

Aquaculture 189 (2000) 361-373

Aquaculture

www.elsevier.nl/locate/aqua-online

Culture potential of the pearl oyster (*Pinctada imbricata*) from the Caribbean.

I. Gametogenic activity, growth, mortality and production of a natural population

H.-Jörg Urban*

Facultad de Ciencias, Departamento de Biología, Sección de Biología Marina, Universidad del Valle, A.A. 25360. Cali. Colombia

Received 26 August 1999; received in revised form 23 February 2000; accepted 4 April 2000

Abstract

Gametogenic activity, growth, mortality and somatic production of an unexploited population of *Pinctada imbricata* from the Cabo de la Vela (Guajira, Colombian Caribbean, 12°10′N, 72°20′W) was studied. *P. imbricata* exhibits a continuous gametogenic cycle with a 5-month period (January to June) of high gametogenic activity. Gametogenesis is inversely correlated to temperature, suggesting a relation between spawning and upwelling-induced food availability. Final growth parameters according to the von Bertalanffy-growth equation, estimated from tagging-recapture data, were $L_{\alpha}=84.0$ mm and K=0.939 year $^{-1}$; total mortality, corresponding to natural mortality M, was calculated as Z=2.687 year $^{-1}$. The P/\overline{B} -ratio for this population estimated with the weight specific growth rate method was 1.515. From the results, it was generally concluded that P. *imbricata* has a large aquaculture potential in this region owing to its continuous gametogenic cycle, and a high growth and production rate. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Pearl oyster; Gametogenesis; Growth; Mortality; Caribbean; Pinctada imbricata

1. Introduction

Pearl oysters (Fam. Pteriidae), have always been of great interest for commercial use and for aquaculture purposes because their meat is used for human consumption and

0044-8486/00/\$ - see front matter © 2000 Elsevier Science B.V. All rights reserved.

PII: S0044-8486(00)00393-8

^{*} Corresponding author. Tel.: +57-2-339-32-43; fax: +57-2-333-49-21. *E-mail address:* jurban@colnet.com.co (H.-J. Urban).

because of their capacity to produce pearls. This is reflected by many publications, principally in the area of reproduction, aquaculture, and spat settlement. In the past, research has been concentrated mainly on three regions. In the Indo-Pacific, *Pinctada albina, P. margaritifera, P. maxima* and *P. maculata* were objects of several studies (Tranter, 1958a,b,c; Rose et al., 1990; Rose and Baker, 1994; Knuckey, 1995; Friedman and Bell, 1996; Sims, 1992). In Japan, where traditionally, pearl oyster culture is used for pearl production, studies mainly on *P. fucata* have been published (e.g. Wada and Komaru, 1994, 1996; Wada et al., 1995). Finally, studies from the Mexican Pacific Coast, deal exclusively with *P. mazatlantica* and *Pteria sterna* (Díaz and Bückle, 1996; Araya-Nuñes et al., 1991; García-Domínguez et al., 1996; Monteforte and García-Gasca, 1994; Bückle et al., 1992; Río-Portila et al., 1992; Gaytan-Mondragón et al., 1993).

In the tropical Atlantic, another *Pinctada* species is found: *P. imbricata* Röding 1798. *P. imbricata* is common in the Caribbean Sea of Colombia, forming dense populations in the Guajira province (12°10′N, 72°20′W and 12°00′N, 72°10′W).

According to recent findings, many of the endemic Pinctada species are now considered as synonyms of one cosmopolitan species (Shirai, 1994). Although the exact classification is not definite, it seems clear that, P. imbricata = P. fucata = P. radiata = P. martensii, with the senior synonym being P. imbricata. However, as this point is still in discussion, in this paper, species will be referred to as they have been cited or identified in the original paper or study.

This is the first paper from a study to examine the culture potential of the pearl oyster, P. imbricata, from the Caribbean, by comparing a natural population with individuals reared under culture conditions and in the laboratory. This paper gives results on gametogenic activity, growth, mortality and production of a natural P. imbricata population from the Guajira province (Colombia).

2. Materials and methods

2.1. Study area and sampling

The studies were carried out at the "'Cabo de la Vela'', a Peninsula located in the Guajira province, Colombia (12°10′N, 72°20′W and 12°00′N, 72°10′W, Fig. 1). Northeast winds during the entire year are the major reason for an upwelling system causing comparatively low temperatures of approximately 25°C and a high salinity of 36 ‰. Apart from colder waters, nutrients also reach the surface and yield a high primary production. A characteristic seagrass (*Thalassia testudinum*) community is nourished by these favorable conditions, giving a suitable substrate for a *P. imbricata* population.

At monthly intervals, quantitative samples (two replicates, $0.25~\text{m}^{-2}$) were taken every 50 m following a transect perpendicular to the beach until no bivalves were found (approximately 500 m from the beach). Every month, the transect was located 100 m to the right from the last sampling month (Fig. 1). From the quantitative samples, two sub-samples of 30-40 individuals each were selected randomly, covering the entire growth range, thus obtaining monthly samples of 1 year (March 1997 to March 1998). Sea-surface temperature and salinity were recorded at each sampling. Maximum length

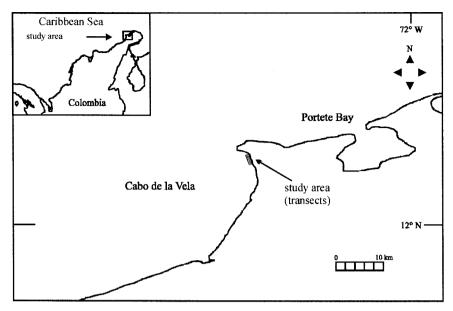


Fig. 1. The study area on the Peninsula, Cabo de la Vela. The location of sampling transects is indicated.

on the antero-posterior axis (shell length) was recorded for all individuals with vernier calipers. One sub-sample was used for gametogenic analysis (gonad histology); the second sub-sample was used to study body condition (body weight cycle).

2.2. Gametogenic activity and condition

For the body weight cycle, all soft parts were removed and dried at 70°C to constant weight to determine the shell-free dry weights (SFDW). Ash-free dry weight (AFDW) was obtained by ignition of dried soft parts at 550°C for 5 h. The constants "a" and "b" of the monthly relationships between shell length and AFDW (Eq. (1)) were estimated by non-linear regression analysis (SIMPLEX algorithm, Press et al., 1986). An annual weight cycle for a standard individual of 50 mm shell length was calculated as

$$AFDW = aSL^b$$
 (1)

where AFDW is in grams and SL, the shell length [mm].

Such a body weight cycle (or condition cycle) can be used to identify spawning events (decreasing weight between 2 successive months). However, as weight changes also depend on feeding conditions, it is necessary to interpret them in connection with gonad studies. Therefore, every month, the reproductive stage of 20 individuals was determined by microscopic observation on fresh gonad material (smear samples) using a scale modified from Guillou et al. (1990):

• *indifferent*: no gonads visible. This has two possible explanations: adults with recuperating gonads after spawning events (1) or immature juveniles (2).

- developing 1: gonad tissues visible, but it is very difficult to distinguish sexes. No mature elements are present.
- developing 2: gonad tissues are evident and sexes can be distinguished. Gametes are abundant, but the majority of the spermatozoids are hardly moving and pedunculate oocytes are present.
- ripe: gonads with rapid moving spermatozoids or spherical oocytes. Spawning is imminent.
- spent: gonads are empty and thin. Coexistence of cells being reabsorbed, and mature cells

2.3. Growth and mortality

Individuals were tagged in situ with dymo-tape labels on telephone wire around the shells. Growth increments corresponding to shell length were measured with vernier calipers approximately every 3 months. In total, 82 individuals were recovered alive and were used for growth parameter estimation. For growth estimation, the von Bertalanffygrowth-function (von Bertalanffy, 1938) was used:

$$L_{t} = L_{\infty} \cdot \left(1 - e^{(-K(t - t_{0}))}\right) \tag{2}$$

where L_{∞} is the asymptotic length [mm], K, the growth constant [year⁻¹], t, the age [year] and t_0 , the age at zero length. Growth parameters were estimated using Fabens' method (Fabens, 1965), by fitting a rearranged function of Eq. (2) to tagging recapture data using an iterative non-linear least-square method (SIMPLEX algorithm, Press et al., 1986):

$$L_2 = L_1 + (L_{\infty} - L_1) \cdot (-e^{(-K(t_2 - t_1))})$$
(3)

where L_1 is the length at the beginning and L_2 , the length at the end of the time interval t_2-t_1 .

Total mortality Z was calculated with the single negative exponential model on pooled length frequency data, taken from the monthly quantitative samples:

$$N_t = N_0 e^{-Zt} \tag{4}$$

where t is the time and N_0 is the number of individuals at t = 0. The length converted catch curve method (Pauly, 1983) was applied, where mortality Z is estimated by linear regression analysis:

$$\operatorname{Ln}\left(\frac{N_i}{\Delta t_i}\right) = a + bt_i; Z = -b. \tag{5}$$

2.4. Production

The weight-specific growth rate method (Crisp, 1984) was used to calculate somatic production of the population P (in g AFDW m⁻² year⁻¹) from the mean of quantitative

samples, pooled length–frequency data, the growth parameters of the von Bertalanffy-growth-function and the length–weight relationship (Eq. (1)):

$$P = \sum N_i W_i G_i \tag{6}$$

where N_i is the mean density of individuals [N m⁻²], W_i , the mean body weight [g AFDW] in length class i and G_i , the weight-specific growth rate [year⁻¹]:

$$G_i = bK \left[\left(\frac{L_{\infty}}{L_i} \right) - 1 \right] \tag{7}$$

where b is the exponent of the length-weight relationship (Eq. (1)), L_{∞} and K are VBGF parameters and L_i is the mean length in length class i. Individual somatic production $P_{\rm ind}$ (in g AFDW m⁻² year⁻¹) was calculated as:

$$P_{\text{ind}} = \sum W_i G_i \tag{8}$$

and mean biomass \overline{B} (in g AFDW m⁻² year⁻¹) of the population as:

$$\overline{B} = \sum N_i W_i. \tag{9}$$

The P/\overline{B} ratio of the population was calculated from somatic production P and mean biomass.

3. Results

3.1. Gametogenic activity and condition cycle

Fig. 2A and B show the distribution of gonad stages in relation to the condition index and the sum of the gonad stages ''ripe'' and ''spent'' (as a measure of high gametogenic activity). Temperature- and salinity cycles are shown in Fig. 2C. Based on Fig. 2, *P. imbricata* clearly has a continuous gametogenic cycle, with ''developing 2'' and ''ripe'' gonad stages present through the entire year and ''spent'' stages found during 8 of 12 months. According to Fig. 2B, gonad stages ''ripe'' and ''spent'' correlate well with the condition cycle (Spearman: gonad stage/condition = 0.403, Table 1) revealing two principal peaks and a minor peak. The two major peaks correspond to a long (principal) phase of high reproductive output between January and June. A second minor spawning activity is indicated in October. Temperature is negatively correlated with gametogenic activity (Spearman: gonad stage/temperature = -0.614, Table 1), with low values between January to July and higher values during the rest of the year.

3.2. Growth and mortality

With the direct fit of Fabens' Eq. (3) to the tagging recapture data, growth parameters K=1.605 and $L_{\infty}=63.9$ cm were estimated (Table 2). Misleading values of L_{∞} can be obtained if the variability of the growth data is large. This was the case in the present study, as indicated by the Gulland and Holt plot (Fig. 3), a linear approach to estimate

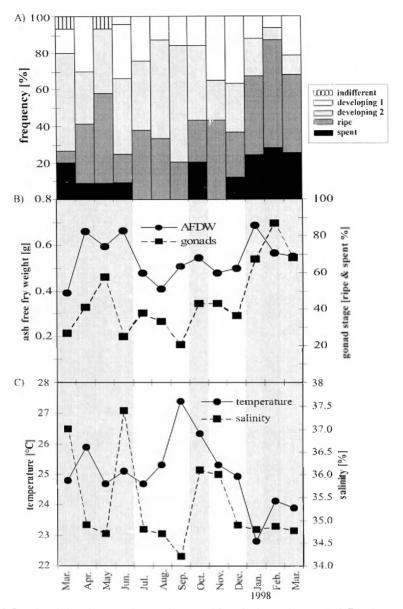


Fig. 2. (A) Gonad cycle based on gonad stages determined from fresh gonad material of P. imbricata from the Colombian Caribbean. (B) Overlay of gonad cycle (=ripe & spent stages) and AFDW cycle corresponding to (A). (C) Temperature and salinity cycle for the same area corresponding to (A). Shadowed bars indicate period(s) of high gametogenic activity.

growth parameters by means of a linear regression (Gulland and Holt, 1959), giving a coefficient of determination of only $r^2 = 0.376$. A large deviation between maximum

Table 1 Spearman correlation matrix of the gonad stage "ripe and spent", salinity, temperature and condition (AFDW = ash-free dry weight) of P. imbricata

	Temperature	Salinity	SFDW	
Salinity	0.109			
AFDW	-0.230	0.011		
Gonad stage	-0.614	-0.086	0.403	

Table 2 Growth parameters (estimated with ''free'' and ''fixed'' routine), total mortality rate estimated with the catch curve method, and results of the production estimation (mean abundance, mean body weight, mean biomass, mean somatic production and productivity) of *P. imbricata*

	Fabens (free)	Fabens (fixed $L_{\infty} = 84$)	Catch curve	Weight- specific
confidence interval)				growth rate
L_{∞} [mm]	63.9 ± 9.3	84.0 ± 12.2		
$K[year^{-1}]$	1.605 ± 0.535	0.939 ± 0.313		
L_{\max} [mm]		83.8		
$Z[year^{-1}]$			2.687 ± 0.234	
Mean abundance $[n m^{-2}]$				7.2 ± 1.5
Mean body weight [AFDW g m ⁻²]				0.441
Mean biomass [AFDW g m ⁻²]				3.173
Mean somatic production [AFDW g m ⁻²]				4.808
P/\overline{B} ratio				1.515

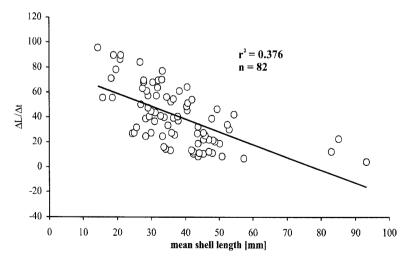


Fig. 3. Gulland and Hold plot corresponding to tagging recapture data of P. imbricata from the Colombian Caribbean.

length ($L_{\rm max}=83.8$ mm, taken from population length–frequency data, Table 2) and L_{∞} (= 63.9 mm) indicates that L_{∞} was underestimated. Thus, K was overestimated because the two growth parameters are inversely related (Pauly, 1979). In order to recalculate the values and to obtain correct growth parameters, the growth routine was therefore re-run with fixed values of L_{∞} (= 84.0 mm). These values are given in Table 2 and the corresponding growth curve is plotted in Fig. 4A.

With the growth parameter of Fig. 4A, a total mortality of $Z = 2.687 \text{ year}^{-1}$ (Table 2) was estimated using the length converted catch curve method (Fig. 4B).

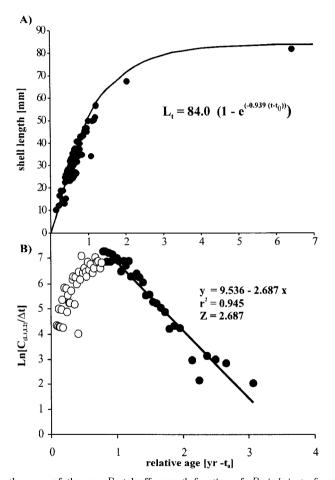


Fig. 4. (A) Growth curve of the von Bertalanffy-growth-function of P. imbricata from the Colombian Caribbean. The independent variable is relative age $(year-t_0)$ because t_0 is not known. To plot tagging-recapture data together with the growth curve, the age of L_2 from tagging-recapture data was estimated with the inverse von Bertalanffy-growth-function, $[age=\frac{-1}{K}ln(\frac{1-L_{max}}{L_{\infty}})]$, this age was plotted against L_1 . (B) Length-converted catch curve of P. imbricata from the Colombian Caribbean, based on monthly pooled length-frequency data. $Open\ data\ points$: excluded from regression, $closed\ data\ points$: used for regression. Regression equation and Z-value are given.

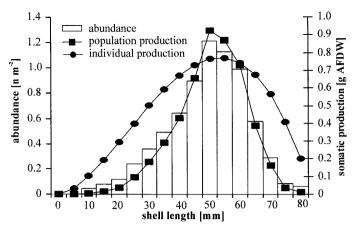


Fig. 5. Individual somatic production, population somatic production, and mean abundance for different length classes of *P. imbricata* from the Colombian Caribbean.

3.3. Production

Fig. 5 shows individual somatic production, somatic production of the population, and abundance distributed among length classes. Abundance distribution is clearly unimodal and approximately normal with a peak at 55 mm shell length. Individual production increases to its highest value at 50 mm and decreases thereafter. Population production follows exactly the abundance distribution pattern. Table 2 concludes the results of the production estimation. With an annual mean somatic population production of 4.808 [g AFDW m $^{-2}$] and a mean biomass of 3.173 [g AFDW m $^{-2}$], this population has a comparatively high productivity given by a P/\overline{B} -ratio of 1.515.

4. Discussion

In order to decide whether a bivalve species is suitable for culture or not, it is first necessary to obtain information on the population dynamics of, if possible, undisturbed natural populations. In a second phase, the behavior and adaptation in and to culture systems should be evaluated and compared with results of the natural population. Population dynamics include reproduction cycle and strategy, giving information on the best season to obtain spat. Growth rates indicate how much time is required until a certain marketable size and weight is reached. Natural mortality rate gives information on the losses that can be expected, indicating the need for special protective devices. Finally, productivity is a widely used index to compare the potential biomass growth of the particular population studied.

The results on gametogenesis clearly indicate a continuous cycle with a long spawning season. This is typical for many tropical bivalve species, where the major abiotic factors temperature and food availability vary little during the year. As the length of the gametogenic activity determines the availability of spat during the year, it is often

a crucial element for the success of a developing aquaculture. This is mostly because hatchery-based spat production is initiated later, after aquaculture of a certain species has been established. The present results are, therefore, also discussed in a latitudinal context considering commercial bivalves from temperate areas. Barnes (1957) stated that under tropical conditions with rather constant temperature and food conditions, seasonal breeding is superimposed. Urban and Campos (1994) and Urban (1996) studied the reproductive cycle of six bivalve species from Chile at 37°S. All six species had a definite short spawning season in summer (3 months: November to January). One of these species (Gari solida), studied closer to the equator at 14°S in Peru, had two spawning seasons per year, one in summer, the second in winter (Urban and Tarazona, 1996). Considering that the condition cycle (AFDW) correlates well with ripe and spent stages, for *P. imbricata*, studied in the tropics at 12°N, a long spawning season from January to June (5 months) can be concluded. Most likely, small parts of the population spawn also between July and December; indicated by the presence of spent stages in October and December. A similar pattern was observed by Rose et al. (1990) for P. maxima, which has a main spawning period in September/October and a secondary spawning in March/April.

The high positive correlation between condition and gonad stages (both having an inverse relationship to the temperature cycle) might be explained in the following way. Between January to June, lower temperatures are caused by increasing upwelling; thus, nutrients reach the surface and these fuel high primary production (Arntz and Fahrbach, 1991; Urban and Tarazona, 1996). This energy is used for build up of gonads (ash free body dry weight increases), which is reflected by a higher reproductive output (ripe and spent stages increase). Between July and December, higher temperature might be explained by a reduction of the upwelling process. Thus, fewer nutrients and less phytoplankton are reflected in reduced body weight, and fewer ripe and spent stages. This finding also implies that the gametogenic cycle depends more on the food availability and is not triggered by temperature. This is also supported by the fact that annual temperature variability is slight: only 4°C (23–27°C).

It was not possible to estimate a seasonal growth curve, due to the large variability of the tagging-recapture data. Such large variability in growth increments of tagging recapture has been observed for other bivalve species from the same area (*Pteria colymbus, Pinna carnea, Arca zebra*, Urban, unpublished data). The reasons most likely for this variability are the uncoupled growth rates between shell growth and weight growth (Rajagopal et al., 1998). This is to be expected in tropical species with continuous developing cycles and long spawning seasons (see above). Therefore, based on these assumptions, a non-seasonal growth curve presenting the mean growth for the population was estimated and this is in accordance with the low temperature variability. According to Fig. 3A, *P. imbricata* reaches a marketable size of 50 mm shell length in less than a year.

No exploitation of the population was observed during the study period. Therefore, it can be assumed that estimated total mortality (Z) corresponds to natural mortality (M). The distribution of the length–frequencies is approximately normal (Fig. 5), implying a small number of young individuals or recruits. This is to be expected for a species with a continuous reproduction strategy, recruiting few individuals continuously throughout the

year. On the other hand, the normal distribution also implies a small number of large individuals and thus, a high mortality rate among all age classes. Urban (1996) estimated total mortality rates of six infaunal clam species from Chile at 37° S. Z-values fluctuated around 1 year⁻¹, while Z = 2.687 year⁻¹ was estimated for P. imbricata in this study. Urban (1996) argued that infaunal clams, owing to a thick shell and a deep burrowing depth, can minimize natural predation after attaining a certain size. P. imbricata, on the other hand, is an epifaunal species with a comparatively thin shell and a high productivity rate of 1.515. In comparison, productivity of six clams from Chile was about 0.3 (Urban, 1996).

5. Conclusions

With the continuous gametogenic cycle of *P. imbricata*, larvae and spat are probably present throughout the entire year. However, abundance peaks of these early stages are to be expected between January and June. Growth rate is high and a marketable size can be achieved within 1 year. Nevertheless it has to kept in mind that even higher growth rates have been recorded for other bivalve species (especially scallops) from the same area (Urban, unpublished data). One negative effect for aquaculture might be expected from the high mortality. This may be controlled by protective culture units (i.e. mesh size, etc.). In conclusion, *P. imbricata* presents a culture potential for the region, owing to its high productivity.

Acknowledgements

This study was carried out in the frame of a larger project ''Culture of Bivalves from the Colombian Caribbean (01/97–04/99)'', at the Instituto de Investigaciones Marinas y Costeras (INVEMAR-Santa Marta), financed by the Inter-American Bank for Development (BID), the Colombian Ministry of Environments (''BPIN'') and the Centrum für Internationale Migration und Entwicklung (CIM-Germany). Special thanks to Juan Pablo Assmus for working on the samples as well as to Carolina Gárcia for her collaboration in the field.

References

- Araya-Nuñes, O., Ganning, B., Bückle-Ramirez, F., 1991. Gonad maturity, induction of spawning, larval breeding, and growth in the American Pearl-Oyster (*Pteria sterna*, Gould). Calif. Fish Game 77 (4), 181–193.
- Arntz, W.E., Fahrbach, E., 1991. El Niño. Klimaexperiment der Natur. In: Physikalische Ursachen und biologische Folgen. Birkhäuser-Verlag, Berlin, p. 264.
- Barnes, H., 1957. Process of restoration and synchronization in marine ecology. The spring diatom increase and the spawning of the common barnacle *Balanus balanoides* (L.). Ann. Biol. 33, 67–85.
- von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws II). Hum. Biol. 10, 181–213.

- Bückle, L.F., Voltolina, D., Morales, E., Valenzuela, F., 1992. Spat settlement and growth of *Pteria sterna* (Gould) (Mollusca, Bivalvia) in Bahía de los Angeles, Baja California, Mexico. Trop. Ecol. 33 (2), 137–147.
- Crisp, D.J., 1984. Energy flow measurements. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos. Blackwell. London, pp. 284–372.
- Díaz, A.H., Bückle, L.F., 1996. Ciclo gonádico de Pteria sterna (Gould, 1851) (Mollusca, Bivalvia) in Baja California. Mexico. Cienc. Mar. 22 (4), 495–509.
- Fabens, A.J., 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29, 265-285.
- Friedman, K.J., Bell, J.D., 1996. Effects of different substrata and protective mesh bags on collection of spat of the pearl oysters, *Pinctada margaritifera* (Linnaeus, 1758) and *Pinctada maculata* (Gould, 1851). J. Shellfish Res. 15 (3), 535–541.
- Garcia-Dominguez, F., Ceballos-Vazquez, B.P., Tripp-Quezada, A., 1996. Spawning cycle of the pearl oyster, Pinctada mazatlanica (Hanley, 1856), (Pteriidae) at isla Espiritu Santo, Baja California Sur, Mexico. J. Shellfish Res. 15 (2), 297–303.
- Gaytan-Mondragon, I., Caceres-Martinez, C., Tobias-Sanchez, M., 1993. Growth of the Pearl Oyster *Pinctada mazatlanica* and *Pteria sterna* in different Culture Structures at La Paz Bay, Baja California Sur, México. J. World Aquacult. Soc. 24 (4), 541–546.
- Guillou, J., Bachelet, G., Desprez, M., Ducrotoy, J.P., Madani, I., Rybarczyk, H., Sauriau, P.G., Sylvand, B., Eikaim, B., Glemarec, M., 1990. Les modalites de la reproduction de la coque (*Cerastoderma edule*) ser le littoral français de la Manche et de l'Atlantique. Aquat. Living Res. 3, 29–41.
- Gulland, J.A., Holt, S.J., 1959. Estimation of growth parameter for data at unequal time intervals. J. Cons. CIEM 25 (1), 47–49.
- Knuckey, I.A., 1995. Settlement of *Pinctada maxima* (Jameson) and other bivalves on artificial collectors in the Timor Sea, Northern Australia. J. Shellfish Res. 14 (2), 411–416.
- Monteforte, M., Garcia-Gasca, A., 1994. Spat collection studies on pearl oysters *Pinctada mazatlanica* and *Pteria sterna* (Bivalvia, Pteriidae) in Bahía de La Paz, South Baja California, Mexico. Hydrobiologia 291, 21–34.
- Pauly, D., 1979. Gill size and temperature as governing factors in fish growth: A generalization of von Bertalanffy's growth formula. Ber. Inst. Meereskd., Kiel 63, 1–156.
- Pauly, D., 1983. Length converted catch curve curves: A powerful tool for fisheries research in the tropics (Part I). Fishbyte 1, 9–13.
- Press, W.H., Flannery, B.P., Teukolsky, S.A., Vetterling, W.T., 1986. Numerical Recipes, The Art of Scientific Computing. Cambridge Univ. Press, Cambridge.
- Rajagopal, S., Venugopalan, V.P., Nair, K.V.K., Velde, G., Jenner, H.A., den Hartog, C., 1998. Reproduction, growth rate and culture potential of the green mussel, *Perna viridis* (L.) in Edaiyur backwater, east coast of India. Aquaculture 162, 187–202.
- Río-Portila, M.A., Re-Araujo, A.D., Voltolina, D., 1992. Growth of the pearl oyster *Pteria sterna* under different thermic and feeding conditions. Mar. Ecol.: Prog. Ser. 89, 221–227.
- Rose, R.A., Baker, S.B., 1994. Larval and spat culture of the Western Australian silver- or goldlip pearl oyster, *Pinctada maxima* (Jameson) (Mollusca: Pteriidae). Aquaculture 126, 35–50.
- Rose, R.A., Dybdahl, R.E., Harders, S., 1990. Reproductive cycle of the western Australian silverlip pearl oyster, *Pinctada maxima* (Jameson) (Mollusca: Pteriidae). J. Shellfish Res. 9 (2), 261–272.
- Shirai, S., 1994. Pearls and pearl oysters of the world. Marine Planning, Okinawa.
- Sims, N.A., 1992. Abundance and distribution of the black-lip pearl oyster, *Pinctada margaritifera* (L.), in the Cook Islands, South Pacific. Aust. J. Mar. Freshwater Res. 43, 11409–11421.
- Tranter, D.J., 1958a. Reproduction in Australian pearl oyster (Lamellibranchia): II. Pinctada albina (Lamarck): Gametogenesis. Aust. J. Mar. Freshwater Res. 9 (1), 144–164.
- Tranter, D.J., 1958b. Reproduction in Australian pearl oysters (Lamellibranchia): III. *Pinctada albina* (Lamarck): Breeding season and sexuality. Aust. J. Mar. Freshwater Res. 9 (2), 190–217.
- Tranter, D.J., 1958c. Reproduction in Australian pearl oysters (Lamellibranchia): IV. Pinctada margaritifera (Linnaeus). Aust. J. Mar. Freshwater Res. 9 (4), 509–524.
- Urban, H.-J., 1996. Population dynamics of the bivalves *Venus antiqua, Tagelus dombeyi* and *Ensis macha* from Chile at 36°S. J. Shellfish Res. 15 (3), 719–727.

- Urban, H.-J., Campos, B., 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.
- Urban, H.-J., Tarazona, J., 1996. Effects of El Niño/Southern Oscillation on the Population Dynamics of a *Gari solida*-population (Bivalvia, Psammobidae) from Bahía Independencia, Peru (14°S). Mar. Biol. 125, 725–734.
- Wada, K.T., Komaru, A., 1994. Effect of selection for shell coloration on growth rate and mortality in the Japanese pearl oyster, *Pinctada fucata martensii*. Aquaculture 125, 59–65.
- Wada, K.T., Komaru, A., 1996. Color and weight of pearls produced by grafting the mantle tissue from a selected population for white shell color of the Japanese pearl oyster *Pinctada fucata martensii* (Dunker). Aquaculture 142, 25–32.
- Wada, K.T., Komaru, A., Ichimura, Y., Kurosaki, H., 1995. Spawning peak occurs during winter in the Japanese subtropical population of the pearl oyster, *Pinctada fucata fucata* (Gould, 1850). Aquaculture 133, 207–214.