

Testing the habitat harshness hypothesis: The reproductive biology of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) from three Argentinian sandy beaches with contrasting morphodynamics

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The 'habitat harshness hypothesis' (HHH) Defeo *et al.* (2001; 2003) predicts that (i) at the community level, reflective beaches will exhibit lower species richness, diversity and abundance while (ii) at the population level, they will be characterised by lower abundance, growth, fecundity, reproductive output and higher mortality rates.

However, other recent investigations suggest that populations co-occurring in sandy beaches with a range of contrasting morphodynamics do not conform consistently to these predictions:

- no significant changes in abundance of macrobenthic communities between intermediate and reflective beaches (Veloso & Cardoso 2001),
- the isopod *Excirrolana braziliensis* exhibited higher abundance at a reflective beach than at a dissipative one (Defeo *et al.* 1997, Defeo & Martínez 2003),
- the amphipod *Pseudorchestoidea brasiliensis* presented greater abundance, egg production potential and recruitment levels and lower natural mortality at a reflective beach (Gómez & Defeo 1999),
- the amphipod *Atlantorchestoidea brasiliensis* shows clear population responses to physical variables in direct opposition to those predicted by the HHH, including an increase in abundance and individual size from dissipative to reflective beaches (Defeo & Gómez 2005),
- the decapod *Emerita brasiliensis* did not vary between dissipative and reflective beaches and at the latter beach type displayed higher male growth rates as well as lower natural mortality (Defeo *et al.* 2001).

In summary, these studies suggest that beach morphodynamics might not be the primary factor affecting abundance, population dynamics and life history traits of macrobenthic species. However, the HHH has not been tested comprehensively with respect to reproductive biology. The only investigation dealing with this subject to date was a 13 month study in which 150 Uruguayan wedge clams from two different beach

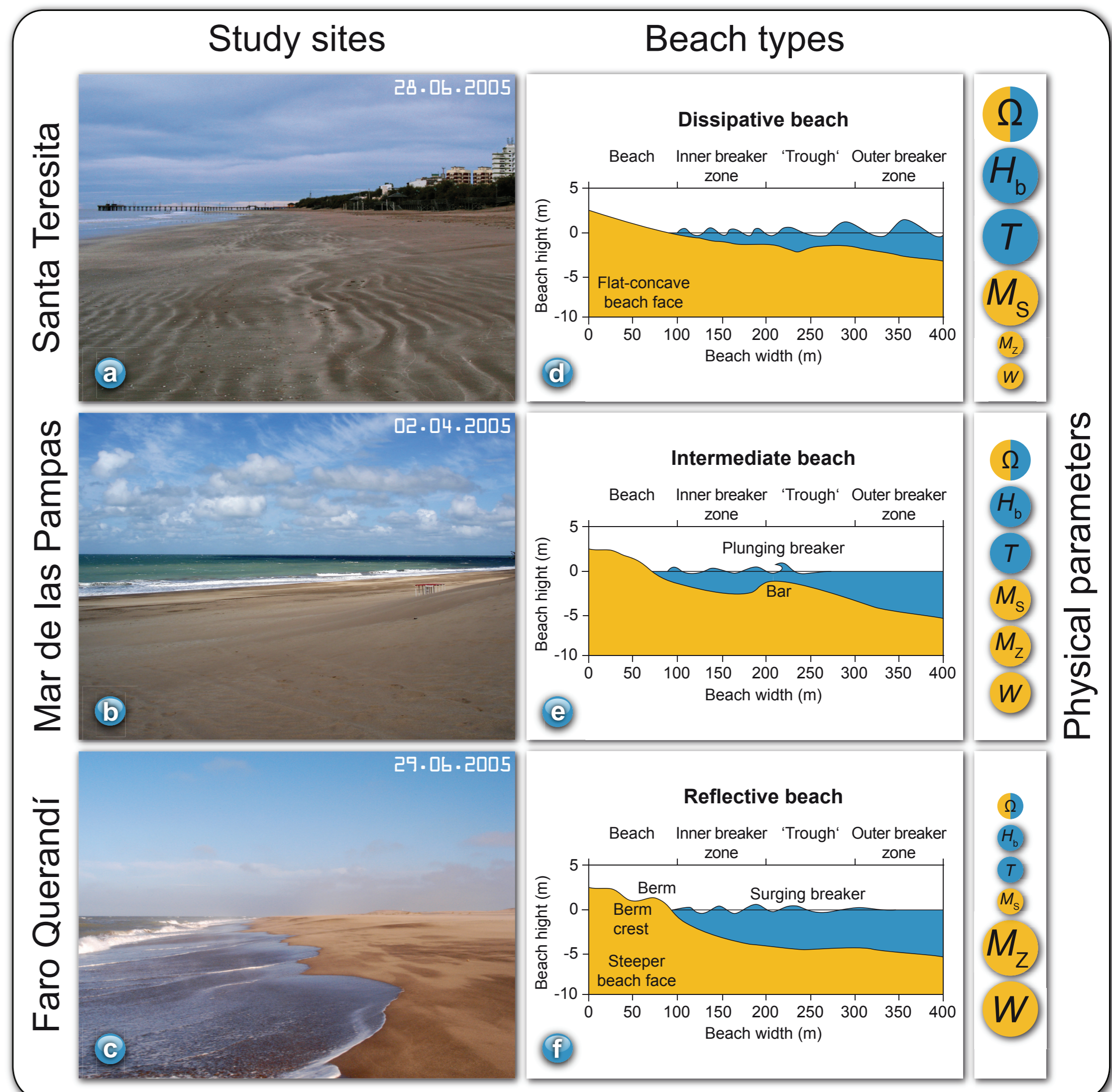


Fig. 1: Study sites (a) Santa Teresita, (b) Mar de las Pampas and (c) Faro Querandí with contrasting beach morphodynamics (d-f, respectively) and corresponding physical parameters: (Ω) Dean's parameter, (H_b) wave height (m), (T) wave period (s), (M_s) mean slope of tidal, (M_z) mean grain size (mm) and (W) sand fall velocity ($m\ s^{-1}$). Size of letters indicate respective trends.

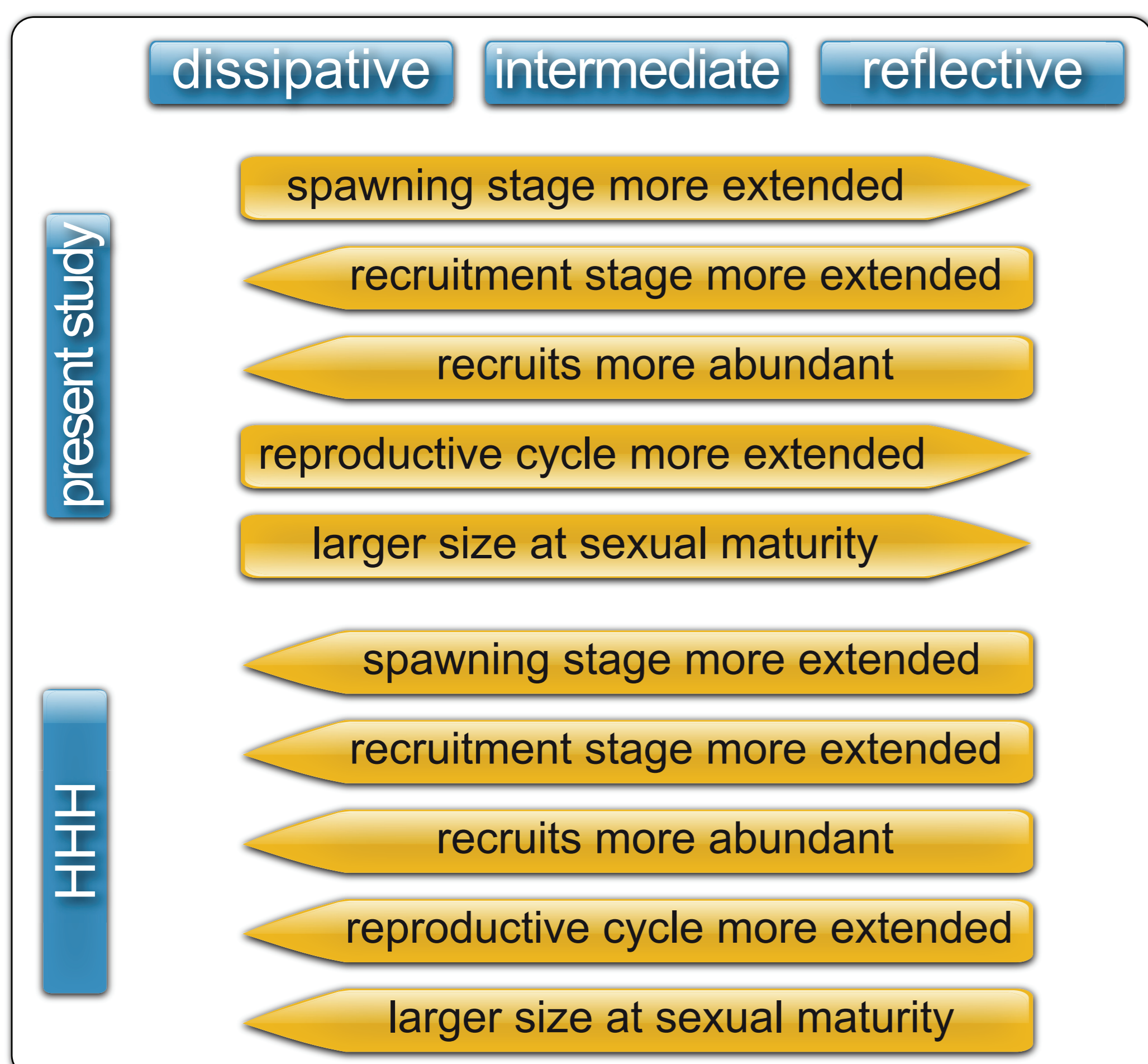


Fig. 2: The reproductive biology of *D. hanleyanus*, reflecting beach morphodynamics of a dissipative (Santa Teresita), intermediate (Mar de las Pampas) and reflective beach (Faro Querandí) compared to predictions of the HHH.

morphotypes were examined. The results in that instance appeared to confirm the HHH (Delgado & Defeo 2007). The present study tests the HHH at the population level, comparing the reproductive biology of *D. hanleyanus* from three Argentinian sandy beach habitats, one dissipative, one intermediate and one reflective. Following predictions of the HHH, we sought to determine whether *D. hanleyanus* at the dissipative beach do indeed exhibit greater abundance of recruits, larger size at first sexual maturity, larger maximum individual size and mass and extended periods of reproduction, recruitment and spawning.

The results of the present study obtained from three beaches over 25 months demonstrate that at the population level *D. hanleyanus* respond systematically to beach morphodynamics in a manner opposite to that predicted by the HHH:

- the population at the dissipative beach exhibited a greater abundance of recruits and an extended recruitment period,
- spawning events were registered twice each year at the dissipative and intermediate beaches, whereas continuous gamete release was noted at the reflective beach,
- size at first maturity and biomass at first maturity were lower at the dissipative beach,
- monthly mean abundance was higher at the reflective beach.

Finally, the current study demonstrated that the 'hypothesis of habitat safety' (HHS), originally postulated by Defeo & Gómez (2005) for supralittoral species, may be extended to intertidal species; the combination of narrow swashes and steep slopes make reflective beaches a safer and more stable environment for supralittoral and intertidal species such as *D. hanleyanus*.

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