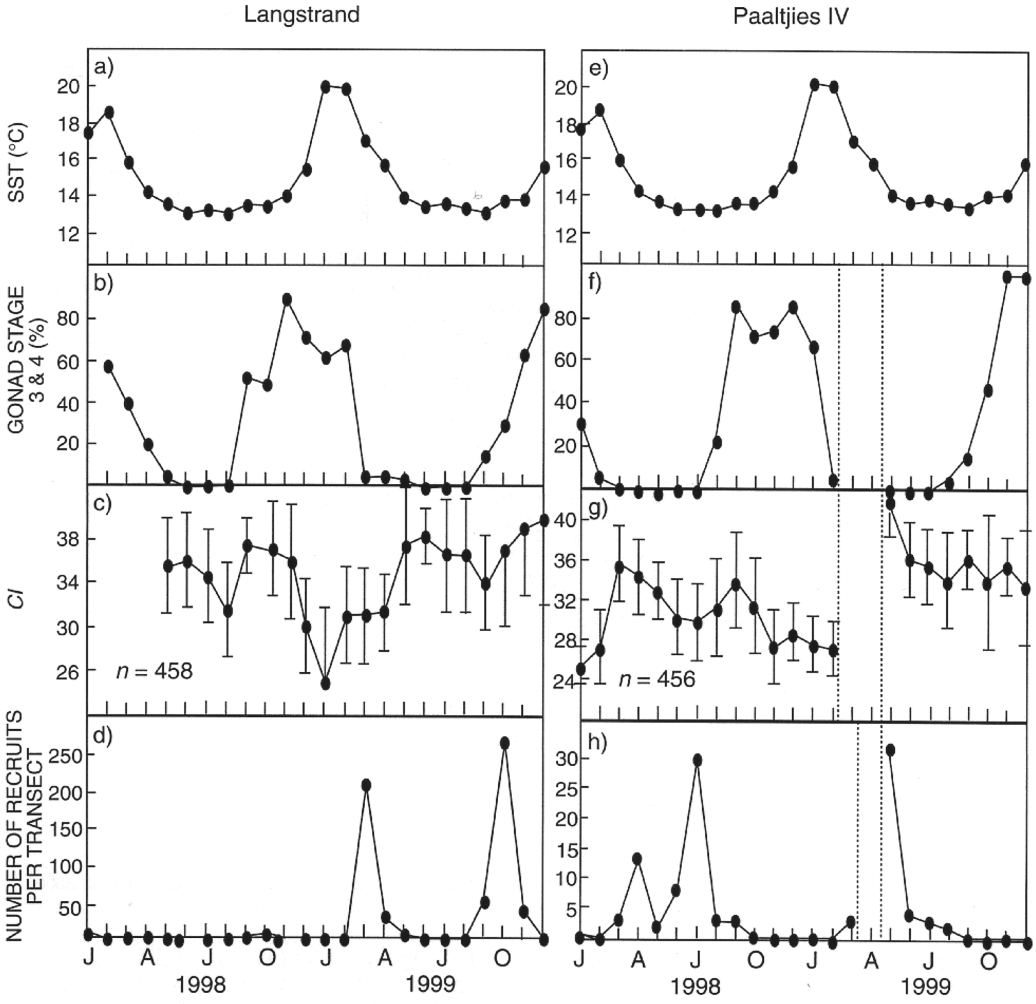

Fig. 3: (a) and (e) Mean SST measured daily (07:00) at Swakopmund, January 1998 to December 1999, the percentage of gonad stages ripe (Stage 3) and spawning (Stage 4) at (b) Langstrand and (f) Paaltjies IV, the mean condition index (*CI*) for monthly samples of adult *D. serra* at (c) Langstrand and (g) Paaltjies IV, and the number of *D. serra* recruits (2–6 mm) recorded per monthly transect at (d) Langstrand and (h) Paaltjies IV. Times when no collections were made are indicated

Paaltjies IV during autumn and winter, peaking in July 1998 and May 1998, and were found for a longer period than at Langstrand (March–September 1998, March–August 1999; Fig. 3h). To preclude possible methodological error, populations were sampled at 300-m intervals; the distribution was apparently uniform at each sampling site and date.

DISCUSSION

Seasonality

The annual reproductive cycle of Namibian *D. serra* is negatively correlated with the *CI*. The decrease of

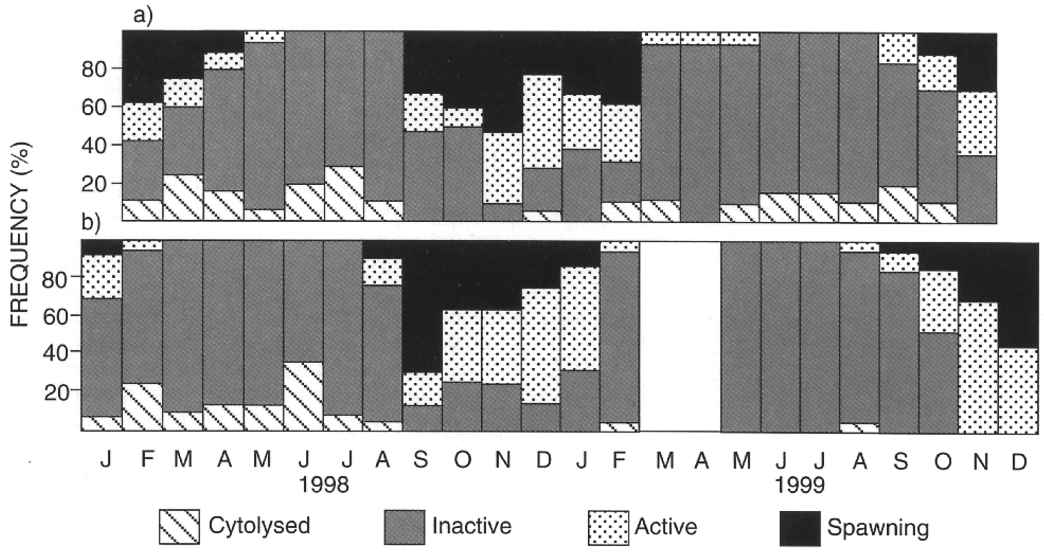

Fig. 4: Distribution of gonad states in mature *D. serra* gonads (both sexes; after De Villiers 1975) sampled at (a) Langstrand and (b) Paaltjies IV. Note sampling time between locations was shifted two weeks between full moon (Langstrand) and new moon (Paaltjies IV)

the *CI* in spring 1998 clearly marked the main period of spawning activity. As a consequence of the prolonged spawning period of the population, all reproductive stages were present (Fig. 4a, b). At Langstrand the decrease was not that evident because a high proportion of the clams was still maturing. During the main spawning season, most of the clams analysed had released their germ cells, resulting initially in a low *CI* but then an increase as some animals began recovering towards the end of the spawning period (January–February 1999; Fig. 3b, c). At Paaltjies IV, the *CI* deceased during autumn 1998 despite the fact that the gonads were still undeveloped; this may have been caused by the degeneration of residual gametes (highest recorded percentage, see Fig. 4b) and a corresponding weight loss of the visceral mass. A decrease as a result of spawning activity in summer 1999/2000 could not be identified, clearly showing that histological analysis is the only way to clarify the spawning cycle of the species.

Hanekom (1975) studied the reproductive cycle of *D. serra* in South Africa's Eastern Cape on the basis of histological sections. In his one-year study he observed a distinct cycle, but with spawning in late summer (February–April). In contrast, McLachlan and Hanekom (1979) and Van der Horst (1986) found more-or-less discrete spawning peaks during summer and winter in the same region. Similar distinct reproductive cycles and spawning events in summer were reported for clams of the Humboldt Current upwelling system by Urban and Campos (1994). In contrast, gametogenic cycles of *D. serra* are less distinct in South Africa's Western Cape (De Villiers 1975, Birkett and Cook 1987).

The recruitment pattern seen here provides clear evidence that juvenile surf clams occur only sporadically and that recruitment varies from year to year, agreeing with the findings of other authors (e.g. Arntz *et al.* 1987). In contrast to the observations of Lastra and McLachlan (1996), who worked on the beaches of South Africa's Eastern Cape, the 2–6 mm cohort was apparently uniformly distributed at the Namibian study sites. There was also no evidence that recruitment events may have been missed, because each new cohort was subsequently tracked (unpublished data). The present study showed that the *D. serra* belt is inhabited by similar size-classes, in accord with the findings of Schoeman (1997), who also worked on beaches of South Africa's Eastern Cape. The zone occupied by recruits varies, according to the slope of the beach, between a minimum breadth of 12 m and a maximum of 40 m (Fig. 5). The larger juveniles

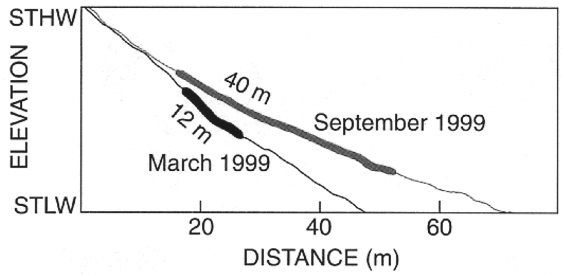

Fig. 5: Beach profile from the spring tide high water mark (STHW) to the spring tide low water mark (STLW) and the related distribution of *D. serra* recruits for March 1999 and September 1999 at Langstrand. With a steeper beach slope the width of the recruit belt becomes narrower

populate a narrower belt in the intertidal.

The juvenile abundance pattern (Fig. 3d) found at Langstrand in March and April 1999 was the result of the spawning event that took place between September 1998 and February 1999. Recruits appeared in the intertidal zone during two months only, even though it is likely that they were released over a period of six months. The duration of the planktonic period of donacids inhabiting upwelling regions is still unknown (McLachlan *et al.* 1996) and the current results regrettably remain inconclusive in terms of *D. serra*. The presence of recruits during March 1999 may indicate that the larval phase lasts at least two months, but there are several possible explanations for the appearance of juveniles in September/October 1998, including:

- Settlement could be of the very first recruits of a spawning, indicating a larval period of <4 weeks (in agreement with the suggestion of Donn 1987);
- Planktonic remnants of the pool of larvae spawned in summer 1997/98 (molluscan larvae may delay metamorphosis and settlement under unfavourable conditions – see Pechenik 1985, Coon *et al.* 1990). It may therefore be possible for the larvae to delay their settlement until after the four winter months (*circa* Birkett and Cook 1987);
- Additionally, recruits from 1997/98 could have settled deeper (Donn 1987, Lastra and McLachlan 1996) as a result of hydrodynamic processes, greater stability of the substratum or geotaxis (Coon *et al.* 1985, Jackson 1986). Insignificant growth of such recruits during winter is possible (as observed for juveniles, unpublished data), so migration to the intertidal may have taken place during spring 1998.

Unfortunately, neither the hydrodynamics of the sample sites nor larval behaviour are sufficiently well known to discuss these possibilities authoritatively. At Paaltjies IV (Fig. 3h), the abundant recruits found between March and September 1998 are likely to be the offspring from summer 1997/98. Juveniles observed there between March and August 1999 were presumably spawned between August 1998 and January 1999.

Although the adult populations showed a nearly synchronous gametogenic cycle, the temporal settlement pattern of recruits varied considerably between sites. Only in January 1999 were recruits found in the intertidal of both beaches simultaneously. Such variation agrees with observations on the behaviour of mussels in the same region (Harris *et al.* 1998). Lastra and McLachlan (1996) also reported temporal variations in *D. serra* spat distribution, although they found recruits throughout the year.

Duration of the larval period and recruitment success are strongly influenced by the actual time of release and the associated environmental conditions (Olson and Olson 1989), probably explaining the observed asynchronous pattern and temporal differences in recruitment strength. Food limitation may cause starvation (Langdon 1983, Olson and Olson 1989) or prolonged development, resulting in longer exposure to possibly unfavourable conditions in the plankton (e.g. predators, hydrogen sulphide; Sale 1990, Diaz and Rosenberg 1995). Further, unfavourable hydrodynamic processes (currents, wave action) may increase the meroplanktic period and influence dispersal and settlement patterns (Roughgarden *et al.* 1988, Zimmerman and Pechenik 1991, Harris *et al.* 1998). Owing to the hydrodynamics (specifically the current patterns) of the Benguela, larvae may have been spawned south of the collection sites and transported northwards. In such a case, recruitment would not be expected to be related to the condition of the adults inhabiting the collection sites, but more related to the oceanographic processes pertaining at any point in time. What is clear, however, is that future research should focus on the larval biology of *D. serra*, specifically trying to determine the duration of the planktonic stage.

De Villiers (1975) reported on the results of a 28-month study of South African west coast populations of *D. serra*. He failed to find a repeated pattern of settlement, but noted that juveniles were most abundant in spring and early summer, but were found all year round. De Villiers' findings agree with those of Lastra and McLachlan (1996), who observed sporadic recruitment events in Eastern Cape populations of the same species, with periods of maximum spat density during summer. Berry (1978) and Harris *et al.* (1998) also noted that rocky shore bivalves around southern Africa recruit in summer.

Table I: Comparison of spawning periods at four southern African sandy beaches sorted by increasing SST difference between winter and summer. The lack of complete overlap in the spawning period of the two Namibian populations under study can be explained by the two-week shift in sampling time

Location	Latitude	Spawning period	Temperature (°C)	SST difference (°C) between summer and winter	Reference
Melkbosstrand	33°41′S	No distinct seasonal cycle	12–16	4.0	De Villiers (1975)
Paaltjies IV	22°59′S	Aug.– Jan. 1998/99	12–19	5.6	This study
Langstrand	22°47′S	Sep.– Feb. 1998/99	12–20	5.6	This study
St Francis Bay	33°59′S	Feb.– May 1974	12–25	6.5	Hanekom (1975)

Potential spawning triggers

Maturation and spawning of bivalves are triggered by changes in SST (Urban and Campos 1994, Sasaki *et al.* 1997). During winter, SST off Namibia is relatively stable, in contrast to the dynamic temperature variations of spring and summer. Therefore, maturation of germ cells in *D. serra* may be triggered by a long period of stable but cold SST and/or some warmer days in late winter/early spring, i.e. before the temperature starts to rise appreciably and consistently. Spawning would then take place when the temperature is higher, possibly favouring larval growth and metamorphosis (Roosenburg *et al.* 1984, Walker *et al.* 1995). Hanekom (1975) hypothesized that the wider annual range in SST on South Africa's south-east coast (6.5°C) compared to the West Coast (4°C) could be a determining factor for the distinctly different gametogenic cycles in South African *D. serra* populations. Table I compares spawning periods at four southern African sandy beaches, with emphasis on the annual range of SST. The results presented here are in line with earlier findings: a SST range of 4.0°C is associated with a pattern of continuous reproduction, a range of 5.6°C with a spawning period of >6 months, and a range of 6.5°C with a spawning period of 4 months. Therefore the results of this study clearly support the hypothesis that the reproductive cycle of *D. serra* is related to annual SST.

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LITERATURE CITED

ARNTZ, W. E., BREY, T., TARAZONA, J. and A. ROBLES 1987 — Changes in the structure of a shallow sandy-beach community in Peru during an *El Niño* event. In *The Benguela and Comparable Ecosystems.* Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 645–658.

BERRY, P. F. 1978 — Reproduction, growth and production in the mussel *Perna perna* (Linnaeus), on the east coast of South Africa. *Investl Rep. oceanogr. Res. Inst. S. Afr.* **48**: 28 pp.

BIRKETT, D. A. and P. COOK 1987 — Effect of the Benguela temperature anomaly, 1982–1983, on the breeding cycle of *Donax serra* Röding. In *The Benguela and Comparable Ecosystems.* Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 191–196.

COON, S. L., BONAR, D. B., and R. M. WEINER 1985 — Induction of settlement and metamorphosis of the Pacific oyster, *Crassostrea gigas* (Thunberg), by L-DOPA and catecholamines. *J. expl mar. Biol. Ecol.* **94**: 211–221.

COON, S. L., FITT, W. K. and D. B. BONAR 1990 — Competence and delay of metamorphosis in the Pacific oyster *Crassostrea gigas. Mar. Biol.* **106**: 379–387.

DE VILLIERS, G. 1975 — Reproduction of the white sand mussel, *Donax serra* Röding. *Investl Rep. Sea Fish. Brch S. Afr.* **102**: 33 pp.

DIAZ, R. L. and R. ROSENBERG 1995 — Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. In *Oceanography and Marine Biology. An Annual Review* **33**. Ansell, A. D., Gibson, R. N. and M. Barnes (Ed.). London; UCL Press: 245–303.

DONN, T. E. 1987 — Longshore distribution of *Donax serra* in two log-spiral bays in the Eastern Cape, South Africa. *Mar. Ecol. Prog. Ser.* **35**: 217–222.

DONN, T. E. and A. C. COCKCROFT 1989 — Macrofaunal community structure and zonation of two sandy beaches on the central Namib coast, South West Africa/Namibia. *Madoqua* **16**(2): 129–135.

HANEKOM, N. 1975 — A study of *Donax serra* in the Eastern Cape.

M.Sc. thesis, University of Port Elizabeth: 70 pp.
HARRIS, J. M., BRANCH, G. M., ELLIOTT, B. L., CURRIE, B., DYE, A. H., McQUAID, C. D., TOMALIN, B. J. and C. VELASQUEZ 1998 — Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *S. Afr. J. Zool.* **33**(1): 1–11.
JACKSON, G. A. 1986 — Interaction of physical and biological processes in the settlement of planktonic larvae. *Bull. mar. Sci.* **39**: 202–212.
JARMAN, N. G. and R. A. CARTER 1981 — The primary producers of the inshore regions of the Benguela. *Trans. R. Soc. S. Afr.* **44**(3): 321–325.
LANGDON, C. J. 1983 — Growth studies with bacteria-free oyster (*Crassostrea gigas*) larvae fed on semi-defined artificial diets. *Biol. Bull. mar. biol. Lab., Woods Hole* **164**: 227–235.
LASTRA, M. 1994 — Recruitment dynamics and spat distribution of *Donax serra*. In *White Sand Mussels: Ecology, Status and Conservation – a Public Symposium*. McGwynne, L. E. (Ed.). University of Port Elizabeth Institute for Coastal Research Report **36**: p. 17.
LASTRA, M. and A. McLACHLAN 1996 — Spatial and temporal variations in recruitment of *Donax serra* Röding (Bivalvia: Donacidae) on an exposed sandy beach of South Africa. *Revta Chilena Hist. nat.* **69**: 631–639.
McLACHLAN, A. 1980 — The definition of sandy beaches in relation to exposure: a simple rating system. *S. Afr. J. Sci.* **76**(3): 137–138.
McLACHLAN, A. 1985 — The ecology of two sandy beaches near Walvis Bay. *Madoqua* **14**(2): 155–163.
McLACHLAN, A. (Ed.) 1986 — *Ecological Surveys of Sandy Beaches on the Namib Coast*. Port Elizabeth; University of Port Elizabeth: 134 pp. (Institute for Coastal Research Report **13**).
McLACHLAN, A. and N. HANEKOM 1979 — Aspects of the biology, ecology and seasonal fluctuations in biochemical composition of *Donax serra* in the East Cape. *S. Afr. J. Zool.* **14**(4): 183–193.
McLACHLAN, A., DUGAN, J. E., DEFEO, O., ANSELL, A. D., HUBBARD, D. M., JARAMILLO, E. and P. PENCHAS-ZADEH 1996 — Beach clam fisheries. In *Oceanography and Marine Biology. An Annual Review* **34**. Ansell, A. D., Gibson, R. N. and M. Barnes (Ed.). London; UCL Press: 163–232.
OLSON, R. R. and M. H. OLSON 1989 — Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success? *A. Rev. Ecol. Syst.* **20**: 225–247.
PECHENIK, J. A. 1985 — Delayed metamorphosis of marine molluscan larvae: current status and directions for future research. *Spec. Ed. Am. malacol. Bull.* **1**: 85–91.
ROMEIS, B. 1989 — *Mikroskopische Technik*, 17th ed. Böck, P. (Ed.). Munich; Urban & Schwarzenberg: 697 pp.
ROOSENBURG, W. H., WRIGHT, D. A. and M. CASTAGNA 1984 — Thermal tolerance by embryos and larvae of the surf clam *Spisula solidissima*. *Environ. Res.* **34**(1): 162–169.
ROUGHGARDEN, J., GAINES, S. and H. POSSINGHAM 1988 — Recruitment dynamics in complex life cycles. *Science* **241**(4872): 1460–1466.
SALE, P. F. 1990 — Recruitment of marine species: is the bandwagon rolling in the right direction? *Trends Ecol. Evol.* **5**(1): 25–27.
SASAKI, K., OTA, H. and M. SAEKI 1997 — Morphological development of veliger larval and juvenile stages of the surf clam *Spisula sachalinensis*. *Fish. Sci.* **63**(1): 81–89.
SCHOEMAN, D. S. 1997 — Spatial and temporal dynamics of *Donax serra* in St Francis Bay: implications for a potential fishery. Ph.D. thesis University of Port Elizabeth: 200 pp.
SCHULZ, K. 1982 — The vertical distribution of calanoid copepods north of Cape Blanc. In *The Canary Current: Studies of an Upwelling System. A Symposium held in Las Palmas, April 1978*. Hempel, G. (Ed.). *Rapp. P-v. Réun. Cons. int. Explor. Mer* **180**: 297–302.
URBAN, H-J. and B. CAMPOS 1994 — Population dynamics of the bivalves *Gari solida*, *Semele solida* and *Protothaca thaca* from a small bay in Chile at 36°S. *Mar. Ecol. Prog. Ser.* **115**: 93–102.
VAN DER HORST, G. 1986 — *Donax serra*: reproduction as an r-strategist and potential for aquaculture. In *Biology of the genus* Donax *in Southern Africa*. Donn, T. E. (Ed.). University of Port Elizabeth Institute for Coastal Research Report **5**: 13–14.
WALKER, R. L., O'BEIRN, F. X. and D. H. HURLEY 1995 — Embryonic and larval development of the southern surf clam, *Spisula solidissima similis* (Say, 1822). In *Triennial Meeting of the Fish Culture Section of the American Fisheries Society, World Aquaculture Society and the National Shellfisheries Association. J. Shellfish Res.* **14**(1): p. 281.
ZIMMERMAN, K. M. and J. A. PECHENIK 1991 — How do temperature and salinity affect relative rates of growth, morphological differentiation, and time to metamorphic competence in larvae of the marine gastropod *Crepidula plana*? *Biol. Bull. mar. biol. Lab., Woods Hole* **180**: 372–386.