

*Biogenic calcareous growth on the
ribbed mussel Aulacomya atra (Bivalvia:
Mytilidae) favours polydorid boring
(Polychaeta: Spionidae)*

**M. E. Diez, N. Vázquez, P. da Cunha
Lana & F. Cremonte**

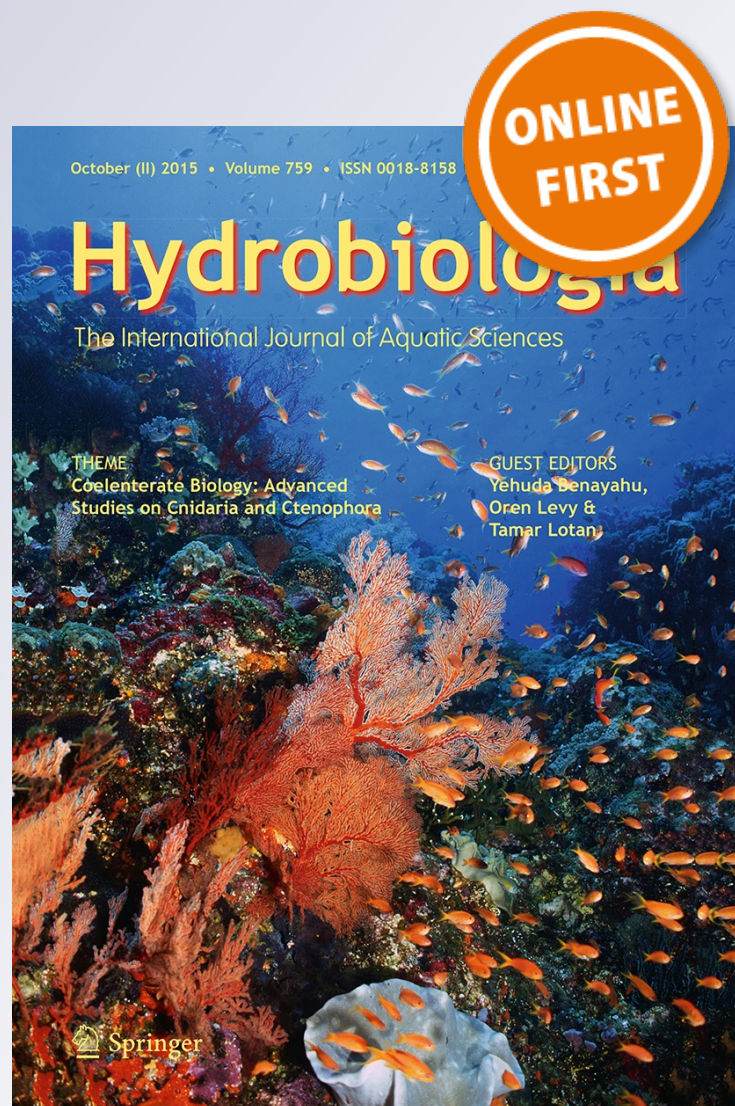
Hydrobiologia

The International Journal of Aquatic
Sciences

ISSN 0018-8158

Hydrobiologia

DOI 10.1007/s10750-015-2467-y



Your article is protected by copyright and all rights are held exclusively by Springer International Publishing Switzerland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Biogenic calcareous growth on the ribbed mussel *Aulacomya atra* (Bivalvia: Mytilidae) favours polydorid boring (Polychaeta: Spionidae)

M. E. Diez · N. Vázquez · P. da Cunha Lana · F. Cremonte

Received: 23 April 2015 / Revised: 27 August 2015 / Accepted: 28 August 2015
© Springer International Publishing Switzerland 2015

Abstract Shells of the ribbed mussel *Aulacomya atra* from the Patagonian gulfs of San Matías and San José (Argentina) are commonly bored by polydorids and covered by serpulids and crustose coralline algae. As the co-occurring mussel *Mytilus edulis* is neither bored by polydorids nor covered by coralline algae, we hypothesize that early or previous calcareous growth would favour larval settlement and boring by polydorids. Generalized Linear Model analyses showed that polydorid boring is indeed positively correlated with the abundance of serpulids and crustose coralline alga. Infestation by polydorids is higher in larger, older ribbed mussels due to their correspondingly higher available area for larval settlement. Increasing polydorid infestation adversely affects the condition index of *A. atra*.

Keywords Polydorid · Infestation · Ribbed mussel · Patagonia

Introduction

Both wild populations and marine cultured molluscs are often covered by epibionts, such as algae, sponges, bryozoans, barnacles, other molluscs, ascidians and polychaetes (Carraro et al., 2012). There are many reports of coralline algae influencing larval settlement or recruitment of encrusting or boring species. Such interspecific interactions may cause negative (Smyth, 1988, 1989; Steele, 1998) or positive (Gee, 1965; Morse & Morse, 1984; Pearce & Scheibling, 1988; Rowley, 1989; Whalan et al., 2012) effects.

The ribbed mussel *Aulacomya atra* (Molina, 1782) is exploited by artisanal fisheries along the Patagonian coasts (Ciocco et al., 1998). Polydorid infestation is a matter of increasing concern for regional shellfisheries (Ciocco et al., 2006). Diez et al. (2011) have recently reported the polydorid polychaetes *Polydora rickettsi* Woodwick, 1961 and *Dipolydora* cf. *giardi* (Mesnil, 1896) boring into shells of *A. atra*, which are often covered by crustose coralline algae and serpulid tubes. A similar positive correlation between the presence of shell boring mytilid *Leiosolenus patagonicus* (d'Orbigny, 1842) and the boring polychaetes *P. rickettsi*, *Dodecaceria* cf. *choromyticola* Carrasco, 1977 and *Caulleriella* cf. *bremecae* Elias & Rivero, 2008 was also locally observed on the oyster *Ostrea puelchana* d'Orbigny, 1842 (Diez et al., 2014). As the co-occurring mussel *Mytilus edulis* Linnaeus, 1758 is neither bored by polydorids nor covered by the algae, we hypothesize that such biogenic calcareous growth

Handling editor: Vasilis Valavanis

M. E. Diez (✉) · N. Vázquez · F. Cremonte
Centro Nacional Patagónico (CONICET), Bvd. Brown
2915, U9120ACF, Puerto Madryn, Chubut, Argentina
e-mail: emiliadiez@cenpat-conicet.gob.ar

P. da Cunha Lana
Centro de Estudos do Mar, Universidade Federal do
Paraná, Av. Beira Mar s/n, Pontal do Paraná,
Paraná CP 50002, Brazil

would favour larval settlement and boring by polydorids.

By using a generalized linear model (GLM) analysis, we test the prediction that polydorid infestation and the presence of epibiont (expressed by the abundance of serpulid polychaetes and percent cover by the algae) are positively correlated on shells of *A. atra* and affected by geographic location and average shell length.

Materials and methods

Study area and sampling

San José is a shallow, semi-enclosed gulf (817 km²; mean depth 30 m) located on the northern Patagonian coast in Argentina. It opens to the north into the much larger San Matías Gulf (18,000 km²) through a narrow (6.9 km) mouth (Amoroso et al., 2011). During January 2012, 186 specimens of *A. atra* were collected at Puerto Lobos (42°S, 65°01'W) in the San Matías Gulf and 164 specimens at Larralde (42°45'S, 65°02'W) in the San José Gulf, northern Patagonian

coast (Fig. 1). The ribbed mussels were collected by scuba diving at about 15 m depth, taken to the laboratory and maintained in aquaria with aerated seawater until processing (up to 48 h). Maximum valve length (mm) was measured, and the valves and soft parts were separately weighted to calculate the condition index (Lucas & Benninger, 1985).

Valves were examined under a stereomicroscope, and the presence of polydorids serpulids and the cover algae was recorded per individual. The abundances of polydorids and serpulids were calculated as the number of specimens and tubes, per individual, respectively. Percent cover by the algae was determined using the Image J software on photographs of each individual, and it was estimated as follows: 0: clean (absence of algae), 1: very slight (up to 20% of cover), 2: slight (up to 40%), 3: moderate (up to 60%), 4: heavy (up to 80%) and 5: very heavy (up to 100%).

Both the presence/absence (binary data) and abundance of polydorids (count data) as response variables were evaluated by GLMs with binomial distribution with a logit link function and Poisson distribution with a log link function (Agresti, 2007), respectively. Different models were used to test these variables with regard to the predictor variables: locality, shell length, host condition index, abundance of serpulids, intensity of the algae infestation and the interaction between these two epibionts. The Akaike information criterion (AIC) was used to determine the best model for the analysed dataset. Model selection was performed with an IT approach using the AIC and model averaging (Grueber et al., 2011). The AIC values and the AIC for small samples (AICc) were calculated for each model. From the AICc differences (Δ_i), where $\Delta_i = \text{AICc}_i - \text{AICc}_{\min}$, Akaike weights (w_i) (Akaike, 1978) were obtained for all candidate models. Models were ranked by their w_i values for each dataset. The model with the highest w_i was considered the one with the best supporting data. Model averaging was calculated using candidate models, which together account for the 95% confidence level. The top model set was averaged using a zero method (Symonds & Moussalli, 2011), where the best AIC model was not strongly weighted. The global model was performed in R (R Development Core Team, 2012) and the standardized function to input variables is available within the 'arm' (Data Analysis Using Regression and Multilevel/Hierarchical Models) package (Gelman et al., 2009). Model selection and averaging were calculated with

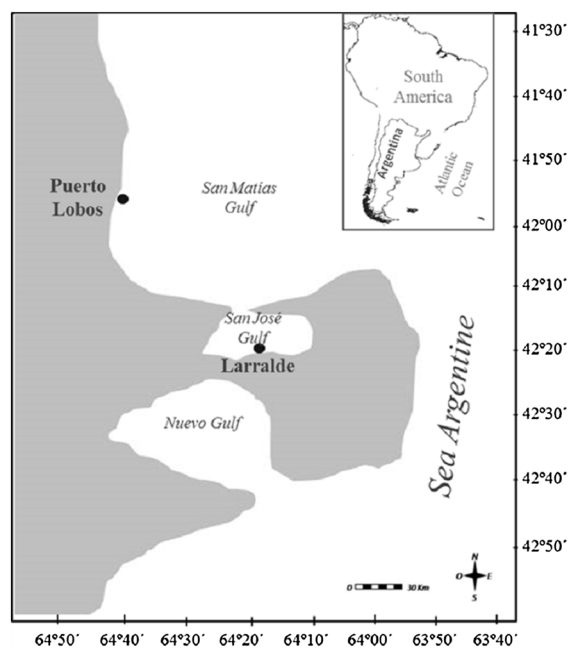


Fig. 1 *Aulacomya atra* (Bivalvia, Mytilidae) sampling sites in northern Patagonian gulfs: Puerto Lobos (San Matías Gulf) and Larralde (San José Gulf), Argentina

the MuMIn package (Barton, 2009). The predictor variables in the top models were reported with their relative importance weights, model-averaged parameter estimates, unconditional standard error and 95% confidence intervals. Results were expressed in terms of odds ratios. The odds were calculated as the exponential of the coefficient of each parameter corresponding to the averaging model.

Results

The presence and abundance of polydorids and crustose algae were higher in *A. atra* valves from San José Gulf than in those from San Matías Gulf. Conversely, valves of *A. atra* with serpulid polychaetes were more prevalent in San Matías Gulf (Table 1).

The presence of polydorid was positively correlated with the abundance of serpulid polychaetes and the percent cover by the algae (Table 2). Polydorids were often reported boring into the serpulid tubes and the algae (Fig. 2). The model analysis resulted in six top models with $\Delta\text{QAIC} < 2$ of the best model (Table 2). Serpulid abundance and the percent cover by crustose algae emerged as the most robust predictor variables, with relative importance weights of 1.00 and a 95% confidence interval that did not include zero (Table 2). The probability of finding a ribbed mussel shell bored by polydorids was 12 times higher in a valve heavily covered by crustose algae than in a “clean” valve (Table 2).

Polydorid abundance was also related to geographic location, shell length and condition index of the host. Model analysis resulted in three top models with $\Delta\text{QAIC} < 2$ of the best model (Table 2), and all explanatory variables considered in the global model were included in at least one model in the top model set. Geographic location, condition index and shell

length were the most robust predictor variables, with relative importance weights of 1.00 and a 95% confidence interval bounded away from zero (Table 2). The probability of finding a ribbed mussel hosting more polydorids in the San José Gulf was 0.3 times higher than in the San Matías Gulf. Polydorid abundance also increased with increasing shell length (Fig. 3). It would show for Puerto Lobos that irrespective of shell length, the polydorid abundance would be low, whereas for Larralde, there would be a clearer relationship between size and number of worms (Fig. 3). There was a negative relationship between condition index and polydorid abundance (Table 2), indicating a poorer physiological condition in infested ribbed mussels (Fig. 4). However, serpulid abundance was not significantly related to polydorid abundance since it had a lower relative importance weight (0.78) and its confidence interval included zero (Table 2).

Discussion

GLM analyses showed that polydorid boring is indeed positively correlated with the abundance of serpulids and crustose coralline algae on the shells of *A. atra*. Adults of many species of *Polydora* are known to bore into various calcareous substrata, including shells of commercially valued molluscs, such as oysters, scallops and mussels (Blake & Evans, 1973; Sato Okoshi & Takatsuka, 2001; Radashevsky et al., 2006; Cremona, 2011). Polydorids are known even to inhibit the settlement of other organisms with calcareous structures, such as serpulid polychaetes (Martin & Britayev, 1998) and coralline algae (Hartman, 1969; Blake, 1975). We present and discuss a distinct interaction pattern, in which polydorid infestation was positively related to the abundance of serpulid

Table 1 The shell length range (in mm), presence (P) and abundance (A) (mean followed by range in parenthesis) of epibiont organisms on the ribbed mussel *Aulacomya atra* from San Matías and San José gulfs, Northern Patagonian coast, Southern Atlantic Ocean

Locality	N	Shell length mean (range)	Polydorid polychaetes		Serpulid polychaetes		Crustose coralline algae P (%)
			P (%)	A	P (%)	A	
Puerto Lobos (San Matías Gulf)	186	89 (61–133)	20	0.4 (0–8)	92	10 (0–67)	87
Larralde (San José Gulf)	164	99 (77–122)	32	3 (0–53)	79	9 (0–122)	91

Table 2 Predictor variables from top models for each response variable in the ribbed mussel *Aulacomya atra*

Response	Parameter	Coefficient	Adjusted SE	Confidence Interval	Relative importance
The presence of polydorid polychaetes	Intercept	−3.1700	0.786	−4.710	−1.630
	Percent cover 1 by algae	1.4200	0.889	−0.319	3.170
	Percent cover 2 × by algae	2.2000	0.852	0.526	3.870
	Percent cover 3 × by algae	1.9800	0.890	0.232	3.720
	Percent cover 4 × by algae	2.0900	0.919	0.293	3.900
	Percent cover 5 × by algae	2.4800	0.811	0.892	4.070
	Geographic location	−0.2420	0.308	−0.847	0.362
	Condition index	0.0658	0.177	−0.281	0.413
	Abundance of serpulids*	1.0100	0.318	0.391	1.640
	Shell length	0.0457	0.167	−0.282	0.374
Abundance of polydorid polychaetes	Intercept	−0.32300	0.467	−1.2400	0.593
	Percent cover 1 by algae	−0.03790	0.545	−1.1100	1.030
	Percent cover 2 by algae	0.00676	0.481	−0.9490	0.936
	Percent cover 3 by algae	0.07690	0.455	−0.8140	0.968
	Percent cover 4 by algae	0.04050	0.538	−1.0100	1.090
	Percent cover 5 by algae	0.26100	0.571	−0.8580	1.380
	Geographic location*	−1.21000	0.401	−2.0000	−0.425
	Condition index*	−0.75900	0.315	−1.3800	−0.143
	Abundance of serpulids	0.18700	0.149	−0.1050	0.479
	Shell length*	0.81000	0.398	0.0296	1.590

Coefficient estimates, their unconditional standard error (SE), 95% confidence interval (CI) and relative importance weights (w(i)) after model averaging are shown for each variable. Variables with * have a 95% confidence interval bounded away from zero (significant results). Percent cover 0 by the crustose coralline algae and Puerto Lobos geographic location were the reference category

polychaetes and crustose algae. The evidence of a relationship between larval settlement and the presence of coralline algae has been well documented (Gee, 1965; Rodriguez et al., 1993; Roberts et al., 2010). Additional calcareous substrates provided by serpulid tubes would further increase the available surface area, favouring the settlement of polydorids with added protection on the ribbed mussel shells. The settlement of polychaete larvae may be triggered by chemical cues produced by coralline algae (Gee, 1965) or by the microbial film on the algal surface (Lau & Qian, 2001). Rough surfaces are known to attract more clam larvae than smooth-surfaced tiles (Neo et al., 2009). Day & Blake (1979) have also reported that larval settlement of *Dipolydora giardi* is induced by previously settled worms or by crustose algae, among other offered substrates. Smyth (1989) showed that infestation by *Polydora* sp. occurs randomly on gastropod shells heavily encrusted by corallines. Thus, our own observations strongly suggest that the

preference of polydorids for *A. atra* valves, contrary to what happens with *Mytilus edulis*, is associated with a previous or early calcareous cover by the algae. Such interactions now need to be further assessed by experimental studies of substratum preferences by polydorid larvae.

The higher presence and abundance of polydorids in *A. atra* from Larralde (San José Gulf) as opposed to Puerto Lobos (San Matías Gulf) may be related to varying geographic location conditions. Amoroso & Gagliardini (2010) suggested that a combination of circulation, tidal currents, coastal topography and bathymetry in San José creates conditions for high primary productivity and larval retention. The San José Gulf is divided into western and eastern oceanographic domains with distinct hydrographic regimes. The western domain is connected with the San Matías Gulf and is highly turbulent due to the formation of vortices and dipoles during the tidal cycle. The eastern domain is less turbulent and more

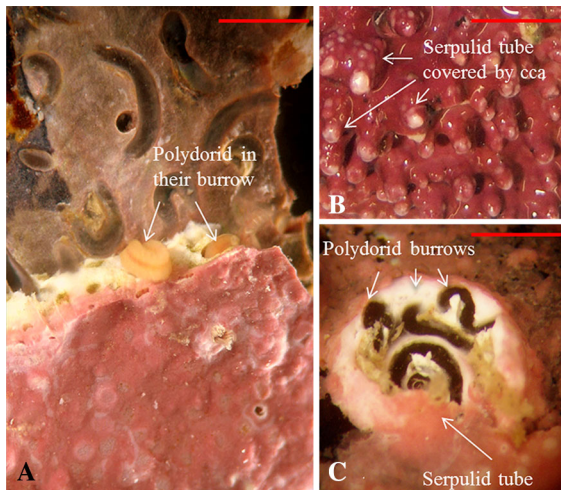


Fig. 2 Ribbed mussel *Aulacomya atra* shell infested by polydorid polychaetes. **A** the crustose coralline algae was removed of the upper half of the valve, showing the polydorid polychaetes in their burrows, **B** crustose coralline algae (cca) covering polydorid and serpulid tubes, **C** serpulid tubes bored by polydorid polychaetes. Bar scales **A** 1 cm, **B** 0.5 cm, **C** 0.25 cm

homogeneous, allowing for the “trapping” of terrigenous nutrients and marine larvae (Amoroso & Gagliardini, 2010; Amoroso et al., 2011). Larralde is located almost in the middle of the two domains, slightly towards the East, where the oceanographic characteristics would favour the time of the retention of the polychaete larvae.

Polydorid abundance was also positively related to the length of *A. atra*. Shell size is a major driver of boring intensity (White, 1969; Diez et al., 2014), since the longer exposure of older bivalves with correspondingly larger shell areas would naturally lead to higher infestation rates. It would show for Puerto

Fig. 3 Abundance of polydorids polychaetes in the ribbed mussel *Aulacomya atra* versus the shell length in **A** Puerto Lobos (San Matías Gulf) and **B** Larralde (San José Gulf), Argentina

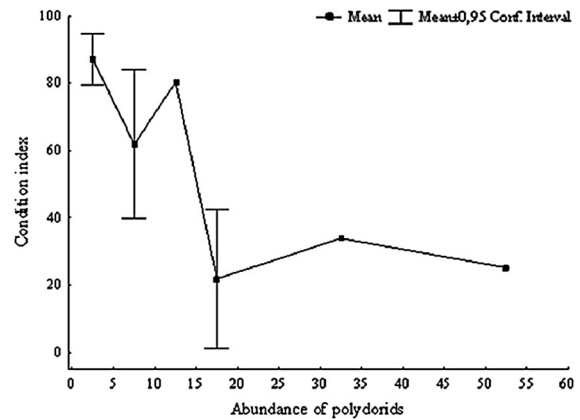
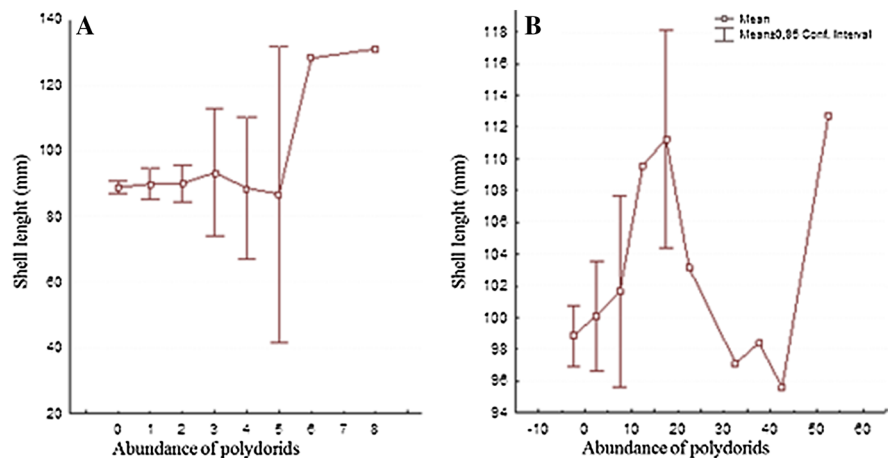


Fig. 4 Abundance of polydorids polychaetes in the ribbed mussel *Aulacomya atra* versus the condition index

Lobos that irrespective of shell length, the polydorid abundance would be low, whereas for Larralde, there would be a clearer relationship between size and number of worms. Orrhage (1969) did not find *P. ciliata* (Johnston, 1838) boring in shells of *Littorina littorea* (Linnaeus, 1758) smaller than 10 mm. Small abalone *Haliotis* shells are not infested by the sponge *Cliona celata* (Hansen, 1970), and larger shells of the snail *Buccinum undatum* Linnaeus, 1758 are more likely to be infested by the barnacle *Trypetesa lampas* (Hancock, 1849) than smaller ones (White, 1969).

In addition, worsening of the physiological condition of *A. atra*, expressed by lower condition indexes, was significantly related to polydorid infestation levels, a pattern also reported by Kent (1979) for *Mytilus edulis* and McDiarmid et al. (2004) for the abalone *Haliotis rubra* Leach, 1814. Such negative effect on the condition index of hosts may be attributed

to the energetic cost involved in the deposition of extra shell layers to repair the bored valves.

Our paper is the first to model the relationship between surface fouling of *A. atra* shells with encrusting coralline algae and serpulid shells with polydorid infestation. We have provided sound correlational evidence, through Generalized Linear Models, that a previous or early cover by calcareous epibionts favours infestation by polydorid polychaetes on shells of *A. atra*. Our models also showed that infestation is affected by geographic location and shell length and by its turn seems to affect the condition index of hosts. Future experimental studies are still needed to better assess such complex interactions.

Acknowledgements M.E. Diez, N. Vázquez and F. Cremonte are members of CONICET. The field work was conducted in a Protected Natural Área of Chubut Province with permits of the Secretaría de Turismo y Areas Protegidas. The financial support was provided by the PADI Foundation and ANPCyT (PICT 2013-1702 and PICT 2013-2582).

References

- Agresti, A., 2007. An Introduction to Categorical Data Analysis, 2nd Edition. New York: Wiley: 400 pp.
- Akaike, H., 1978. A Bayesian analysis of the minimum AIC procedure. *Annals of the Institute of Statistical Mathematics* 30: 9–14.
- Amoroso, R. O. & D. A. Gagliardini, 2010. Inferring complex hydrographic processes using remote-sensed images: turbulent fluxes in the Patagonian gulfs and implications for scallop metapopulation dynamics. *Journal of Coastal Research* 26: 320–333.
- Amoroso, R. O., A. M. Parma, J. M. Orensanz & D. A. Gagliardini, 2011. Zooming the macroscope: medium-resolution remote sensing as a framework for the assessment of a small-scale fishery. *ICES Journal of Marine Science* 68: 696–706.
- Barton, K., 2009. MuMIn: Multi-model Inference. R Package, Version 0.12.2. <http://r-forge.r-project.org/projects/mumin>.
- Blake, J. A., 1975. Phylum Annelida: Class Polychaeta. In Smithand, R. I. & J. A. Carlton (eds), *Light's Manual, Intertidal Invertebrates of the Central California Coast*. University of California Press, Berkeley: 151–243.
- Blake, J. A. & J. W. Evans, 1973. *Polydora* and related genera as borers in mollusc shells and other calcareous substrates. *Veliger* 15: 235–249.
- Carraro, J. L., G. S. Rupp, B. Mothes, C. Lerner & N. L. Würdig, 2012. Characterization of the fouling community of macroinvertebrates on the scallop *Nodipecten nodosus* (Mollusca, Pectinidae) farmed in Santa Catarina, Brazil. *Ciencias Marinas* 38: 577–588.
- Ciocco, N. F., M. L. Lasta & C. S. Bremec, 1998. Pesquerías de bivalvos: mejillón, vieiras (tehuelche y patagónica) y otras especies. In Boschi, E. E. (ed.), *El Mar Argentino y sus recursos pesqueros*. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata: 143–166.
- Ciocco, N. F., M. L. Lasta, M. Narvarte, C. Bremec, E. Bogazzi, J. Valero & J. M. Orensanz, 2006. Argentina. In Shumway, S. E. & G. J. Parsons (eds), *Scallops: Biology, Ecology and Aquaculture*, Vol. 26. Elsevier, Amsterdam: 1251–1292.
- Cremonte, F., 2011. Enfermedades de moluscos bivalvos de interés comercial causadas por metazoos. In Figueras, A. & B. Novoa (eds), *Enfermedades de moluscos bivalvos de interés en Acuicultura*. Observatorio Español de Acuicultura, Madrid: 331–385.
- Day, R. L. & J. A. Blake, 1979. Reproduction and larval development of *Polydora giardi* Mesnil (Polychaeta: Spionidae). *Biology Bulletin* 156: 20–30.
- Diez, M. E., V. I. Radashevsky, J. M. Orensanz & F. Cremonte, 2011. Spionid polychaetes (Annelida: Spionidae) boring into shells of molluscs of commercial interest in northern Patagonia, Argentina. *Italian Journal of Zoology* 78: 497–504.
- Diez, M. E., N. Vázquez, D. Urteaga & F. Cremonte, 2014. Species associations and environmental factors influence borers' activity on *Ostrea puelchana* of the northern Patagonian coast. *Journal of Molluscan Studies* 80: 430–434.
- Gee, J. M., 1965. Chemical stimulation of settlement in larvae of *Spirorbis rupestris* (Serpulidae). *Animal Behaviour* 13: 181–186.
- Gelman, S., Y.-S. Su, M. Yajima, J. Hill, M. G. Pittau, J. Kerman, T. Zheng & V. Dorie, 2009. Arm: Data Analysis Using Regression and Multilevel Hierarchical Models. R package, version 9.01. <http://CRAN.R-project.org/package=arm>.
- Grueber, C. E., S. Nakagawa, R. J. Laws & I. G. Jamieson, 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24: 699–711.
- Hansen, J. C., 1970. Commensal activity as a function of age in two species of California abalones (Mollusca: Gastropoda). *Veliger* 13: 90–94.
- Hartman, O., 1969. Atlas of the sedentary polychaetous annelids from California. Allan Hancock Foundation, University of Southern California: 812 pp.
- Kent, R. M. L., 1979. The influence of heavy infestations of *Polydora ciliata* on the flesh content of *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom* 59: 289–297.
- Lau, S. C. K. & P. Y. Qian, 2001. Larval settlement in the serpulid polychaete *Hydroides elegans* in response to the bacterial films: an investigation of the nature of putative larval settlement cue. *Marine Biology* 138: 321–328.
- Lucas, A. & P. G. Benninger, 1985. The use of physiological condition indices in marine bivalve aquaculture. *Aquaculture* 44: 187–200.
- Martin, D. & T. A. Britayev, 1998. Symbiotic polychaetes: review of known species. *Oceanography and Marine Biology: An Annual Review* 36: 217–340.
- McDiarmid, H., R. Day & R. Wilson, 2004. The ecology of polychaetes that infest abalone shells in Victoria, Australia. *Journal of Shellfish Research* 23: 1179–1188.
- Morse, A. N. C. & D. E. Morse, 1984. Recruitment and metamorphosis of *Haliotis* larvae induced by molecules

- uniquely available at the surfaces of crustose red algae. *Journal of Experimental Marine Biology and Ecology* 75: 191–215.
- Neo, M. L., P. A. Todd, S. L.-M. Teo & L. M. Chou, 2009. Can artificial substrates enriched with crustose coralline algae enhance larval settlement and recruitment in the fluted giant clam (*Tridacna squamosa*)? *Hydrobiologia* 625: 83–90.
- Orrhage, L., 1969. On the shell growth of *Littorina littorea* (Linne) (Prosobranchiata, Gasteropoda) and the occurrence of *Polydora ciliata* (Johnston) (Polychaeta Seden-taria). *Zoologiska bidrag från Uppsala* 38: 137–153.
- Pearce, C. M. & R. E. Scheibling, 1988. Larval settlement in the green sea urchin. *Strongylocentrotus droebachiensis*. *American Zoologist* 28: 365.
- R Development Core Team 2012. R: A Language and Envi-ronment for Statistical Computing. R Foundation for Sta-tistical Computing, Vienna, Austria. ISBN 3-900051-07-0
- Radashevsky, V. I., P. C. Lana & R. C. Nalesso, 2006. Mor-phology and biology of *Polydora* species (Polychaeta: Spionidae) boring into oyster shells in South America, with the description of a new species. *Zootaxa* 1353: 1–37.
- Roberts, R. D., M. F. Barker & P. Mladenov, 2010. Is settlement of *Haliotis iris* larvae on coralline algae triggered by the alga or its surface biofilm? *Journal of Shellfish Research* 29: 671–678.
- Rodriguez, R., F. P. Ojeda & N. I. Inestrosa, 1993. Review: settlement of benthic marine invertebrates. *Marine Ecol-ogy Progress Series* 97: 193–207.
- Rowley, R., 1989. Settlement and recruitment of sea urchins (*Strongylocentrotus* spp.) in a sea-urchin barren ground and a kelp bed: are populations regulated by settlement or post-settlement processes? *Marine Biology* 100: 484–494.
- Sato, Okoshi W. & M. Takatsuka, 2001. *Polydora* and related genera (Polychaeta, Spionidae) around Puerto Montt and Chiloé Island (Chile), with description of a new species of *Dipolydora*. *Bulletin of Marine Science* 68: 485–503.
- Symonds, M. R. E. & A. Moussalli, 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* 65: 13–21.
- Smyth, M. J., 1988. *Penetrantia clionoides* sp. nov. (Bryozoa), a boring bryozoan in gastropod shells from Guam. *Biologi-cal Bulletin* 174: 276–286.
- Smyth, M. J., 1989. Bioerosion of gastropod shells: with emphasis on effects of coralline algal cover and shell microstructure. *Coral Reefs* 8: 119–125.
- Steele, M. A., 1998. The relative importance of predation and competition in two reef fishes. *Oecologia* 115: 222–232.
- Whalan, S., N. S. Webster & A. P. Negri, 2012. Crustose cor-alline algae and a cnidarian neuropeptide trigger larval settlement in two coral reef sponges. *PLoS ONE* 7: e30386.
- White, F., 1969. Distribution of *Trypetesa lampas* (Cirripedia, Acrothoracica) in various gastropod shells. *Marine Biol-ogy* 4: 333–339.