Cah. Biol. Mar. (2002) 43 : 17-26

Review of the literature on bivalve cytogenetics in the last ten years

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Abstract: This paper provides a review of the studies on bivalve chromosomes since 1992, in order to gather available data and to highlight the recent progress in different fields of cytogenetics: karyotype and chromosome markers, genome size, aneuploidy, natural and induced polyploidy, and hybridization.

Résumé: *Revue des travaux des dix dernières années sur l'étude cytogénétique des bivalves*. Cet article présente une revue sur l'étude des chromosomes des bivalves depuis 1992 afin de rassembler les données disponibles et de souligner les progrès récents dans les différents domaines de la cytogénétique : caryotype et marqueurs chromosomiques, taille du génome, aneuploïdie, polyploïdie naturelle et induite, et hydridisation.

Keywords: Bivalvia, Chromosomes, Cytogenetics

Introduction

Cytogenetic studies encompass different levels of biological organization ranging from the morphological to the molecular, depending on the applicable technology. Chromosomes can be studied as a morphological manifestation of the genome in terms of their microscopically visible size, shape, number and behaviour during meiosis and mitosis. At another level, banding studies reveal finer details of chromosomal morphology. Studies of natural or induced deviation from the diploid chromosome number also contribute significant cytogenetic data.

Among bivalves, the first investigations concerned the chromosome number (see Patterson review, 1969). Then, pre-treatment with colchicine and hypotonic treatment, combined with the air drying technique, permitted accurate assessments of chromosome morphology (see Nakamura review, 1985). Later, the development of banding techniques which allowed chromosome identification in karyotypes began to be applied in bivalves (see Thiriot-Quiévreux review, 1994). Since these reviews, the study of bivalve chromosomes has greatly progressed in karyological as well as molecular information, as a result of routine application of several banding techniques and the development of techniques for in situ hybridization.

The aim of this paper is to provide a review of the studies on bivalve chromosomes since 1992, in order to gather available data and to highlight the recent progress in the different fields of bivalve cytogenetics.

Karyotypes and Chromosome markers

Data on standard karyotypes, banding techniques and FISH are given in Table 1, in which bivalve classification follows that of Boss (1982). Since 1992, new karyological data have been added for 65 bivalve species among which the first karyotype data are given for 49 species. Within the bivalve class, the most frequent chromosome number of 2n=38,

Reçu le 1er juin 2001 ; accepté après révision le 20 septembre 2001.
Received 1st June 2001; accepted in revised form 20 September 2001.

Table 1. Recent data on bivalve chromosomes: standard karyotype, banding techniques and FISH.
° : species with first karyotype description; * : species without known commercial importance
NORs: silver staining, C: C-banding, Fluo: fluorochrome staining, RE: restriction enzyme treatment, G: G-banding; N: N-banding, RB: replication pattern
FISH: fluorescence in situ hybridization, rDNA: ribosomal genes, sat DNA: satellites DNA, T: telomere sequences; ( ): in situ hybridization only
m: metacentric, sm: submetacentric, st: subtelocentric, t: telocentric
Tableau 1 : Données récentes sur les chromosomes de bivalves : caryotype standard, techniques de marquages et FISH.

Family/Species	Origin	2n	Karyotype	NORs	C	Fluo	RE	G	N	RB	FISH	References
Nuculidae												
Acilia insignis ° *	Japan	24	9 m, 1 sm/m, 2 sm									Ieyama, 1992
Nuculanidae												
Yoldia notabilis ° *	Japan	38	9 m, 5 sm, 5 st									Ieyama, 1992
Mytilidae												
Brachidontes minimus ° *	W Mediterranean	28	5 m, 9 st									Thiriot-Quiévreux, unpublished
Brachidontes pharaonis ° *	Sicily, Mediterranean	28	6 m/sm, 8 st	+		+					rDNA	Vitturi et al., 2000
Brachidontes rodriguezi ° *	Argentina	32	2 m, 12 st, 2 t	+		+				+	rDNA	Torreiro et al., 1999
Choromytilus chorus °	Chile	30	10 m, 5 sm									Palma-Rojas et al., 1997
Limnoperna fortunei ° *	Japan	30	10 m, 4 sm, 1 st									Ieyama, 1996
Mytilaster lineatus ° *	North East Italy	26	6 m, 4 sm, 1 st, 2 t									Libertini et al., 1996
Mytilaster solidus ° *	North East Italy	28	5 m, 3 sm, 2 st, 2 t									Libertini et al., 1996
Mytilus californianus	Canadian Pacific	28	7 m, 7 sm	+								Martinez-Lage et al., 1997
	Canadian Pacific	28									rDNA	Gonzalez-Tizon et al., 2000 b
Mytilus edulis	French Atlantic coast	28	6 m, 6 sm,2 st	+								Cornet, 1993
	North West Europe	28	6 m, 8 sm/st	+								Insua et al., 1994
	North sea	28	6 m, 8 sm/st	+	+	+						Martinez-Lage et al., 1995
	North Sea	28	6 m, 8 sm/st	+	+	+						Martinez-Lage et al., 1996
Mytilus galloprovincialis	French Mediterranean	28	5 m, 9 sm/st	+								Insua et al., 1994
	Galicia, Spain	28	6 m, 8 sm/st		+	+	+	+				Martinez-Lage et al., 1994
	Galicia, Spain	28		+								Martinez-Exposito et al., 1994 a
	Galicia, Spain	28								+		Martinez-Exposito et al., 1994 b
	Galicia, Spain	28		+	+	+						Martinez-Lage et al., 1995
	Iberian peninsula	28	6 m, 8 sm/st + or 5 m, 9 sm/st	+	+	+						Martinez-Lage et al., 1996
	NW Iberian peninsula	28			+							Pasantes et al., 1996 a
	Galicia, Spain	28								+		Pasantes et al., 1996 b
	Galicia, Spain	28		+	+	+			+		(rDNA,T)	Martinez-Exposito et al., 1997
	Galicia, Spain	28		+							rDNA	Insua & Mendez, 1998
Mytilus trossulus °	Gdansk Bay, Baltic Sea	28	6 m, 8 sm/st	+								Insua et al., 1994
	Dahme, Baltic Sea	28	6 m, 8 sm/st	+	+	+						Martinez-Lage et al., 1995
	Dahme, Baltic Sea	28	6 m, 8 sm/st	+	+	+						Martinez-Lage et al., 1996
	Canadian Pacific	28	7 m, 7 sm	+								Martinez-Lage et al., 1997
	Canadian Pacific	28									rDNA	Gonzalez-Tizon et al., 2000 b
Perna canaliculus °	New Zealand	30	1 m, 3 sm, 9 st, 2 t									Libertini et al., 1996
Perna perna	NW Gulf Mexico	28	10 m/sm, 4 st									Holland et al., 1999
Hormomya mutabilis ° *	Japan	30	1 m, 6 sm, 7 st, 1 t									Ieyama et al., 1994
Modiolus arcuatulus ° *	Egypt	24	5 m, 7 sm									Ghobashy et al., 1995
Modiolus barbatus °	North East Italy	32	6 m, 8 sm, 2 st									Libertini et al., 1996

Table 1. Continued 1.
Tableau 1 : suite 1.

Family/Species	Origin	2n	Karyotype	NORs	C	Fluo	RE	G	N	RB	FISH	References
Arcidae												
Barbatia fusca ° *	Egypt	38	2 m, 17 t									Ebied, 1999
Barbatia tenella ° *	Egypt	36	4 m, 14 t									Ebied, 1999
Scapharca subcrenata	Haiyang, China	38	9 m, 8 sm, 1 st, 1 t									Wang et al., 1998 b
Pteriidae												
Pinctada imbricata	Venezuela	28	9 m, 4 sm, 1 t									Marquez, 1992
Pinctada margaritifera	Egypt	28	5 m, 2 sm, 3 st, 4 t									Ebied, 1999
Pinctada radiata °	Egypt	26	5 m, 2 sm, 2 st, 4 t									Ebied, 1999
Ostreidae												
Ostrea angasi °	South Australia	20	5 m, 3 sm, 2 st	+	+							Li & Havenhand, 1997
Ostrea cucullata °	Quingdao, China	20	10 m									Wang et al., 1998 a
Ostrea edulis	La Tremblade, France	20		+								Thiriot-Quiévreux & Insua, 1992
Ostrea puelchana °	Argentina	20	4 m, 5 sm, 1 st	+								Insua & Thiriot-Quiévreux, 1993
Tiostrea chilensis °	Chile	20	7 m, 3 sm	+								Ladron de Guevara et al., 1994
Crassotrea angulata	Portugal	20	9 m, 1 sm	+				+				Leitao et al., 1999 a, b
Crassostrea ariakensis °	New Jersey, USA	20	8 m, 2 sm	+								Leitao et al., 1999 a
Crassotrea gasar °	Senegal	20	6 m, 4 sm	+								Leitao et al., 1999 a
Crassostrea gigas	La Tremblade, France	20		+								Thiriot-Quiévreux & Insua, 1992
	La Tremblade, France	20	10 m					+				Leitao et al., 1999 b
	Galway, Ireland	20									sat.DNA	Clabby et al., 1996
	Rutgers, USA	20									T	Guo & Allen, 1997 a
	Rutgers, USA	20	10 m								rDNA	Xu et al., 2001
Crassostrea rhizophorae	Venezuela	20	8 m, 2 sm									Marquez, 1992
Crassostrea virginica	Venezuela	20	6 m, 4 sm									Marquez, 1992
	Louisiana, USA	20	7 m, 3 sm									Zhang et al., 1999 a
	Louisiana, USA	20									rDNA	Zhang et al., 1999 b
	New Brunswick, Can.	20	8 m, 2 sm	+				+				Leitao et al., 1999 a,b
	Rutgers, USA	20	9 m, 1 sm								rDNA	Xu et al., 2001
Saccostrea commercialis °	Australia	20	8 m, 2 sm	+								Leitao et al., 1999 a
Saccostrea cucullata °	West Pakistan	20	10 m									Goswamy, 1992
Pectinidae												
Aequipecten opercularis °	Galicia, Spain	26	6 m, 7 t	+	+						rDNA	Insua et al., 1998
Argopecten purpuratus °	Chile	32	2 m, 14 st or t									Alvarez & Lozada, 1992
Euvola ziczac °	Venezuela	38	5 m, 6 sm, 7 st, 1 t									Basoa et al., 2000
Nodipecten nodosus °	Brazil	38	6 m, 6 sm, 7 st	+	+							Pauls & Affonso, 2000
	Venezuela	38	4 m, 5 sm, 7 st, 3 t									Basoa et al., 2000
Placopecten magellanicus °	St Lawrence R., Can	38	5 sm, 10 st, 4 t									Xiang et al., 1993

Table 1. Continued 2.
Tableau 1 : suite 2.

Family/Species	Origin	2n	Karyotype	NORs	C	Fluo	RE	G	N	RB	FISH	References
Anomiidae												
Anomia ephippium ° *	W Mediterranean	12	1 m, 2 sm, 3 st									Thiriot-Quiévreux, unpublished
Unionidae												
Hyriopsis cumingii °	China	38	12 m, 5 sm, 2 st		+							Wang et al., 2000
Unio conus ° *	Ukraine	38	11 m, 7 sm, 1 st									Melnychenko, 2000
Unio elongatus ° *	Egypt	28	10 m, 4 sm									Ebied, 1998
Unio pictorum *	Ukraine	38	13 m, 6 sm									Melnychenko, 2000
Mutelidae												
Mutela rostrata ° *	Egypt	20	2 m, 2 sm, 6 t									Ebied, 1998
Laseidae												
Lasaea australis ° *	Australia	36	4 m, 6 sm, 3 st, 5 t									Thiriot-Quiévreux, 1992
Lasaea colmani ° *	Australia	40	5 m, 9 sm, 5 st, 1 t									O Foighil & Thiriot-Quiévreux, 1999
Cardiidae												
Cerastoderma edule	Galicia, Spain	38	12 sm, 4 st, 3 t									Insua & Thiriot-Quiévreux, 1992
	Galicia, Spain										rDNA	Insua et al., 1999
Cerastoderma glaucum °	Baltic Sea	38	3 m, 10 sm, 6 st	+								Thiriot-Quiévreux & Wolowicz, 1996 a
	Sète, Mediterranean		4 m, 9 sm, 6 st	+								Thiriot-Quiévreux & Wolowicz, 1996 a
Mactridae												
Mactra chinensis °	Japan	38	9 sm, 9 st									Wada & Komaru, 1993
Spisula solidissima °	Magdalen Islands, Can.	38	4 m, 5 sm, 10 st/t									Xiang et al., 1993
Tresus capax °	Canadian Pacific	34	10 m, 7 sm								rDNA	Gonzalez-Tizon et al., 2000 b
Solenidae												
Solen constrictus ° *	Haiyang, China	38	15 m, 3 sm, 1 st									Wang et al., 1998 b
Tellinidae												
Macoma balthica *	Gdansk Bay, Baltic Sea	38	11 m, 2 sm, 6 st									Wolowicz & Thiriot-Quiévreux, 1997
Macoma nasuta ° *	Canadian Pacific	38	8 m, 6 sm, 5 st									Gonzalez-Tizon et al., 2000 b
Psammobiidae												
Nuttalia nuttallii ° *	Canadian Pacific	38	7 m, 12 sm								rDNA	Gonzalez-Tizon et al., 2000 b
Sinonovacula constricta °	Qingdao, China	38	13 m, 4 sm, 1 st, 1t	+		+						Wang et al., 1998 c
Corbiculidae												
Corbicula colorata ° *	Korea	38	1 m, 18 st									Park et al., 2000
Corbicula fluminalis ° *	Egypt	26	6 m, 7 sm									Ebied, 1998
Veneridae												
Ruditapes philippinarum	Haiyang, China	38										Wang et al., 1998 b
Venerupis pullastra °	Galicia, Spain	38	3 m, 8 sm, 8 st									Insua & Thiriot-Quiévreux, 1992
Venerupis rhomboides °	Galicia, Spain	38	4 m, 8 sm, 4 st, 3 t									Insua & Thiriot-Quiévreux, 1992
Myidae												
Mya arenaria °	Gdansk Bay, Baltic Sea	34	10 m, 7 sm	+								Thiriot-Quiévreux et al., 1998

reported by Nakamura (1985) and Thiriot-Quiévreux (1994), is here confirmed.

Most bivalve karyotypes known before 1992 included a majority of metacentric and submetacentric chromosomes. However, since the majority of bivalve species studied were of commercial importance, this may have biased cytotaxonomical comparisons within the bivalve class. Looking at the 49 new species investigated, 21 are without known commercial importance of which 13 show karyotypes with a majority of subtelocentric-telocentric chromosomes. Thus, as more species are examined, the variety of karyotypes is increasing.

The families Mytilidae and Ostreidae have been intensively investigated, showing for some species, such as *Mytilus galloprovincalis* or *Crassostrea virginica,* distinct karyotypes according to different authors. This may be due either to their different geographical origin, leading to intraspecific polymorphism, or to differences in the techniques used. The recent use of statistical methods applied to computer-based measurements of chromosomes has allowed accurate cytotaxonomic comparisons (Insua et al., 1994; Ladron de Guevara et al., 1996; Leitão et al., 1999a; Zhang et al., 1999a).

Positive silver staining Ag-NORs have been observed in 21 bivalve species since 1992. The number of NOR bearing chromosome pairs varies from one to three among the studied species. The chromosomal location of Ag-NORs in most species was terminal on the short or long chromosome arm. Among the species, the overall tendency was for Ag-NORs to be found on metacentric-submetacentric chromosomes which are the dominant type of chromosomes in studied bivalves (Insua et al., 2001). Intraspecific heteromorphism involving the number of active Ag-NORs per cell was detected in all species. It has been suggested that chromosomal Ag-NORs can serve as characters for inferring phylogenetic relationship, such that a single pair of chromosomal NORs may represent a plesiomorphic character (Amemiya & Gold, 1990). For example, among the Ostreidae, *Crassostrea gigas* may be considered a more primitive species than the other studied species of Ostreidae (Thiriot-Quiévreux & Insua, 1992).

Techniques of chromosome banding have been successfully employed in eight species with C-banding and in five species with fluorochrome staining. N-banding and restriction enzyme treatment have only been successful in *Mytilus galloprovincialis*. Chromosomal markers, such as Ag-NoR staining, C-banding and flurochrome staining, have allowed three species within *Mytilus* to be characterized at a cytogenetical level (Martínez-Lage et al., 1995, 1996). G-banding has been performed in *Mytilus galloprovincialis* and in three *Crassostrea* species*, C. gigas*, *C. angulata* and *C. virginica*, these latter showing specific G-banding patterns, allowing the individual identification of all chromosome pairs (Leitão et al., 1999). Replication banding pattern has been obtained in *Mytilus galloprovincialis* (Martínez-Expósito et al., 1994b) and in *Brachidontes rodriguezi* (Torreiro et al., 1999).

The chromosomal location of specific DNA sequences has been determined in several bivalve species mainly by fluorescence in situ hybridization (FISH). Satellite DNA was first employed as a probe in *Crassostrea gigas*, showing two distinct heterochromatic regions on two chromosome pairs (Clabby et al., 1996). Vertebrate telomere probes yielded strong hybridization signals in telomeres of *Mytilus galloprovincialis* and *Crassostrea gigas.* The chromosomal location of ribosomal RNA genes (rDNA) was performed for 5S rDNA in *Aequipecten opercularis* and *Cerastoderma edule* (Insua et al., 1999), while 18S-28S have been reported in eleven bivalve species (see Table 1 for references). Therefore, the data presented here is restricted to physical mapping of genes or DNA fragments within bivalve species. These results are far behind the cytogenetic progress in other organisms. For example, in humans, the application of FISH using specific-chromosome probes or whole chromosome probes has opened the way for comprehensive studies on chromosome abnormalities, especially in tumors (e.g. Tsukamoto et al. 2001).

Recent molecular studies in bivalves have provided gene sequences in bivalves (e.g. Frisher et al. 2000) which are clarifying taxonomic relationships (e.g. O Foighil et al., 1995) and provide new insights into phylogenetic inferences (e.g. Josefowicz & O Foighil, 1998; Canapa et al., 2000).

Genome size

Nuclear DNA content has been determined in 32 bivalve species (Table 2). The DNA content per diploid nucleus ranged from 1.82 pg in *Crassostrea gigas* to 3.94 pg for the venerid *Tapes philippinarum* (Gonzalez-Tizon et al., 2000) and 4.24 pg for *Lithophaga curta* (Ieyama et al., 1994). In a previous exhaustive study on 53 bivalve species (Hinegardner, 1974), the range of diploid DNA content (2C) was 1.38 to 4.12 pg looking at the same bivalve families as in Table 2.

Intra and interspecific variation of genome size was observed by Rodriguez-Juiz et al. (1996) who studied 20 individuals per species. There is a low correlation between nuclear DNA content and chromosome number (Méndez et al., 2001). For example, the DNA content (2.33 pg) of *Ostrea edulis* (2n= 20) is almost identical to that of *Spisula solidissima* (2.32 pg) (2n=36). Hinegardner (1974) stated that the more generalized molluscs tend to have a higher amount of DNA than the specialized species. But, according to González-Tizón et al. (2000), this assumption cannot be considered universal. Further studies on an increasing

Table 2: DNA content of bivalve species analysed since 1992.
Tableau 2: Contenu en ADN dans les espèces de bivalves étudiées depuis 1992.

Family/*Species*	Origin	2n	diploid DNA content pg	References
Mytilidae				
Aulacomya ater maoriana	New Zealand	unknown	2.24	Libertini et al., 1996
Limnoperna fortunei	Japan	30	2.96 *	Ieyama,1996
Mytilaster solidus	North East Italy	28	3.08 *	Libertini et al., 1996
Mytilus californianus	Canadian Pacific	28	3.21	Gonzalez-Tizon et al., 2000 b
Mytilus coruscus	Japan	28	3.80 *	Ieyama et al., 1994
Mytilus edulis	Northern Europe	28	3.42	Rodriguez-Juiz et al., 1996
Mytilus edulis eoteanus	New Zealand	28	3.20 *	Libertini et al., 1996
Mytilus galloprovincialis	Japan	28	2.70 *	Ieyama et al., 1994
	Galicia, Spain		3.84	Rodriguez-Juiz et al., 1996
Mytilus trossulus	Canadian Pacific	28	3.02	Gonzalez-Tizon et al., 2000 b
Perna canaliculus	New Zealand	30	2.22 *	Libertini et al., 1996
Septifer keenae	Japan	28	2.12 *	Ieyama et al., 1994
Septifer virgatus	Japan	28	2.16 *	Ieyama et al., 1994
Musculista senhousia	Japan	30	2.32 *	Ieyama et al., 1994
Lithophaga curta	Japan	32	4.24 *	Ieyama et al., 1994
Hormomya mutabilis	Japan	30	3.58 *	Ieyama et al., 1994
Modiolus auriculatus	Japan	32	3.36 *	Ieyama et al., 1994
Ostreidae				
Crassotrea gigas	Canadian Pacific	20	1.82	Gonzalez-Tizon et al., 2000 b
Ostrea edulis	Galicia, Spain	20	2.33	Rodriguez-Juiz et al., 1996
Pectinidae				
Chlamys hastata	Canadian Pacific	38	3.28	Gonzalez-Tizon et al., 2000 b
Chlamys opercularis	Galicia, Spain	26	2.23	Rodriguez-Juiz et al., 1996
Hinnites giganteus	Canadian Pacific	unknown	2.57	Gonzalez-Tizon et al., 2000 b
Pecten maximus	Galicia, Spain	38	2.83	Rodriguez-Juiz et al., 1996
Cardiidae				
Cerastoderma edule	Galicia, Spain	38	2.73	Rodriguez-Juiz et al., 1996
Mactridae				
Spisula solidissima	Galicia, Spain	36	2.32	Rodriguez-Juiz et al., 1996
Tresus capax	Canadian Pacific	34	3.27	Gonzalez-Tizon et al., 2000 b
Tellinidae				
Macoma nasuta	Canadian Pacific	38	3.90	Gonzalez-Tizon et al., 2000 b
Psammobiidae				
Nuttalia nuttallii	Canadian Pacific	38	3.48	Gonzalez-Tizon et al., 2000 b
Veneridae				
Protothaca staminea	Canadian Pacific	38	3.50	Gonzalez-Tizon et al., 2000 b
Ruditapes decussatus	Galicia, Spain	38	3.62	Rodriguez-Juiz et al., 1996
Tapes philipinarum	Canadian Pacific	38	3.94	Gonzalez-Tizon et al., 2000 b
Venerupis pullastra	Galicia, Spain	38	3.56	Rodriguez-Juiz et al., 1996
Venerupis rhomboides	Galicia, Spain	38	3.23	Rodriguez-Juiz et al., 1996

* : original values are given in haploid DNA content

number of species studied with the same techniques could help to elucidate if a trend exists within bivalves.

Aneuploidy

Aneuploid cells have been observed in natural populations of *Ostrea angasi* (Li & Havenhand, 1997) and of *Mytilus* (Martínez-Expósito et al., 1992). The study of chromosome loss in somatic cells of *Crassostrea gigas* has been extended to several populations (Thiriot-Quiévreux et al., 1992; Zouros et al., 1996). The consistency of the negative relationship between aneuploidy and growth rate has been observed over a ten year survey (Leitão et al., 2001b). Experimental evidence has suggested the existence of a genetic basis for the control of aneuploidy level (Leitão et al., 2001a). Evidence of differential chromosome loss has been demonstrated in aneuploid karyotypes. Only four out of the ten chromosome pairs of *C. gigas* are affected by the loss of one homologous chromosome (Leitão et al., 2001c). This differential susceptibility opens a field for new investigations.

Polyploidy

Natural polyploidy has been observed in *Argopecten purpuratus* (Alvarez & Lozada, 1992), *Sphaerium striatinum* (Lee, 1999) and *Corbicula* spp. (Park et al., 2000). In the genus *Lasaea*, australian polyploid clonal lineages share an exclusive common ancestor despite differences in developmental modes, polyploidy and reproductive modes (Ó Foighil & Thiriot-Quiévreux, 1999).

High chromosome numbers have been reported and related to neoplastic disorders in *Macoma balthica* (Thiriot-Quiévreux & Wolowicz, 1996b; 2001) and in *Mya arenaria* (Reno et al., 1994), or to polyploidy in *Mytilus trossulus* (González-Tizón et al., 2000a). Cytogenetic disturbances due to ecotoxic factors have also been observed in other bivalve species (Barsiene & Lovejoy, 2000).

Polyploidy has been induced in several commercially important bivalve species (Beaumont & Fairbrother, 1991). The main methods of ploidy assessment are chromosome counts, polar body counts, image analysis, flow cytometry, microfluorometry, nuclear size and electrophoresis. Only papers dealing with chromosome counts will be included in the following paragraph.

Chromosome counts were scored in 6-8 h embryos (Guo et al., 1994) and in three-month-old viable tetraploids of *Crassostrea gigas* (Guo & Allen, 1994a), these latter showing 67% tetraploids, the remaining being aneuploid, diploid, triploid and mosaics.

The effect of blocking polar body I complicates subsequent chromosome segregation (Guo et al., 1992) and has been reported in triploids (Guo & Allen, 1994b; Que et al., 1997) and tetraploids (Guo & Allen, 1997b) of *C. gigas*. Tetraploids showed more aneuploids than normal diploids (Guo & Allen, 1997b). According to Wang et al. (1999), oysters tolerate a number of aneuploids without obvious growth retardation in triploid production of *C. gigas*. Chromosome counts of induced triploids in the Chilean blue mussel, *Mytilus chilensis*, were scored in 20-hour-old embryos and showed a high proportion of aneuploids (Toro & Sastre, 1995). In the scallop *Chlamys ferreri*, patterns of chromosome segregation were observed in induced triploids and tetraploids, producing different ploidies in embryos (Yang et al., 2000a, b). Karyotype analyses of 6-hour–old embryos of *Pinctada fucata martensii* (3n x 2n cross) revealed high levels of aneuploidy, while ploidy examination of 4-month-old juveniles showed only diploid and triploid chromosome numbers indicating that aneuploid larvae had died (Komaru & Wada, 1994). Chromosome counts in induced tetraploids (one-year-old) in *Pinctada martensii* showed different levels of ploidy (He et al., 2000).

These studies highlight that ploidy manipulation of bivalves results in different proportions of aneuploids, diploids and polyploids, but the question remains to assess the threshold of tolerance of aneuploid conditions. Research on the accurate assessment of karyological features of triploid and tetraploid bivalves provide a direct method for ploidy verification.

Interspecific hybridization

Numerous attempts at hybridization in the genus *Crassostrea* have been reported (Gaffney & Allen, 1993) as well as naturally occurring hybrids in the genus *Mytilus* (e.g. Gardner, 1994), in *Mercenaria* (e.g. Bert & Arnold, 1995) and in scallops (Beaumont, 2000). Genetic or biochemical controls yield confirmation of hybrid status. Cytogenetic studies of bivalve hybrids are very rare. In hybrids of *Crassostrea virginica* x *Crassostrea corteziensis* and of *Crassostrea virginica* x *Crassostrea rhizophorae,* the hybrid karyotypes were close to the progenitors (Rodriguez-Romero & Gasca-Montes, 1995; 1998). Chromosomal examination of parents and offsprings in hybridization experiments may contribute to the confirmation of a hybrid status.

Acknowledgements

I would like to thank A. Insua and A. Leitão for constructive comments, and P. Chang and E. Houliston for their help in english editing.

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