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Arturo Aguirre-Velarde

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Arturo Aguirre-Velarde

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Sciences de l'environnement

La bioénergétique du pétoncle
péruvien (*Argopecten
purpuratus*) dans un contexte
environnemental limitant
en oxygène.

Thèse soutenue le 15 décembre 2016
devant le jury composé de :

Miguel Avendaño

Professeur, Université d'Antofagasta (Chili) / Rapporteur

Laurent BARILLÉ

Professeur, Université de Nantes / Rapporteur

Jocelyne FERRARYS

Directrice de recherche, IRD UMR ENTROPIE / Examinatrice

Frédéric JEAN

Professeur, UBO, CNRS, LEMAR - IUEM / Directeur de thèse

Gérard THOUZEAU

Directeur de recherche, CNRS, LEMAR - IUEM / Directeur de
thèse

Jonathan FLY SAINTE MARIE

Maître de Conférences, UBO, LEMAR - IUEM / Directeur de
thèse

UNIVERSITÉ DE BRETAGNE OCCIDENTALE - BREST
École doctorale des Science de la Mer - IUEM

Thèse de Doctorat de l'UNIVERSITÉ DE BRETAGNE OCCIDENTALE
Spécialité : Océanologie biologique

La bioénergétique du pétoncle péruvien (*Argopecten purpuratus*) dans un contexte environnemental limitant en oxygène

par

Arturo Aguirre Velarde

Composition du Jury

Miguel AVENDAÑO	<i>Professeur</i> , Université d'Antofagasta (Chili)	Rapporteur
Laurent BARILLÉ	<i>Professeur</i> , Université de Nantes, MMS	Rapporteur
Jocelyne FERRARIS	<i>Directrice de recherche</i> , IRD, UMR ENTROPIE	Examinatrice
Frédéric JEAN	<i>Maitre de Conférences</i> , UBO, CNRS, LEMAR-IUEM	Directeur de thèse
Gérard THOUZEAU	<i>Directeur de recherche</i> , CNRS, LEMAR-IUEM	Directeur de thèse
Jonathan FLYE-SAINTE-MARIE	<i>Maitre de Conférences</i> , UBO, LEMAR-IUEM	Directeur scientifique

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RÉSUMÉ

Au cours des deux dernières décennies, la culture du pétoncle (*Argopecten purpuratus*) s'est développée dans les baies côtières péruviennes. La disponibilité trophique liée au système d'upwelling est favorable à la production du pétoncle. Cependant, les côtes péruviennes sont également connues pour présenter une forte variabilité environnementale sur tout en domaine océanique. Bien que les élevages du pétoncle soient vulnérables aux aléas de production (mortalité, croissance faible), la variabilité environnementale dans les baies côtières du Pérou et ses effets sur la croissance, la reproduction et survie de cette ressource socialement sensible ont été peu étudiés. La baie de Paracas au Pisco-Pérou est une zone traditionnelle de culture du pétoncle où des hauts et des bas productifs liés aux conditions environnementales ont été enregistrées au long de son histoire. Dans le but d'approfondir nos connaissances sur cette problématique, cette étude se pose sous trois approches : (1) l'observation *in situ*, (2) l'expérimentation en physiologie et (3) la modélisation du bilan énergétique de *A. purpuratus*.

Un suivi environnemental mené dans la baie de Paracas montre que la variabilité océanographique peut être important, en particulier pendant l'été. Des variations de température de $\pm 8^{\circ}\text{C}$ et des conditions oxiques allant de la sursaturation à l'anoxie (absence d'oxygène) dans le cours d'une journée ont été observés. L'enregistrement haute fréquence a permis de révéler une exposition chronique, sévère et prolongée de la baie de Paracas aux conditions hypoxiques. Les pétoncles cultivés sur le fond, où l'exposition à l'hypoxie était importante (47 % du temps observé) ont montré une croissance et les conditions de reproduction plus faibles. Cependant, au cours de l'été, les événements hypoxiques prolongés et sévères ont touché les deux profondeurs de culture - les pétoncles cultivées en suspension comme sur le fond-, causant des pertes de poids de tissu somatique ainsi que l'arrêt de la reproduction. Durant les expériences en laboratoire, les pétoncles ont montré une importante capacité à réguler leur respiration face à la diminution de la saturation en oxygène jusqu'à $\approx 24\%$. De manière surprenante, nous avons trouvé que cette espèce est capable de maintenir une filtration, quoique diminuée, même à des saturations en oxygène basses (5%).

Sur la base des réponses physiologiques du pétoncle face à l'hypoxie et le rendement énergétique moindre du métabolisme anaérobie par rapport au métabolisme aérobie nous faisons l'hypothèse d'une diminution de l'ensemble du métabolisme à des saturations en oxygène en dessous de la capacité de régulation de l'espèce. Des simulations d'un modèle incluant cette restriction énergétique (sur les flux d'assimilation et de mobilisation de la réserve) en conditions d'hypoxie parviennent à reproduire avec succès les observations de terrain effectuées dans la baie de Paracas : une plus grande exposition à l'hypoxie a pour conséquence une croissance réduite et un arrêt de la reproduction.

Alors que le pétoncle possède des adaptations physiologiques/métaboliques pour faire face à des conditions limitantes en oxygène, la croissance et la reproduction peuvent être compromis, affectant ainsi la productivité des cultures de cette espèce (cela en fonction de la fréquence, durée et intensité de l'hypoxie). Les résultats des observations, des expériences et des simulations réalisées lors de cette étude fournissent des informations utiles pour mieux gérer la culture de pétoncle péruvien. Sur la base de ces travaux, des estimations de capacité de charge des baies, et des évaluations de zones et profondeurs favorables pour la culture de ces pétoncles pourront être réalisées.

Keywords: *Argopecten purpuratus* ; variabilité environnementale ; bioénergétique ; physiologie ; modélisation ; hypoxie ; aquaculture ; Pérou.

ABSTRACT

During the past two decades, the scallop (*Argopecten purpuratus*) culture developed in the Peruvian coastal bays. The trophic availability linked to the upwelling system supports the production scallop. However, the Peruvian coast are also known to have a high environmental variability especially in oceanic domain. Although scallop farms are vulnerable to production hazards (mortality, low growth), environmental variability in coastal bays of Peru and its effects on growth, reproduction and survival of this socially sensitive resource have been poorly studied. Paracas Bay in Pisco Peru is a traditional farming area where scallop highs and lows in productivity related to environmental conditions were recorded throughout its history. In order increase our knowledge on this issue, this study arises from three approaches : (1) observation *in situ*, (2) experimental physiology and (3) modelling of the energy budget of *A. purpuratus*.

An environmental monitoring conducted in the Paracas Bay shows that the oceanographic variability can be important, especially during the summer. Temperature variations of $\pm 8^{\circ}\text{C}$ celsius and oxic conditions ranging from supersaturation to anoxia (absence of oxygen) in the course of a day were observed. The high frequency monitoring has revealed a chronic, severe and prolonged hypoxic conditions in Paracas Bay . Scallops grown on the bottom, where exposure to hypoxia was important (47% of the observed time) showed lower growth and reproductions conditions. However, during the summer, prolonged and severe hypoxic events affected both deep culture - scallops grown in suspension and on bottom - causing weight somatic tissue losses and cessation of reproduction. During the laboratory experiments, scallops showed significant ability to regulate their oxygen uptake face to decreased oxygen saturation up to $\approx 24\%$. Surprisingly, we found that this species is able to maintain filtration, although diminished, even at low oxygen saturations (5%).

Based on the physiological responses of the Peruvian scallops face to hypoxia and the energy performance aerobic and anerobic metabolism ; it is hypothesized that there exist a restriction in the energy flow available for metabolism at oxygen saturations below the regulation capacity of the organism. Model simulations including this energy restriction (on assimilation and reserves mobilization fluxes) against hypoxia can reproduce successfully field observations of Paracas Bay : greater exposure to hypoxia results in a reduced growth and reproductive conditions.

Although the scallop has physiological adaptations/metabolism to deal with limited oxygen conditions, growth and reproduction can be compromised, affecting culture productivity of this species (according to the frequency, duration and intensity hypoxia). The results of observations, experiments and simulations obtained during this study provide useful information to better manage of Peruvian scallop cultures (ex. Load capacity estimates in the bays, evaluations of adequate areas/depths for culture, etc.).

Keywords: *Argopecten purpuratus* ; environmental variability ; bioenergetics ; physiology ; modelling ; hypoxia ; aquaculture ; Peru.

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Chapitre 1

Introduction

Au Pérou, l'histoire de l'aquaculture marine peut être racontée à travers l'histoire du pétoncle péruvien. De nos jours, les pêcheurs qui sont devenus aquaculteurs associés à des entreprises privées, ont réussi à mettre en place une activité de production importante dans le secteur alimentaire. De grandes exploitations aquacoles sur la côte péruvienne se sont développées au cours des 20 dernières années. Deux systèmes de culture sont principalement utilisés : l'élevage sur le fond marin (dans les enclos en filet) utilisé essentiellement par les pêcheurs et l'élevage dans des cages suspendues ("long-line") utilisé par des entreprises privées. L'aquaculture de pétoncle a profondément modifié l'économie de certaines zones côtières en devenant une source d'emplois et de revenus majeure pour les populations locales (ex. Sechura, Casma). Une chaîne de production qui comprend la fourniture des semis jusqu'à l'exportation vers les marchés européen et nord-américain sous forme de produits congelés a généré un secteur économique très dynamique. En 2013 l'exportation nationale a représenté 159 millions de Dollars américains (PRODUCE, 2015) et 25000 emplois rien que dans la région de Piura. Cependant, bien qu'il existe des conditions qui ont favorisé la croissance de cette activité comme la productivité phytoplanctonique naturelle disponible, il y a aussi des facteurs qui ont nui aux cultures de pétoncle. Des faibles productivités et survie des élevages ont été enregistrées dans certaines zones de culture comme les baies de Paracas, Sechura et Samanco (Comunidades IMARPE). En fait, c'est une activité très vulnérable aux aléas de l'environnement (ex. El Niño, marées rouges, anoxies). En plus, des épisodes de mortalités massives ont été enregistrés dans les principales zones de production telles que les baies de Paracas et Sechura depuis le début de l'activité aquacole (González-Hunt, 2010) avec des conséquences économiques graves pour les producteurs de pétoncle. Malgré cela, les variables environnementales qui affectent la croissance, la reproduction et la survie du pétoncle dans les zones de production sur la côte péruvienne sont peu étudiées et encore mal connues.

La variabilité environnementale le long de la côte péruvienne peut être très importante. Dans des conditions "normales", des eaux côtières froides (14-18°C) prédominent. Cette eau froide provient du transport vertical à la côte d'eau profonde en surface par effet de l'upwelling généré par les alizés le long de la côte péruvienne. Cependant, sporadiquement, les vents faiblissent, en conséquence l'upwelling s'arrête et la côte péruvienne est alors envahie par des eaux tropicales chaudes (> 23°C). Ces conditions sont connues comme les événements El Niño (ENSO). Des études comparatives ont montré que les conditions ENSO sont favorables aux populations de pétoncles par rapport aux périodes d'eaux froides (La Niña), au moins dans le centre-sud Pérou et le nord du Chili. Des taux de croissance, de reproduction et de recrutement impor-

tants ont été enregistrés lors des périodes chaudes (Wolff, 1988; Mendo et Wolff, 2003; Avendaño et Cantillánez, 2005; Mendo *et al.*, 2008; Avendaño *et al.*, 2008a). En effet, historiquement des débarquements importants de pétoncles sont liés aux événements El Niño. Wolff (1987) a émis l'hypothèse que cet effet positif pourrait être dû à l'origine tropicale de cette espèce. Cependant, au jour d'aujourd'hui, la production dans les années "normales" (i.e. sans épisodes El Niño ou La Niña) surpasse celle d'années El Niño grâce à la contribution de l'aquaculture. D'autre part, il existe des preuves d'une variabilité de l'environnement côtier qui ne serait pas liée à El Niño. Sears (1954) a observé dans la baie de Paracas (zone traditionnelle d'élevage de pétoncle) des fluctuations de température dans une plage de 10°C sur une échelle de temps hebdomadaire. Ces enregistrements mettent en évidence l'importante variabilité des conditions océanologiques à laquelle le pétoncle est confronté dans son environnement naturel. Curieusement, la dynamique environnementale dans les baies côtières du Pérou a été jusqu'ici peu étudiée.

La Bioénergétique, discipline qui permet d'étudier les flux d'énergie chez les organismes, peut nous aider à mieux comprendre l'effet de la variabilité environnementale sur les processus métaboliques tels que la croissance, la reproduction, la respiration, etc. Kooijman (2010a) avec la théorie du "Dynamic Energy Budget" (DEB) propose un modèle dynamique capable de représenter le cycle de vie d'un organisme. Ce modèle reproduit les variations de multiples flux d'énergie et de la masse en fonction des variations de l'environnement (disponibilité trophique et température). Cet outil a été utilisé pour la réalisation du travail présenté ici afin d'évaluer les conséquences bio-énergétiques de la variabilité de l'hydroclimat de la côte péruvienne sur le pétoncle. En ce sens, ce manuscrit fournit des informations sur les effets des stress métaboliques ou physiologiques qui peuvent être utiles pour la gestion des populations cultivées du pétoncle péruvien.

1.1 Le pétoncle péruvien : science, économie et société

1.1.1 Biologie du pétoncle péruvien

Le pétoncle péruvien, également nommé pétoncle chilien, *Argopecten purpuratus* (Lamarck, 1819), appartient à la famille des *Pectinidés* (Rafinesque, 1815) dont la position systématique est détaillée ci-dessous. Il est généralement nommé "concha de abanico" signifiant littéralement "coquille d'éventail", par les péruviens ou "ostion del norte" par les chiliens du fait de sa répartition géographique.

Embranchement	<i>Mollusca</i>
Classe	<i>Bivalvia</i> (Linné, 1758)
Subclass	<i>Pteriomorphia</i> (Beurlen, 1944)
Ordre	<i>Pectinoidea</i> (Gray, 1854)
Superfamily	<i>Pectinoidea</i> (Rafinesque, 1815)
Famille	<i>Pectinidae</i> (Rafinesque, 1815)
Genus	<i>Argopecten</i> (Monterosato, 1889)
Species	<i>Argopecten purpuratus</i> (Lamarck, 1819)

Le pétoncle péruvien (*Argopecten purpuratus*, Lamarck 1819) est un bivalve épibenthique (fixé ou posé sur le fond). Cette espèce est caractérisée par des valves solides, modérément convexes avec une couleur allant du blanc au rose, brun, violet ou une

combinaison de ceux-ci (Fig. 1.1). Il est distribué principalement le long des côtes péruviennes et du nord du Chili (Pacifique Sud-Est) (Rombouts, 1991). Il habite les baies semi-protégées à substrat sédimentaire (Brand, 1991) avec une préférence pour les fonds sableux à faible courant (Avendaño et Le Pennec, 1996). Cependant, il peut être trouvé sur les fonds vaseux et fixé sur les macroalgues pour les juvéniles (Navarro *et al.*, 1991). On le trouve à des profondeurs comprises entre 2 et 40 mètres (Valdivieso et Alarcón, 1985) et à des salinités variant entre 33 et 35 PSU (Osorio, 2002). *A. purpuratus* peut être trouvé dans des eaux dont la température varie entre 12 et 25°C et son importante capacité d'acclimatation thermique a été soulignée par certains auteurs (Navarro *et al.*, 2000). Comme la plupart des bivalves, le pétoncle péruvien, se nourrit en filtrant la matière particulaire en suspension dans l'eau (seston). Ce qui comprend du phytoplancton mais également des particules inertes de détrit, d'origine organique ou inorganique (pour les Pectinides en general, Shumway et Parsons, 2011).



FIG. 1.1: Le pétoncle péruvien *Argopecten purpuratus* : illustration de la forme et de la variabilité de couleur de valves ainsi que des tissus mous (M : muscle, G : gonade, Ma : manteau, V : valve)

Le pétoncle péruvien est un hermaphrodite simultané (Avendaño *et al.*, 2001), qui atteint sa maturité sexuelle à une hauteur coquillière d'environ 25 mm (Mendo *et al.*, 1989), bien que Disalvo *et al.* (1984) aient trouvé du matériel gonadique dès 13 mm. A partir de la première maturation, des gonades développées peuvent être observées tout au long de l'année, avec des cycles de ponte plus ou moins synchrones (Chavez et Ishiyama, 1989). Il est difficile de trouver une étape de repos sexuel ainsi que des individus matures présentant des gonades entièrement vides (Disalvo *et al.*, 1984). Des études histologiques démontrent que la ponte chez le pétoncle péruvien est partielle, les régions de la gonade vidangées étant rapidement remplacées par de nouveaux gamètes (Brown et Guerra, 1980; Avendaño et Le Pennec, 1996). Au Chili les pontes montrent une certaine saisonnalité, du printemps au début de l'automne (Avendaño et Le Pennec, 1996; Avendano et Le Pennec, 1997). Cependant, (Wolff, 1988) indique que *A. purpuratus* en baie de Paracas pond toute l'année avec un pic à la fin de l'été et durant l'automne. Le recrutement présente des fortes variations inter-annuelles. Avendaño *et al.* (2008b) a observé une survie plus importante de post-larves fixées dans des collecteurs près de la surface par rapport au collecteurs situés plus profonds (Avendaño *et al.*, 2008b). Dans un suivi de captations avec des collecteurs artificiels dans la Baie d'Indépendance, Bandin L. et Mendo (1999) ont montré qu'il existait deux périodes importantes de fixation des postlarves : 1) pendant tout l'été (surtout de février à mars) et 2) à la fin de l'automne et la première moitié de l'hiver. L'addition du substrat sur le fond pourrait améliorer la fixation de post-larves (Pacheco et Stotz, 2006).

Cycle de vie

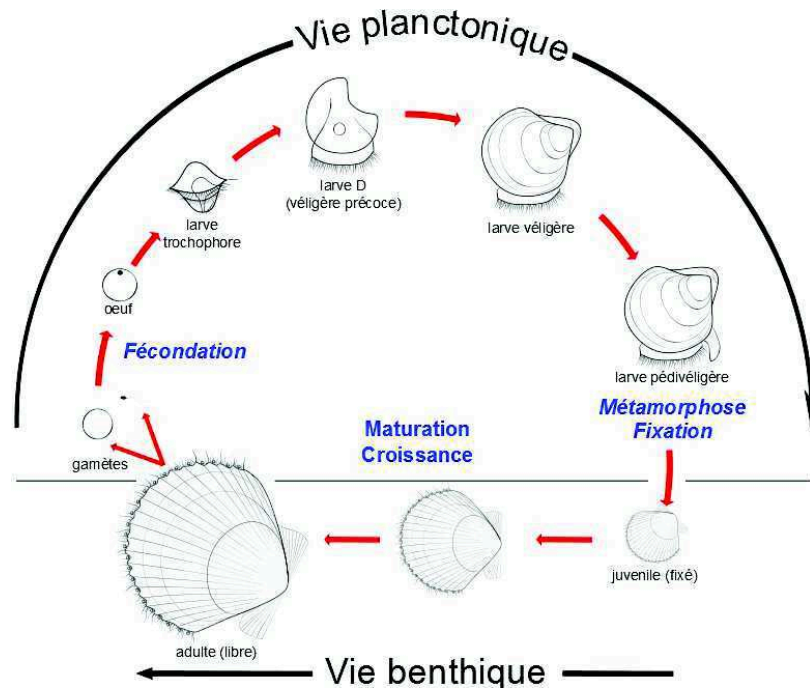


FIG. 1.2: Le cycle de vie benthopélagique d'*A. purpuratus*

Comme l'immense majorité des bivalves, *A. purpuratus* présente un cycle de vie benthopélagique, c'est à dire que son cycle se divise en une phase larvaire pélagique suivie d'une phase post-métamorphique benthique comme illustré dans la Fig. 1.2. Les gamètes sont émis dans la masse d'eau ; la fécondation est externe et est dite ovulipare. Le stade larvaire, durant lequel se succèdent les stades trochophore, larve D, véligère puis pédivéligère, a une durée d'environ 30 jours. Toutefois la durée de ce cycle est influencée par la température et la disponibilité trophique (Wolff *et al.*, 1991). La vie benthique est initiée par la fixation, correspondant au moment où la post-larve se fixe sur le fond à l'aide d'un filament appelé byssus. Dès le stade juvénile, malgré la fixation sur le substrat, *A. purpuratus* est capable d'une certaine mobilité, permettant par exemple de fuir un prédateur (Navarro, 2002).

1.1.2 Quelques éléments de l'écologie du pétoncle péruvien

Répartition géographique

Argopecten purpuratus est une espèce inféodée à la cote pacifique de l'Amérique du sud (Fig. 1.3). Sa répartition géographique s'étend de 12°30' au Nord jusqu'à 33°02' au Sud (González *et al.*, 2002), soit une vaste répartition latitudinaire comprenant des zones tropicales et tempérées. Cependant, sa distribution est associée à des conditions d'upwelling du système de Humboldt, i.e. des eaux productives et relativement froides (14-18°C). Pendant les années 90, le pétoncle péruvien a été introduit dans les régions du sud du Chili (jusqu'à 42°Sud) pour la culture (Uriarte *et al.*, 1996; Uriarte et Farias, 1999). Cependant, ces cultures n'ont jamais été économiquement rentables. En 2008, le pétoncle péruvien a été introduit en Chine (Qingdao, 36°Nord) où des travaux sont

effectués sur l'hybridation avec un autre pétoncle *Argopecten irradians irradians* (Wang *et al.*, 2011; Hu *et al.*, 2013)



FIG. 1.3: Répartition géographique du pétoncle péruvien (González *et al.*, 2002)

Influence de l'environnement sur la croissance, la reproduction et la physiologie

Le pétoncle péruvien est une espèce présentant une croissance relativement rapide. Cette dernière est sans doute favorisée par l'importante productivité primaire générée par le système d'upwelling côtier de Humboldt, connu comme étant l'un des plus productifs au monde. La taille (hauteur) maximale atteinte par cette espèce au Pérou est d'environ 110 mm (Wolff, 1987; Mendo et Jurado, 1993) tandis que Disalvo *et al.* (1984) au Chili documentent des individus atteignant 160 mm. La croissance individuelle d'*Argopecten purpuratus* a été étudiée le long des côtes péruviennes et chiliennes (Wolff, 1987; Yamashiro et Mendo, 1988; Mendo et Jurado, 1993; Stotz et Gonzalez, 1997; Skrabonja et Mendo, 2002; Avendaño D *et al.*, 2007; Cantilláñez *et al.*, 2007; Avendaño *et al.*, 2008a; Tarazona *et al.*, 2007) où on constate des variations latitudinales et temporelles. La plupart de ces études sont basées sur l'analyse de cohortes, le

marquage individuel a plus rarement été utilisé. Souvent un effet positif de la température sur la croissance a été constaté. Mendo *et al.* (2016) à l'aide d'une méta-analyse montre que les performances de croissance (ϕ , voir Pauly et Munro, 1984) sont expliquées à 90% par la température. Thébault *et al.* (2008) ont également observé un effet positif de la température sur la croissance coquillière, alors que des concentrations élevées de matière organique en suspension ont un effet négatif. En outre, le cycle lunaire pourrait avoir une influence sur la croissance. Des comparaisons des systèmes de culture montrent une meilleure croissance chez les pétoncles cultivés en suspension dans la colonne d'eau en comparaison avec ceux élevés sur le fond (Mendo et Jurado, 1993; Aguirre, 2008; Alcazar et Mendo, 2008). Bien que peu de données environnementales soient disponibles pour ces études, Aguirre (2008) attribue la différence de croissance entre les systèmes de culture à la qualité du phytoplancton disponible à chaque profondeur d'élevage. Des différences phénotypiques de la croissance ont été enregistrées par Wolff et Garrido (1991) en fonction de la couleur des valves : des pétoncles de couleur jaune ont montré une croissance inférieure par rapport à ceux de couleur «normale».

Il existe plusieurs facteurs qui influent sur la reproduction des pétoncles notamment la température et la ressource trophique (Shumway et Parsons, 2011). À cet égard, Wolff (1987); Cantillanez *et al.* (2005) ont observé que l'activité reproductrice s'intensifie dans des conditions de température élevée (6-8°C au-dessus la moyenne) durant un événement El Niño. Au cours de ces événements des pontes massives liées à l'augmentation de la température ont été enregistrées. Illanes *et al.* (1985) ont observé dans la baie de Tongoy (Chili) que les températures élevées favorisent la reproduction du pétoncle en produisant la vidange totale des gamètes. L'effet positif des conditions chaudes liées à El Niño sur la croissance et la reproduction de *Argopecten purpuratus* est attribué à ses origines phylogénétiques tropicales/subtropicales (Wolff, 1987). D'autre part, Brown et Guerra (1980) indiquent que la maturation de la gonade du pétoncle dépend directement de la disponibilité en nourriture.

A. purpuratus a la capacité de réguler ses taux physiologiques sur une plage de température comprise entre 16 et 20°C (Navarro *et al.*, 2000). Cependant, Dionicio-Acedo et Flores-Mego (2015) trouvent un effet significatif de la température sur la consommation d'oxygène et le taux de filtration dans la gamme 17-22°C. D'autre part, la composition du régime alimentaire a un effet sur la consommation d'oxygène et sur les taux de filtration et d'ingestion. Navarro *et al.* (1993) et Farias *et al.* (1997) sont d'accords sur le fait que l'augmentation de la qualité de la ressource trophique maximise le gain d'énergie chez *A. purpuratus* grâce à une optimisation des différents paramètres d'alimentation, comme la filtration et l'efficacité d'absorption. En ce qui concerne l'excrétion, Diaz et Martinez (1992) n'ont trouvé aucune différence du taux d'excrétion chez juvéniles d'*A. purpuratus* soumis à des régimes alimentaires composés de différentes combinaisons de microalgues. Une situation similaire a été décrite par Farias *et al.* (1997) chez des adultes pour lesquels aucune corrélation significative entre l'excrétion d'ammonium et la teneur en protéines de la nourriture n'a été observée. Enfin, la salinité aurait un effet significatif sur le bilan énergétique de *A. purpuratus*. Des salinités inférieures à 30 réduisent considérablement l'énergie disponible pour la croissance (scope for growth, Navarro et Gonzalez, 1998).

1.1.3 Brève histoire de l'aquaculture du pétoncle péruvien

L'exploitation de gisements naturels de bivalves sur la côte péruvienne est aussi vieille que les premiers établissements humains dans cette région du monde soit d'en-

viron 10000 ans (Rostworowski de Diez Canseco, 1981). De grands amas coquilliers ont été trouvés sur des sites archéologiques. La présence de valves d'*A. purpuratus* confirme l'importance de ce bivalve en tant que ressource alimentaire des civilisations péruviennes pré-colombiennes (Sandweiss *et al.*, 1989).

Son utilisation comme ressource de subsistance a perduré pendant plusieurs milliers d'années jusqu'à la fin du XIXe siècle, lorsqu'il est apparu de façon régulière sur le marché de la région de Lima (capitale du Pérou). Il est probable que l'arrivée d'immigrants pêcheurs italiens, qui ont importé l'utilisation de la drague comme pratique de pêche du pétoncle, a permis d'approvisionner le marché local de façon importante durant cette période (Murphy, 1925). Cependant, l'exploitation intensive de cette ressource a conduit à plusieurs événements de surexploitation des populations naturelles au cours de l'histoire. Des rapports qui datent de la première décennie du XXe siècle indiquent que dans la région de Callao (proche de Lima), on pensait que le stock de pétoncle péruvien avait été épuisé au moins à deux reprises (Coker, 1907). Plus tard, Ancieta (1952) suggère sa disparition dans la zone de Callao. Ces informations tendent à indiquer que l'espèce a connu des cycles d'abondance et de raréfaction. Selon Schweigger (1947), la pêche commerciale du pétoncle a commencé dans la région de Pisco-Paracas aux alentours des années 30. Il semble que jusqu'au début de la première décennie du XXe siècle, la pêche s'est faite exclusivement à la drague. Ensuite, au cours des années 50, la pêche en plongée semi-autonome au narguilé (compresseur en surface qui envoie de l'air au plongeur à travers un tuyau flexible) aurait été introduite dans les régions de Callao et Pisco-Paracas (Vildoso et Chirichigno, 1956; Espezuá, 1985). L'utilisation de ces deux pratiques de pêche a continué jusqu'au début des années 70 pendant lesquelles la pratique de la drague a complètement disparu (Buse, 1973). Depuis les années 1970, la région de Pisco-Paracas a vu son activité de pêche augmenter jusqu'à devenir la plus importante en termes d'extraction d'espèces de bivalves, et le principal fournisseur du marché de Lima (Ysla, 1987). Actuellement, la pêche du pétoncle représente 80% de l'extraction totale de mollusques benthiques sur la côte péruvienne (PRODUCE, anuario 2014).

l'histoire de la culture du pétoncle péruvien est étroitement liée aux derniers grands événements El Niño des années 1982-83 et 1997-98. D'après Wolff (1984), à la fin des années 70, une famille de pêcheurs de la baie de Paracas (Région de Pisco) aurait commencé à collecter des coquillages pour les placer sur le fond de la baie à l'intérieur d'enclos jusqu'à atteindre la taille commerciale. L'expérience a été couronnée de succès, et en septembre 1982 des entrepreneurs privés ont investi dans cette activité dans la région. En l'absence de législation, c'est à cette époque que le gouvernement a publié divers règlements dans l'optique de promouvoir et de gérer le développement de la mariculture de pétoncles. Le système de culture sur le fond alors pratiqué passait par la construction d'un enclos en utilisant un filet de pêche à l'anchois sur une hauteur de 1 à 2 m. Dans ces enclos, des pétoncles de taille comprise entre 20 et 40 mm capturés sur des banc naturels sont semés jusqu'à atteindre la taille commerciale (> 60 mm). A l'apogée de cette pratique, après le "boom" associé à l'événement El Niño 1982-83, il existait 181 fermes aquacoles dans la baie de Paracas (PRODUCE). En Février 1985, la production a connu une fin brusque due à la mortalité massive des pétoncles associée à la détérioration des conditions environnementales dans la baie de Paracas à cause de déversements d'eaux usées provenant d'une usine de fabrication de farines de poissons. Après cet épisode la production aquacole a été abandonnée et elle ne reprit que lors de l'événement El Niño 1997-98. A cette période toutes les aires d'élevage disponible à Paracas sont mises en production. Toutefois, la production est retombée

quelques années plus tard. Au cours de cette période, également des efforts de gestion et de repeuplement de populations naturelles sont faites (Stotz et Mendo, 2001). Au cours de la dernière décennie du XXe siècle, une nouvelle pratique culturelle, d'origine japonaise, a été introduite : il s'agit de la culture suspendue, utilisé largement sur la côte chilienne (Avendano *et al.*, 2001), qui a permis une reprise de cette activité par des entreprises privées principalement localisées dans la région d'Ancash. Au cours de cette période, bien que la production de l'aquaculture ait été soutenue par le recrutement naturel (des collecteurs de postlarves ont été utilisés) quelques écloséries ont vu le jour. Parallèlement, les pêcheurs de la région de Pisco (Sud) ont migré vers la baie de Sechura (Piura, limite nord de répartition de l'espèce) initiant ce qui constitue aujourd'hui la plus grande zone de production aquacole au Pérou. Dans cette région, il existe environ 150 associations de pêcheurs qui sont engagées dans la culture du pétoncle péruvien (PRODUCE, 2014).

Aujourd'hui, la production de *A. purpuratus* se développe principalement dans les régions de Piura, d'Ancash et d'Ica, atteignant 55100 tonnes (Fig. 1.4) qui représentent environ 115 millions de dollars américains en 2014 (PRODUCE, 2016). La production aquacole dépasse aujourd'hui à la pêche du pétoncle péruvien comme au Chili à la fin des années 90 (Stotz, 2000). Cette production constitue donc une activité économique importante si l'on prend à la fois en compte l'activité aquacole, la transformation des produits frais et l'exportation, et a une importance sociale considérable. Les marchés principaux sont l'Europe, France principalement, et les États-Unis. Cependant l'histoire a montré que cette activité est particulièrement sensible aux conditions environnementales qui peuvent perturber la production. En outre actuellement, des tensions sociales liées à l'exploitation des hydrocarbures se font jour, liées aux conflits d'usages des zones marines côtières.

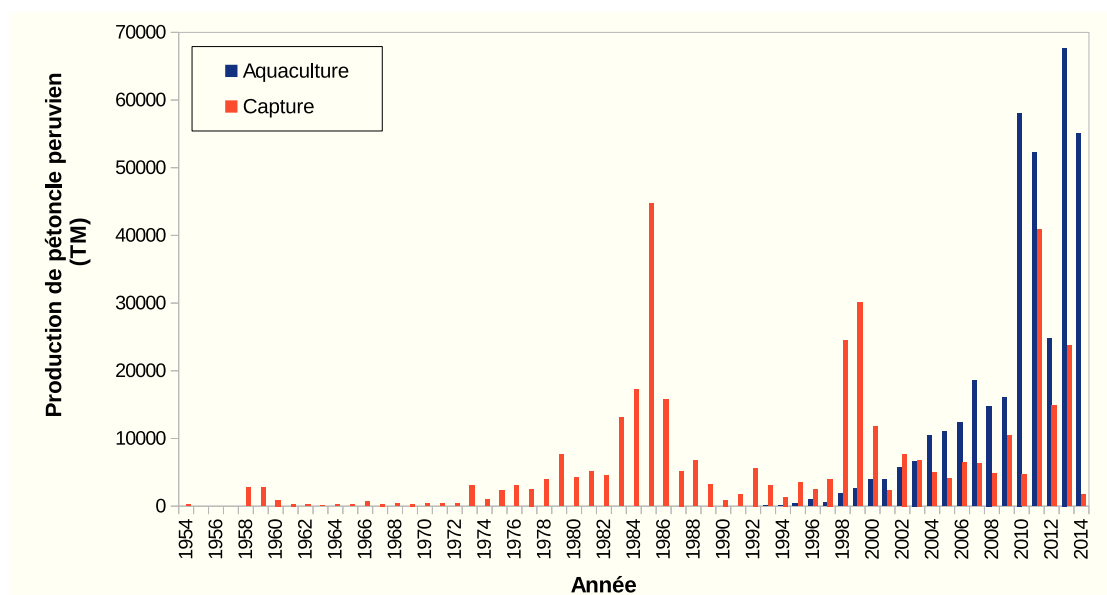


FIG. 1.4: Évolution de la production totale du pétoncle péruvien par pêche et aquaculture au Pérou entre 1954 et 2015 (PRODUCE, 2015)

1.2 L'upwelling côtier péruvien : productif mais pauvre en oxygène

Le Pacifique sud est caractérisé par la présence d'une cellule anticyclonique qui génère des vents longeant les côtes péruviennes, du sud vers le nord en direction de l'équateur, également appelés alizés. Ces vents poussent les eaux de surface vers le large, forçant ainsi les eaux situées en profondeur à remonter (Ekman, 1905). Ce phénomène s'explique par le principe d'Ekman appliquée au bord Est des bassins océaniques et qui donne une relation entre la tension de vent parallèle à la côte et le transport d'eau vers le large. En effet, la composante parallèle à la côte et dirigée vers l'équateur génère un transport vers l'Ouest perpendiculaire à la côte. La zone côtière constitue alors une zone de divergence des eaux de surface. Les masses d'eaux situées en profondeur, plus froides, remontent par conséquent en surface afin de remplacer les eaux de surface divergentes. Cette remontée d'eau s'accompagne d'une remontée des isothermes côtières et de la thermocline. Ce processus, appelé upwelling côtier, se caractérise par l'affleurement d'eaux profondes, froides et riches en nutriments qui entrent dans la zone euphotique, générant ainsi une production primaire importante (Fig. 1.5a). Dans cette zone, l'abondance de phytoplancton soutient d'importantes biomasses de niveaux trophiques supérieurs (zooplancton, poissons, mollusques...). Une position géographique proche de l'Équateur favorisant le rayonnement solaire nécessaire pour la photosynthèse, une saisonnalité peu marquée et l'orientation de la côte sont des caractéristiques qui font des côtes péruviennes l'une des zones de pêche les plus productives au monde. Cependant, ce système océanographique est soumis à une variabilité importante associée au phénomène El Niño, qui a pour conséquence l'affaiblissement des vents et un arrêt de l'upwelling avec des conséquences écologiques/trophiques dramatiques. Lors d'un événement El Niño, les eaux tropicales chaudes envahissent la côte péruvienne et la productivité primaire chute en raison de la limitation en nutriments. Par conséquent, la variabilité environnementale interannuelle voire interdécennale peut être importante.

Si cette productivité importante est capable de soutenir durant les années «normales» une capture de petits pélagiques très importante, la pêche de bivalves n'est pas négligeable non plus (environ 55100 tonnes/an). Cette abondance en phytoplancton grâce à l'upwelling côtier a également soutenu le développement de la culture d'*A. purpuratus* au cours des dernières années. D'autre part, les processus de dégradation de la matière organique qui se dépose en dessous de la zone photique (où il y a une production nette d'oxygène par photosynthèse) consomment rapidement l'oxygène dissous. En conséquence, alors qu'il y a une forte productivité dans les eaux côtières peu profondes, en profondeur il existe une zone à minimum d'oxygène (OMZ, acronyme en anglais) très étendue (Fig. 1.5). Ceci a des implications écologiques fortes qui limitent la répartition des espèces benthiques et pélagiques. L'OMZ au Pérou est relativement peu profonde (< 50m). En l'absence d'oxygène, un processus de dégradation anaérobie de la matière organique peut se produire avec la production de sulfure toxique (H_2S). Le même transport vertical de l'upwelling peut conduire ces eaux pauvres en oxygène et chargées en H_2S à la surface provoquant des impacts négatifs sur les organismes, y compris des mortalités massives. Des images satellites ont permis d'identifier un énorme panache de H_2S dans les environs de la baie de Paracas. Il a été suggéré que l'événement serait lié au transport des eaux profondes par l'upwelling (Schunck *et al.*, 2013).

Dans le contexte du changement climatique et de l'industrialisation, une augmentation des événements à faible teneur en oxygène (hypoxie) est attendue (Levin *et al.*, 2009; Zhang *et al.*, 2010). L'augmentation de la température, l'utilisation intensive d'en-

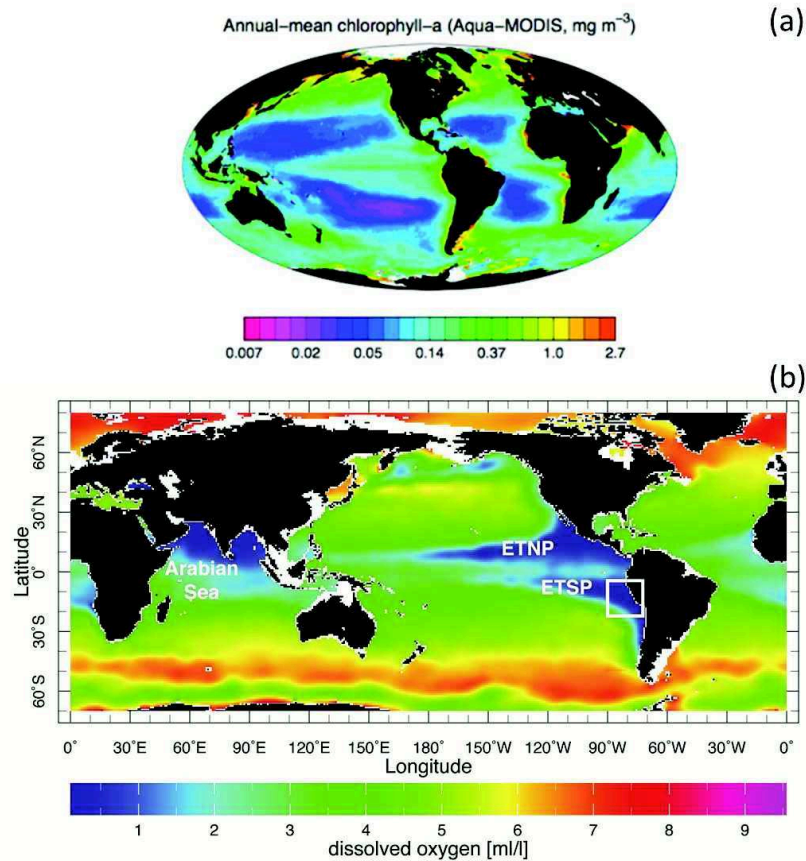


FIG. 1.5: Concentration moyenne de chlorophyll-a (a) et répartition des zones à minimum d'oxygène (OMZ) dans les océans (b). Source : World Ocean Atlas 2009.

grais et d'autres perturbations écologiques augmenteraient le risque d'événements hypoxiques côtiers. Au même temps, l'oxygène dissous dans les OMZ diminue provoquant son expansion horizontale et verticale (Gewin, 2010). En outre, on s'attend dans les zones d'upwelling à une augmentation du transport vertical en réponse à l'intensification des vents (voir Bakun *et al.*, 2010). Cela pourrait entraîner qu'un plus grand volume d'eau dépourvu en oxygène soit pompé vers la surface. Les conséquences d'une limitation accrue en oxygène pourrait avoir des effets négatifs sur les écosystèmes et les ressources exploitées comme *A. purpuratus*.

Étudier les effets des conditions hypoxiques sur *Argopecten purpuratus* permettra d'élaborer des stratégies de production et d'adaptation des pratiques conchylicoles face aux changements climatiques visant à assurer la sécurité alimentaire de la région. En outre, l'étude des organismes benthiques habitant les écosystèmes du Pérou (naturellement soumis à des événements hypoxiques) peut nous aider à comprendre les défis que d'autres organismes marins devront relever ailleurs à l'avenir.

1.3 La baie de Paracas

Dans la baie de Paracas (province de Pisco, département de Ica, Pérou) l'histoire de l'élevage du pétoncle péruvien commence dans les années 80 (Wolff, 1984). Depuis cette date, l'activité aquacole dans cette baie a connu des périodes bonnes (liées à El Niño) et mauvaises (faible recrutement de naissain et mortalités massives). À l'heure actuelle, la production du pétoncle dans la baie n'est pas très importante ; cependant,

les fort taux de croissance et la bonne maturation gonadique dans cette baie ainsi que la facilité de gestion des parcs (accessibilité, entretien et surveillance) permettent de maintenir cette activité dans la zone. D'autre part, la baie de Paracas a de multiples usages en dehors de la mariculture. Des activités liées à la pêche, au tourisme et au port de commerce sont recensées dans la baie. En outre, l'extrême Sud-ouest de la baie se trouve dans une aire protégée (Reserva Nacional de Paracas). Les bords sud et ouest sont plutôt inhabités tandis que sur la côte orientale se situent le village de Paracas, des hôtels et un port de pêche/touristique.

Paracas est une baie semi-fermée, ouverte vers le nord, avec une importante productivité biologique favorisée par l'upwelling environnant. Elle est située entre les parallèles 13°47'48" et 13°51'58" de latitude sud, dans l'extrémité sud de la baie de Pisco. La baie est bordée à l'Ouest et au Sud par la péninsule de Paracas (terrain escarpé avec une altitude maximale de 200m), à l'Est elle est délimitée par le continent. Sa ligne de côte s'étend sur environ 24 Km et sa superficie est d'environ 36 Km². Du Nord au Sud sa longueur est de 8 Km contre 6.5 Km d'Est en Ouest. La profondeur maximale approximative de 14m est située dans l'extrême Nord-Ouest de la baie (face au port San Martín). Cependant, la majeure partie de la baie a moins de 5 mètres de profondeur (Fig. 1.6a).

La baie de Paracas se caractérise par ses eaux calmes presque assimilables à un lagon. Le régime de marée est semi-diurne avec un marnage maximale de 1m. Le fond de la baie est couvert de gravier, sable, mais surtout de vase (Fig. 1.6b).

Les espèces de poissons les plus abondantes dans la baie sont l'athérine (*Odonesthes regia regia*), le mullet (*Mugil cephalus*) et la sole (*Paralichthys adspersus*). Les invertébrés commerciaux les plus communs sont le pétoncle (*Argopecten purpuratus*), 2 espèces de palourde (*Gari solida* et *Semele solida*), un gastéropode (*Thais chocolata*), le poulpe (*Octopus sp.*) et une espèce de crabe (*Cancer setosus*). Cette baie abrite également des prairies de macroalgues qui sont exploitées commercialement. Les principales espèces sont l'algue rouge *Chondracanthus chamissoi*, les algues vertes *Ulva papenfussi* et *Codium sp.* et l'algue brune *Desmarestia peruviana*. Récemment est apparue enregistré l'algue invasive *Caulerpa filiformis* dans la baie de Paracas.

Le vent dominant dans la région comme le long de toute la côte péruvienne est principalement de secteur Sud. En outre, à Pisco et en particulier dans la zone de Paracas, de forts vents (entre 50 et 80 Km/h) sont fréquemment enregistrés avec un important transport de sable et de poussières, connus sous le nom local de "vents Paracas" (viento Paracas). Dans la baie, le régime de vent est en général calme le matin et il augmente à partir de midi. Ces vents sont d'origine thermique.

En raison des multiples activités réalisées dans la baie de Paracas, des études de divers types ont été menées. L'une des premières études visait à comprendre l'écologie de la baie de Pisco y compris Paracas (Sears, 1954). La croissance, la reproduction et le recrutement des pétoncles ont ensuite été étudiés par Wolff (1987, 1988) lors de l'événement El Niño 1982-1983. La croissance du pétoncle en cultures suspendues est mentionné pour une première fois par Mendo et Jurado (1993). Des études des courants, des types de fond et de la distribution des nutriments et des métaux lourds ont également été réalisées (IMARPE, 2010). Le laboratoire côtier de Pisco (IMARPE) a effectué un suivi des variables océanographiques dans la baie de Pisco y compris Paracas en 2009 : les distributions mensuelles de la température et de l'oxygène dissous sont présentés dans la figure 1.7.

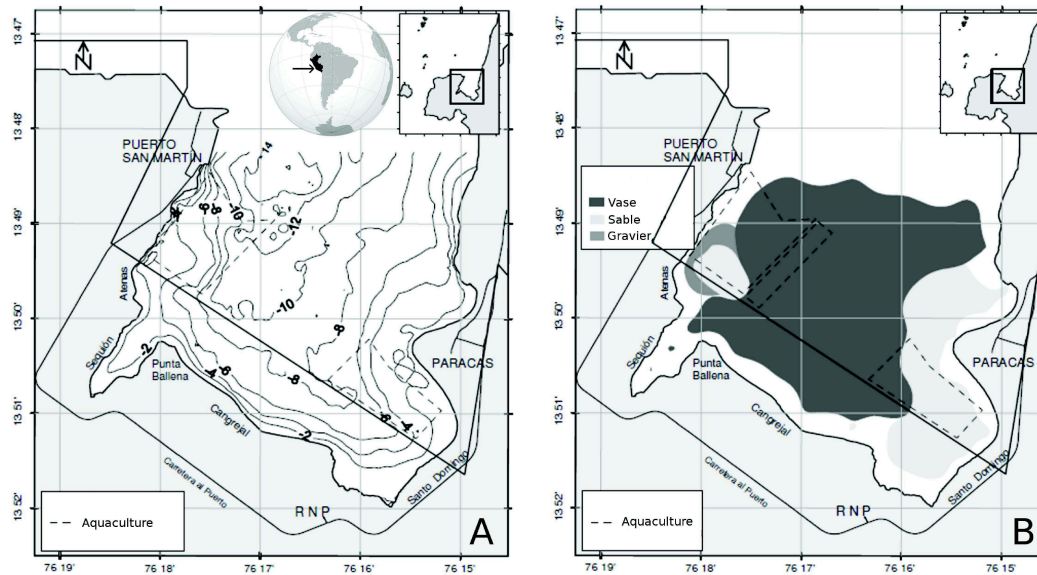


FIG. 1.6: Bathymétrie de la Baie de Paracas (A) et nature sédimentaire des fonds (B). Les lignes pointillées délimitent les zones d'aquaculture du pétoncle péruvien. Source : Laboratorio costero de Pisco, IMARPE (2010)

1.4 La modélisation bioénergétique au niveau individuel

La bioénergétique étudie les flux d'énergie chez les organismes : cela comprend l'assimilation d'énergie du milieu ainsi que son utilisation pour les fonctions métaboliques d'entretien, de croissance et de reproduction. Une vision empirique de la bioénergétique ne propose pas un moyen pratique et unifié pour comprendre les impacts de la variabilité environnementale sur la physiologie des organismes. En revanche, une approche beaucoup plus théorique connue sous le nom de Dynamic Energy Budget (DEB) considère les mêmes processus que les modèles empiriques, mais dans une perspective différente.

Un modèle DEB pour un organisme (individu) décrit les taux auxquels celui-ci assimile et utilise l'énergie pour l'entretien, la croissance et la reproduction, en fonction de l'état de l'organisme et de son environnement (Nisbet *et al.*, 2000). L'état d'un organisme peut être caractérisé par exemple par l'âge, la taille et la quantité de réserves ; l'environnement peut par exemple être décrit par la densité de nourriture disponible et la température.

La théorie DEB développée par Bas Kooijman dans les années 80 (Kooijman, 1986, 2010a) constitue un corpus robuste pour étudier les dynamiques énergétiques des êtres vivants. Elle s'appuie sur un ensemble bien défini d'hypothèses et fournit une caractérisation du cycle de vie complet (embryon, juvénile et adulte) d'un organisme par un modèle. Celui-ci prédit à la fois des variations interspécifiques et intraspécifiques dans les flux d'énergie et de masse dans un environnement biologiquement pertinent.

La théorie DEB décrit l'organisme individuel en fonction de deux variables d'état : la structure corporelle, quantifiée en termes de volume, et les réserves, quantifiée comme densité énergétique. Cette dernière variable s'exprime en termes de réserves par unité de structure. La structure corporelle et les réserves ont toutes les deux une composition chimique constante. Cette hypothèse est appelée l'homéostasie forte (strong homeostasis). La quantité des réserves peut varier par rapport à la structure, par exemple en raison de conditions variables d'alimentation. Ceci implique que la composition chimique de la masse corporelle totale peut varier. Cela implique également qu'un modèle DEB fait

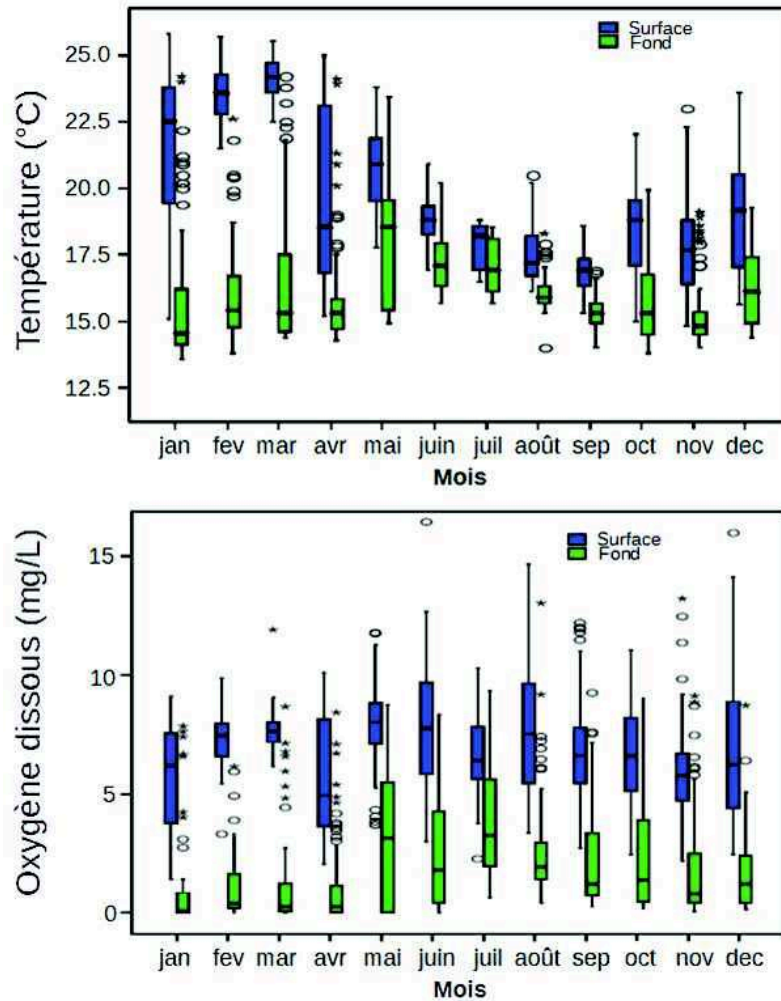


FIG. 1.7: Distribution mensuelle de la température (A) et de l'oxygène dissous (B) des eaux de surface et de fond mesurés en seize points de la Baie de Paracas en 2009. Source : Laboratorio costero de Pisco, IMARPE (2010)

la distinction entre la structure et la réserve. Les organismes sont en mesure de survivre à des périodes prolongées de jeûne, au cours desquelles ils doivent en permanence allouer de l'énergie à l'entretien. Durant le jeûne, ces besoins en énergie ne peuvent pas être immédiatement fournis à partir de l'alimentation, ce qui est un autre argument en faveur de la prise en compte explicite des réserves.

La théorie DEB suppose que ce qui est assimilable à partir de la nourriture ingérée intègre directement les réserves. Alors que le taux d'ingestion est proportionnel à la surface de l'organisme, le taux de maintenance est proportionnel au volume de sa structure. Les coûts de la digestion des aliments sont payés directement à partir de la nourriture consommée. Une fraction fixe κ de l'énergie de la réserve est consacré à la croissance et à l'entretien somatique, le reste $1 - \kappa$ sert au développement de la maturité et à la reproduction. Sur la base de cette règle, le modèle de croissance DEB a été appelé le modèle κ -rule (Fig. 1.8). La priorité est toujours donnée à la maintenance somatique ; si le taux d'utilisation de l'énergie à partir des réserves ne suffit plus pour couvrir les coûts d'entretien somatique, l'individu meurt à force d'utiliser la structure comme source d'énergie.

La théorie DEB utilise l'équation de Van't Hoff-Arrhenius pour décrire la dépendance des taux physiologiques à la température. Kooijman (2010a) souligne que l'équa-

tion de Van't Hoff-Arrhenius est seulement une généralisation statistique et qu'à l'heure actuelle, nous manquons encore d'une compréhension claire de la relation entre la température et le métabolisme à l'échelle de l'organisme.

La version «standard» du modèle DEB possède 13 paramètres. L'estimation des valeurs de ces paramètres nécessite de nombreuses données sur le cycle de vie de l'espèce (Kooijman, 2010a), mais il est possible de faire une première estimation en tirant parti des prédictions théoriques de relations interspécifiques taille-corps (scaling) ou de co-variation des paramètres (Kooijman, 2010a).

Un modèle DEB permet de faire des prévisions quantitatives de la croissance, de la reproduction ainsi que d'une variété de taux physiologiques et des flux d'énergie dans un environnement dynamique. La théorie sur laquelle est basé le modèle nous donne également un cadre pour la compréhension, l'analyse et la discussion des effets environnementaux sur la bioénergétique (métabolisme/physiologie) d'un organisme.

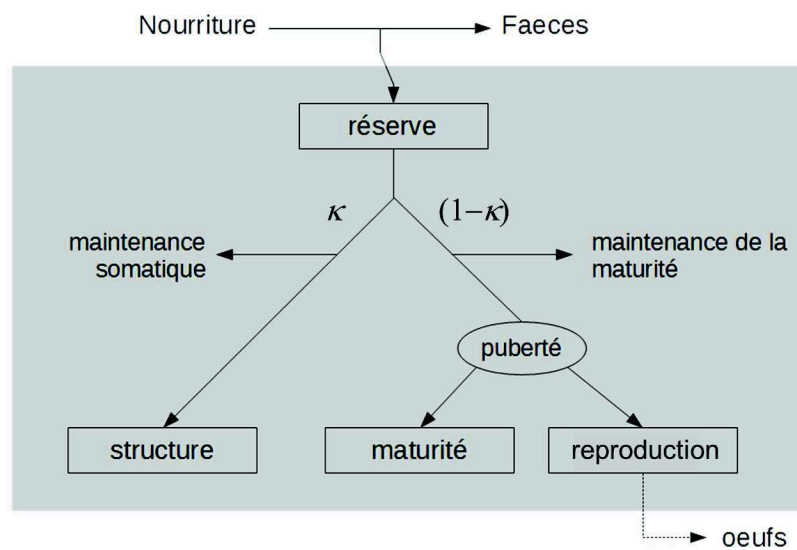


FIG. 1.8: Diagramme schématisique du bilan énergétique (Dynamic Energy budget theory) d'un individu selon Kooijman (2010a)

1.5 Objectifs de la thèse

Dans le contexte ci-dessus exposé, ce travail comprend trois approches : (1) l'observation *in situ* de la variabilité environnementale qui se produit dans les baies de la côte péruvienne dans le but d'identifier les facteurs qui ont une influence sur la croissance et la reproduction d'*A. purpuratus*; (2) l'expérimentation *ex situ*, en laboratoire, qui permet d'évaluer les effets environnementaux (température, concentration en Oxygène, ressource trophique) sur la physiologie (ex. respiration, filtration) et la bioénergétique en conditions contrôlées et (3) la modélisation du bilan énergétique du pétoncle péruvien, qui permet de comprendre les conséquences métaboliques de ces variations environnementales, et constitue un outil permettant d'élaborer des prévisions en fonction de scénarios environnementaux.

Ces trois approches complémentaires ont pour objectif de mieux comprendre, d'une façon intégrée, les effets de la variabilité environnementale sur une ressource aquacole majeure au Pérou. L'ensemble des résultats obtenus sera utile, dans un avenir proche,

pour développer des outils de gestion et de production (ex. capacité de charge des baies)
du pétoncle péruvien.

Première partie

Identification de variables environnementales affectant la bioénergétique d'*A. purpuratus*

Chapitre 2

Environnement et croissance journalière chez *A. purpuratus*

Sclerochronological records and daily microgrowth of the Peruvian scallop (*Argopecten purpuratus*, Lamarck, 1819) related to environmental conditions in Paracas Bay, Pisco, Peru.

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Arturo AGUIRRE VELARDE, Jonathan FLYE-SAINTE-MARIE, Jaime MENDO,
Fred JEAN

Abstract

We investigated the rhythm of micro-striae formation in the shell of *Argopecten purpuratus* and environmental influence on micro-growth increments by monitoring growth over a 98-day period between April and July 2007 under bottom and suspended culture (2m above the bottom) rearing conditions. The transfer of individuals to the study site induced the formation of a notable growth mark that allowed us to count the number of micro-striae formed between transfer and sampling dates. Micro-striae counts showed a deposition rate of one stria per day independent of rearing condition. This result allowed us to analyse the relationships between growth increments and environmental conditions. We therefore examined the deviations between observed growth rates and growth rates predicted from a Von Bertalanffy growth function. Cross-correlation analysis revealed significant correlations, without time-lag, between these deviations and both particulate organic carbon and nitrogen concentrations in the bottom treatment. Additionally, we observed negative correlations with temperature and current speed at this depth with time-lags of 1 and 10 days respectively. In the suspended treatment, we observed a significant negative correlation with temperature, only with a 12-day lag-time. Our results show that growth response to environmental variability is not always instantaneous. This delay can be explained by the time delay over which metabolic processes need to be performed (e.g. digestion, use/movements of reserves, growth, reproduction).

Keywords: *Argopecten purpuratus* growth ; shell microgrowth increments ; periodicity ; sclerochronology ; Paracas Bay .

2.1 Introduction

The Peruvian scallop, *Argopecten purpuratus* (Lamarck, 1819), is a hermaphrodite pectinid bivalve, that occurs mainly along the Pacific coast of Peru and northern Chile (Wolff and Mendo, 2000) in semi-protected coastal and island bays with soft bottom sediment (Brand, 1991). Expansion of *A. purpuratus* stocks in southern Peru, especially near Pisco during El Niño events of 1982-83 and 1997-98, contributed to the intensive exploitation of this resource for export purposes. In the last decade, bottom and suspended cage aquacultures have gradually replaced fishing of the Peruvian scallop. Scallop has become the major aquaculture activity along the Peruvian coast. Paracas Bay represents a major traditional cultivation and fishing area of the Peruvian scallop especially during El Niño events.

This activity has catalyzed widespread studies of *A. purpuratus* stocks along the Peruvian and Chilean coasts (see e.g. Wolff, 1987; Yamashiro and Mendo, 1988; Alarcon and Wolff, 1991; Mendo and Jurado, 1993) that demonstrate significant spatial and temporal variability in growth. Several studies relate temporal variability in the growth of this species to environmental conditions induced by El Niño Southern Oscillation (ENSO) (Wolff, 1987; Mendo and Wolff, 2003; Thébault et al., 2008). Most of these studies are based on a cohort growth monitoring rather than high-frequency individual growth surveys (Thébault et al., 2008). In spite of these studies, the links between short-term growth and environmental parameters (e.g. physico-chemical parameters of seawater, temperature, trophic resource availability/quality) remain poorly known.

Shell growth striae on the surface of many scallops, including *A. purpuratus*, offer a mechanism for high-frequency monitoring of individual growth in bivalves. Although most studies show daily formation of shell striae formation in the genera *Argopecten* (Wrenn, 1972; Clark, 1975; Helm and Malouf, 1983) and *Pecten* (Clark, 1968, 1975; Antoine, 1978; Chauvaud et al., 1998; Chauvaud, 2005) some evidence suggests a 2-day periodicity in the tropical scallop *Comptopallium radula* (Thébault et al., 2005), demonstrating that periodicity must be determined prior to any sclerochronological study. Knowledge of this rhythm allows use of inter-striae distances to determine the growth rate per unit time and evaluation of the relationship between growth rate and environmental conditions. Chauvaud et al. (1998) demonstrated the potential of daily striae for relating growth and environmental variables in *P. maximus*.

The objectives of our study are (1) to determine the periodicity of shell striae formation in *A. purpuratus* and (2) to investigate the influence of environmental parameters on its growth rate in Paracas Bay. We also evaluate the different farming systems of the Peruvian scallop and their consequences in terms of growth.

2.2 Material and methods

2.2.1 Scallop collection and shell marking

The scallops were collected as post-larvae in Samanco Bay using commercial collectors and were maintained suspended in the water column in cultivation lanterns (pearl nets) and remained until they reached ≈ 25 mm average shell height (H). Scallops then were transported in refrigerated seawater ($\approx 10^\circ\text{C}$) to the Paracas Bay experimental site where they were placed on the bottom in a 7-m depth area devoted to commercial farming of this species ($13^\circ 49' 22,817''$ S, $76^\circ 17' 36,985''$ W, Fig. 6.1). The interruption of growth caused by the stress of transport left a visible mark on the valves in all individu-

als. Scallops were kept undisturbed in the field to acclimate for 60 days before starting the experiment.

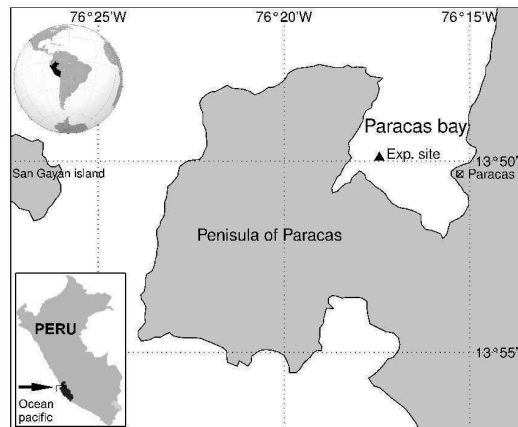


FIG. 2.1: Map of the experimental site in Paracas Bay (Peru; 13°49'22,817" S, 76°17'36,985" W). The experimental site was located in a 7m-deep area dedicated to commercial farming of *Argopecten purpuratus*.

2.2.2 Monitoring of growth

By the end of the acclimation period scallops reached a size of 35-45 mm. We monitored growth periodically during the 98 days between April and July 2007. Over this period, we exposed the scallops to two contrasting growing conditions. Individuals were randomly arranged at a density of 30 individuals per cage within 14 circular cages constructed of a metallic frame and monofilament nylon mesh (diameter = 50 cm, height = 20 cm). Seven cages were placed on the bottom in contact with the sediment (bottom treatment) while the others were suspended at 2 m above the bottom (suspended treatment; Fig. 2.2). Every 14 days, scallops were sampled by removing one cage from bottom and suspended treatments and selecting three or four individuals per cage excluding damaged or heavily fouled individuals. The tissues were completely removed from the shells and valves were dried and stored for subsequent striae measurement.

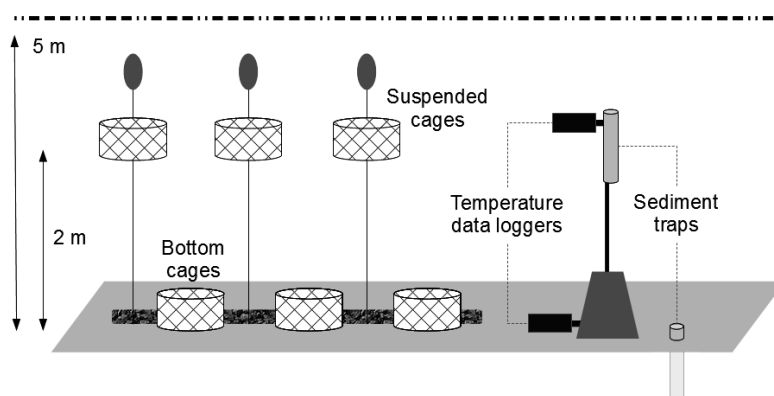


FIG. 2.2: Experimental set-up for the scallop cultures (suspended and bottom) and measurement of environmental parameters.

2.2.3 Monitoring of environmental variables

We measured physico-chemical descriptors of seawater at the depth of each treatment. Temperature was measured with two data-loggers that recorded one datum every hour. Dissolved oxygen and salinity were measured using a multi-parameter sensor HACH (HQ40D) two days per week, in the morning (6 a.m.) and in the afternoon (2 p.m.). Simultaneously, current velocity was measured with a propeller current-meter. Concentrations of chlorophyll-*a* and phaeopigments were measured two days per week from samples collected in the morning and afternoon. For this purpose, we filtered 100 mL of seawater from the sediment-water interface and from the water column at two meters above the bottom through filter GF/F (0.7 μm pore size). Photopigments were extracted for 24 h in 10 mL of acetone 90% and quantified with a fluorometer (TURNER AU-10). Particulate organic material was collected using two sediment traps deployed weekly for 48 h at depths corresponding to each treatment (Fig. 2.2). Trapped material was lyophilized and the particulate organic carbon and nitrogen (POC and PON respectively) quantities were determined with a CHN elemental analyzer (EuroEA). Finally, the mean concentrations of POC and PON in the environment were calculated following Armanini and Ruol (1988) and assuming a sinking velocity of 4.167 m h^{-1} for the sediment, based on diatom data (Alldredge and Gotschalk, 1989).

$$C = \frac{M}{(w \cdot A \cdot \Delta t)} \times 1000 \text{ mg L}^{-1}$$

with:

C : POC or PON concentrations (mg L^{-1})

M : mass of trapped material (mg)

w : settling velocity of the sediment particles (m h^{-1})

A : area of the collection orifice of the trap (m^2)

Δt = deployment time (h)

2.2.4 Shell preparation and observation

Although striae are more visible in the left valves, preliminary trials indicated that fouling would often prevent a complete reading along the maximum growth axis and we therefore performed striae measurement on right valves (Fig. 2.3). The selected valves of *A. purpuratus* were first cleaned with fresh water and immersed in glacial diluted acetic acid for 30 s to remove any fouling. Valves were then rinsed thoroughly and dried before they were encased in polyester resin (SODY 33R). After the resin hardened, valves were sectioned along the dorso-ventral axis, parallel to the central rib, using a low-speed diamond saw (Struers Accutom 50). Sections were grounded and polished to reveal external striae in cross-section. Photographs were taken under a binocular microscope at x20 for the counting of striae and measurement of the interstriae distances as well as umbo-striae distances. In order to determine the rhythm of striae formation, we performed a linear regression (ordinate origin forced to zero) of the number as a function of the number of days between the transport date (t_{initial} = stress mark) and the collection date.

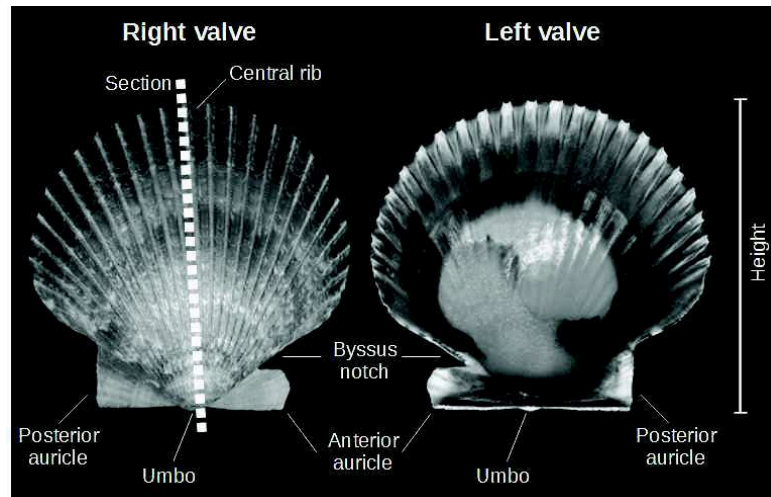


FIG. 2.3: Morphology of *A. purpuratus* valves. The Peruvian scallops rest on their right valve, Sections for the study of striae were performed parallel to the valve central rib in as shown in figure.

2.2.5 Growth modeling and data analysis

Because *A. purpuratus* typically lives on the sediment striae and many striae readings were available, we considered individual growth in the bottom treatment as a reference in order to study the influence of environmental variables. In addition, published growth parameters were available for bottom-living individuals in Paracas Bay. The von Bertalanffy's growth function (VBGF) was adjusted to the observations:

$$H_t = H_\infty \cdot (1 - e^{-K(t-t_0)})$$

with:

H_t = shell height at time t (mm)

H_∞ = asymptotic shell height (mm)

K = growth coefficient (year^{-1})

t_0 = age when shell height equals zero (years)

For this purpose, we fixed H_∞ at 110 mm according to Wolff (1987) and calculated K according to the linearized method suggested by von Bertalanffy (1934):

$$-\ln(1 - H_t/H_\infty) = -K.t_0 + K.t$$

For both treatments, we calculated shell microgrowth rates for height (GR , $\Delta H/\Delta t$ $\mu\text{m}/\text{day}$). In order to remove the natural reduction of growth with size/age (Gulland and Hold, 1959) we adopted the following methodology: for each treatment, we calculated deviations (E) between the observed growth rate and the calculated growth rate expected from adjusted VBGF for bottom individuals ($GR^{\text{calc.bottom}}$) as follows :

$$E_t = \bar{X}_t - GR_t^{\text{calc.bottom}}$$

with:

E_t = growth rate deviation ($\mu\text{m d}^{-1}$) at time t

X_t = observed average growth rate at time t

$GR_t^{calc.bottom}$ = Calculated bottom growth rate at time t (from VBGF)

We also calculated the daily average temperature and weekly averages for the other environmental variables. Analysis of time series of height growth rate deviations (E) and environmental parameters for the bottom was conducted using cross-correlation function analysis (CCF) to highlight possible correlations at time t and with a time offset (t-h). All data treatment and statistical analyses were performed with R software (R Development Core Team, 2009)

2.3 Results

2.3.1 Periodicity of micro-growth striae formation

The stress mark produced during transport was clearly visible on all studied valve sections, showing clear interruption of growth (calcification; Fig. 2.4). Subsequent growth produced an observable discontinuity on valves. Only post-stress striae were visible because abrasion of the shell surface obliterated older striae. We were able to analyze a total of 17 valves from the bottom treatment and 13 from the suspended treatment. The number of growth days (days between stress date and collection date) showed a strong linear relationship with the number of striae ($R^2 = 0.9979$, $p < 0.001$) and a slope of 1.003 striae/day (Fig. 2.5). Differences between treatments were not significant ($p > 0.05$). The slope estimated for the combined individuals did not differ significantly from 1 stria/day ($p > 0.05$). For the last bottom treatment sampling we observed two individuals outside the regression's forecasting confidence interval.

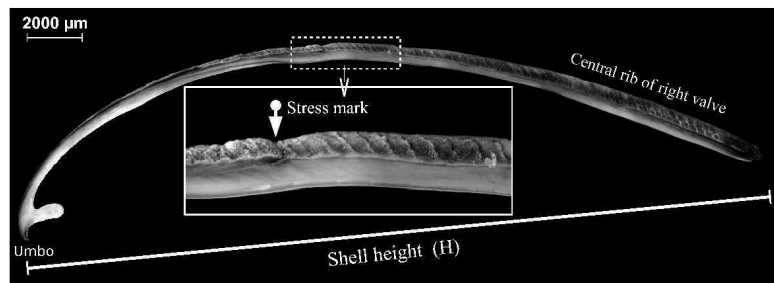


FIG. 2.4: Right valve section view along the dorso-ventral maximum growth axis (height, H), parallel to the central rib. The inset shows a detail of a shell section. Reference stress mark (caused by transport of scallops to the experimental site in Paracas Bay) and striae are visible.

2.3.2 Temporal variation of height microgrowth rates

Next, we considered the difference in height between two striae ($H_{t+1} - H_t$) by height daily microgrowth increment, and we observed a low inter-individual variability of average microgrowth rates (Fig. 2.6): $\approx 30 \mu\text{m d}^{-1}$ on average and rarely exceeding $100 \mu\text{m d}^{-1}$. For the bottom treatment, we show all post stress measurements, whereas for the suspended treatment we report increments from day 60, when individuals were placed in suspension. Fitting a VBGF to the data for the bottom treatment, with H_∞ fixed to 110 mm, gives a value of $K=1.44$ ($R^2 = 0.875$, $p < 0.001$, see Fig. 2.6). Deviations from $GR_t^{calc.bottom}$ were higher in the suspended than in the bottom treatment,

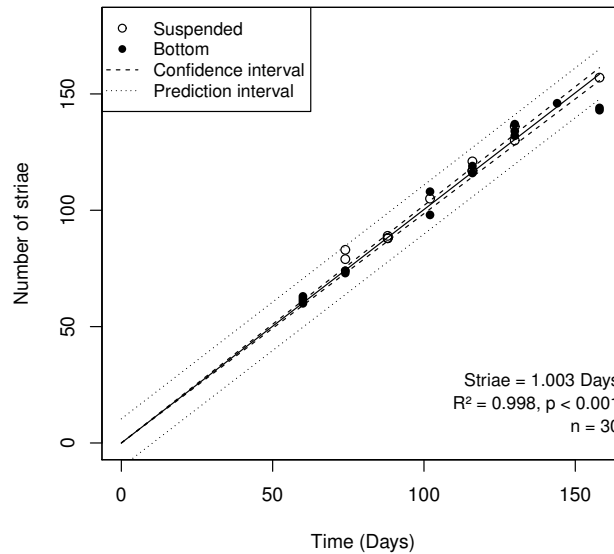


FIG. 2.5: Relationship between the number of striae counted from the stress mark to the ventral margin of the shell and the number of days between the transport and collection date for scallops from bottom and suspended treatments.

especially around days 65, 80, 130 and 140. In the bottom treatment, we observed negative deviations especially in the days prior to the beginning of the experiment (day 60) and around day 75. However, variations in growth rates remained fairly synchronized between the two treatments, except for the last 15 days, where growth suddenly increased in the suspended treatment.

2.3.3 Temporal evolution of environmental variables

During the experiment, temperature ranged from 14.6°C to 22.6°C (Fig. 2.7 a). Bottom and the suspended treatments exhibited similar temperature variation, although temperature in the suspended treatment was approximately one-tenth of a degree higher than in the bottom treatment. Temperature also varied daily of approximately 1°C; and we sometimes observed sharp temperature variations, reaching 4°C per day. Oxygen saturation (Fig. 2.7 b) varied between 4.2 % and 128.2 % in the bottom treatment and from 14.3 % to 138.6 % in the suspended treatment. For both treatments, we consistently observed lower values at 6 a.m. and higher values were at 2 p.m (Fig. 2.8 a). Current speed (Fig. 2.7 c) also exhibited daily variations with low values (close to 0 cm s⁻¹) during the morning and higher values in the afternoon (Fig 2.8b). The maxima observed were 35 cm s⁻¹ in bottom and 50 cm s⁻¹ in suspended treatments. Average current speed was significantly higher in the suspended than in the bottom treatment ($p < 0.05$). Salinity varied between 29.2 and 37.5 in both treatments (Fig 2.7 d), with minima during the first two weeks; after this period salinity remained almost constant for the duration the experiment.

POC concentrations (Fig. 2.7 g) varied between 0.853 and 3.714 mg L⁻¹ in the bottom treatment and between 0.811 and 3.166 mg L⁻¹ in the suspended treatment. POC peaked around days 90 and 150 in the bottom treatment and around days 100 and 150 in the suspended treatment. POC evolution in the two treatments showed similar patterns

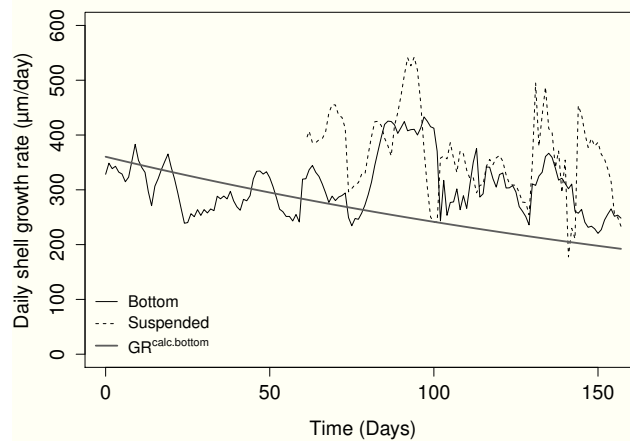


FIG. 2.6: Temporal variations in average daily microgrowth rate ($\mu\text{m d}^{-1}$) for scallops in bottom and suspended treatments. For scallops in bottom treatment, the entire post-stress measurements are shown. For suspended treatment the series starts at day 60, when the individuals were placed in suspension. Stronger gray line indicates growth rate calculated from VBGF for bottom individuals ($GR^{\text{calc.bottom}}$).

except around day 30 when POC concentrations were much higher in the bottom than in the suspended treatment. PON levels (Fig. 2.7 h) ranged between 0.140 and 0.482 mg L^{-1} in the bottom treatment and between 0.128 and 0.446 mg L^{-1} in the suspended treatment; the overall pattern of variation paralleled that observed in POC concentrations. PON concentrations peaked around days 40 and 90 at both depths, but were higher in the bottom than in the suspended treatment. We observed low concentrations of POC and PON during the first four weeks of monitoring.

Chlorophyll-*a* peaked twice during the experimental period: first between days 60 and 70 in the bottom treatment only and again between days 110 and 115 in both treatments. Minimum concentrations occurred around days 80 and 145 for both treatments. In the suspended treatment, phaeopigment concentrations were almost constant and relatively low in contrast to very high values recorded between days 100 and 115. Phaeopigment concentration minima occurred for the two treatments around day 75. Phaeopigment concentration differed significantly between treatments ($p < 0.05$) but chlorophyll-*a* concentration did not.

2.3.4 Environmental influence on microgrowth increments

The CCF analysis in this section (Tab. 2.1) only considers negative time-lags (h) because this approach correlates environmental variables at time t or $t-h$ with growth rate deviations E at time t . We studied E from bottom and suspended treatments (E_{bottom} and $E_{\text{suspended}}$ respectively) in relation to temperature at daily resolution and other environmental parameters were at weekly resolution to correspond to the timing of acquisition of environmental data.

Environmental parameters correlated significantly with E from bottom and suspended treatments at different time-lags (Table 2.1). The E_{bottom} correlates significantly and negatively negative correlations with temperature and currents at specific time-lags (> -7 days). The availability of trophic resources, measured as concentrations of POC and PON, correlated positively with no time-lag. In the case of the $E_{\text{suspended}}$, only

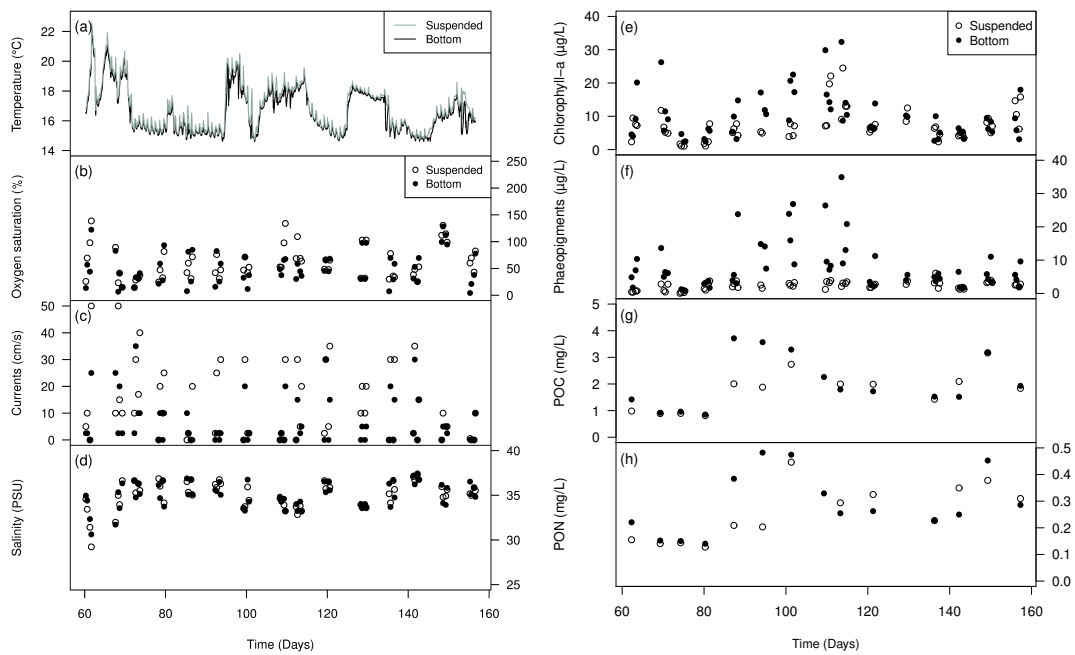


FIG. 2.7: Temporal variation in (a) temperature, (b) dissolved oxygen saturation, (c) currents, (d) salinity, (e) chlorophyll-a concentration, (f) phaeopigments, (g) particulate organic carbon (POC) concentration and, (h) particulate organic nitrogen (PON) concentration in bottom and suspended treatments.

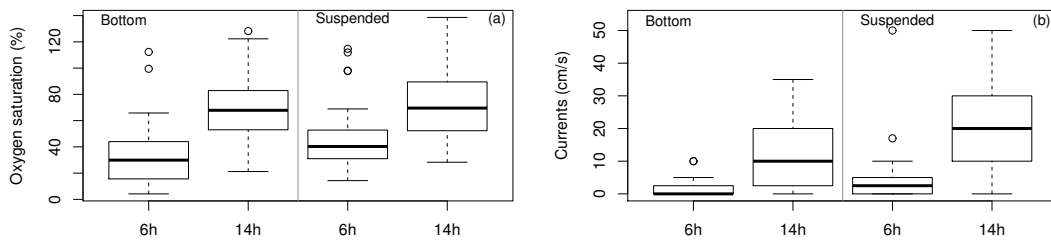


FIG. 2.8: Daily variation (morning and afternoon measurements) in (a) dissolved oxygen saturation and (b) currents in bottom and suspended treatments. Open circles represent outlier values.

temperature correlated significantly (with a significant time-lag) but with a small CCF coefficient.

A significant linear regression ($p < 0.01$) indicates that POC explained 39.8 % of the variation of E_{bottom} .

TAB. 2.1: Summary of significant CCF correlations found between growth rate deviations in bottom (E_{bottom}) and suspended ($E_{suspended}$) treatments as a function of environmental parameters. Only negative time-lags (h) are studied. Given the periodicity of environmental data acquisition, we studied lags for temperature at a daily resolution as opposed to a weekly resolution for other environmental parameters.

	E_{bottom}		$E_{suspended}$	
	Max. CCF*	h (-)	Max. CCF*	h (-)
Temperature	-0.425	10 days	-0.270	12 days
Oxygen saturation	-	-	-	-
Salinity	-	-	-	-
Current	-0.607	1 week	-	-
Chlorophyll-a	-	-	-	-
Phaeopigments	-	-	-	-
POC	0.631	0 weeks	-	-
PON	0.583	0 weeks	-	-

*Significant at $\alpha = 0.05$

2.4 Discussion

2.4.1 Periodicity of microgrowth striae formation

The close relationship between the number of striae and the number of days since the stress mark – with a slope of 1 – clearly indicates a daily formation of shell microstriae in *A. purpuratus* at Paracas Bay, which confirms the assumption of Thébault et al. (2008) and estimation of Gosselin et al. (2013) based on recorded seawater temperature variations for this species. This daily striae formation rhythm confirms results obtained for most other species of *Argopecten*. Such a rhythm has been suggested for *Argopecten irradians* (Wrenn, 1972; Clark, 1975; Wheeler et al., 1975; Helm and Malouf, 1983), *Argopecten gibbus* and *Argopecten circularis* (Clark, 1975) as well as other Pectinidae species including juveniles of *Pecten diegensis* (Clark, 1968), *Pecten vogdesi*, (Clark, 1975) *Chlamys opercularis* (Broom and Mason, 1978) and *Amusium balloti* (Joll, 1988), juveniles and adults of *Pecten maximus* (Antoine, 1978; Chauvaud et al., 1998; Owen et al., 2002) and larvae and post-larvae of *Placopecten magellanicus* (Hurley et al., 1987; Parsons et al., 1993). Photoperiod presumably controls this daily periodicity (Clark, 2005).

However, a recent study carried out in the protected marine area of La Rinconada, Chile, indicates a deposition of one strium every two days in adult individuals of *A. purpuratus* marked with calcein and measured over 140 days (Thouzeau, personal communication). Rhythmic activities are generally assumed to be controlled by endogenous oscillators synchronized by environmental cues acting as zeitgebers (Aschoff et al., 1982). In marine bivalve striae formation corresponds to a growth rate decrease brought about by altered metabolism (Chauvaud et al., 1998). Diurnal, tidal and seasonal environmental cycles are known to drive growth rhythms (Rosenberg and Jones, 1975).

Confirmation of Thouzeau's results would strongly suggest that different zeitgebers synchronize and/or control metabolic rhythms of scallops from the Paracas Bay and from La Rinconada populations. However, reports of 2-day long biological rhythms in nature are unusual. Only *Mercenaria mercenaria* (Pannella and MacClintock, 1968; Kennish and Olsson, 1975) and *Comptopallium radula* (Thébault et al., 2005) were reported to exhibit such a 2-day periodicity of microstriae formation.

In the case of Paracas Bay, rhythm synchronized to the tidal cycle (mixed regime predominantly semidiurnal) is unlikely given the small amplitude (<1 m) in this area. We can also eliminate the daily increase in turbidity resulting from wind-driven turbulence in the water-sediment boundary layer (weak in the morning to strong in the afternoon) as the cause given that the rhythm in suspended scallops, without resuspended sediment particles, was no different. Daily changes in oxygen saturation seem a much more likely driver of periodicity in growth. The low saturation values observed at 6 a.m. (average of 30 % in bottom and 40 % in the suspended treatment) confirm nocturnal hypoxia. Oxygen availability is a key regulator of metabolic processes of marine invertebrates. Aquatic organisms may respond to hypoxia by (1) attempting to maintain oxygen delivery, (2) reducing energy expenditure, and (3) enhancing energetic efficiency and deriving energy from anaerobic sources (Wu, 2002). Bivalves may reduce their metabolic rate in response to hypoxia (Storey and Storey, 2004). This reduced-oxygen stress could stop shell growth during the night, but growth could resume during the day when oxygen saturations are more favorable, thus creating a circadian rhythm as an energetic strategy to cope with high variations in oxygen availability. In the Pectinidae family, particularly in temperate zones, long-term growth deceleration (Krantz et al., 1984; Owen et al., 2002) or even growth cessations occurred during winter. Although our study only integrates a 160-day period between February and July 2007, the periodicity observed during the monitoring likely persists throughout the year given the reduced seasonality in the Paracas Bay area and a year round high primary production is supported by consistent upwelling. However, decreased striae deposition rate occurs in older aged individuals, as in *P. maximus* (Antoine, 1978).

2.4.2 Influence of environmental parameters on microgrowth increments

The positive effect of POC and PON on bottom growth rates found in our study study contradicts the results of Thébault et al. (2008) who hypothesized that an increase in POC concentration above a threshold of 2.5 mg L^{-1} might affect growth negatively. A negative effect of sedimentation of high amounts of organic particles was also suggested for *P. maximus* (Chauvaud et al., 1998; Lorrain et al., 2000; Chauvaud et al., 2001). Nevertheless, we observed no negative effect with concentrations of POC comparable to those measured by Thébault et al. (2008) (between 1 and 4 mg L^{-1}). Perhaps inhibited filtration at high concentrations of POC and PON relates to the size and rate of agglomeration and origin of the particles (e.g. phytoplankton, detrital).

Food availability was apparently higher for scallops living on the bottom in our experiment. Nevertheless, growth rates in suspended scallops were considerably higher in several periods of the study. It is possible that the food availability descriptors that we measured miss certain aspects of seston quality and composition (phytoplankton/detritus/particulate inorganic material) that primarily determine growth. The energy balance of adult *A. purpuratus* depends strongly on diet composition (Navarro et al., 2000) and many laboratory studies show strong effects of food composition and quality on juvenile

growth (Diaz and Martinez, 1992; Martinez et al., 1995; Uriarte and Farias, 1999) and fertility in *A. purpuratus* adults (Farias and Uriarte, 2001). The presence of abundant phaeopigments on the bottom, which was the only measured trophic descriptor that differed significantly between the two treatments, might indicate reduced food quality because these molecules reflect degradation/digestion of chlorophyll.

Inhibition of filtration by high currents, as has been observed in other bivalve species such as *P. magellanicus* (Wildish et al., 1992; Pilditch and Grant, 1999) could explain the negative effect of current velocity observed in our study. In addition, high currents might increase sediment resuspension at the water-sediment interface, which could increase turbidity, resulting in a decreased feeding activity and therefore growth (Sobral, 2000). Furthermore, currents in Paracas Bay are generated almost exclusively by offshore winds, which transport particulate inorganic matter from the adjacent desert. This material might contribute to a degradation of the quality of available seston, and consequently affects scallop feeding. Negative effects of high particulate inorganic matter on bivalve nutrition are well known (see Widdows et al., 1979). In the Paracas Bay environment, particulate inorganic matter spikes could last for several days after a windy event (sandstorm type), which could explain the one week time-lag in our correlation.

Temperature has often been identified as a key regulator of scallop growth (Broom and Mason, 1978; Wilson, 1987; Chauvaud et al., 1998; González et al., 1999; Laing, 2000; Wallace and Reinsnes, 1985; MacDonald and Thompson, 1986). Previous studies in the Paracas area indicated a positive effect of temperature on populations of *A. purpuratus* (Mendo and Jurado, 1993; Mendo and Wolff, 2003). However, depending on the period of year and the cohort, Wolff (1987) observed positive and negative relationships between temperature and growth rates. Thébault et al. (2008) recognized that temperature produced a significant positive effect on *A. purpuratus* shell growth in La Rinconada Marine Reserve, Chile. However, two hypotheses could explain the significant negative relationship in our study. The first is that temperature that exceeds the upper limit of the species' thermal tolerance results in reduced growth (e.g. during an El Niño event; Urban, 1994). However, the relatively low temperature (rarely exceeding 20°C) during our study period precludes this explanation. Although *A. purpuratus* acclimates well metabolically to temperature (10°C - 18°C González et al., 2002) rapid initiation of warm periods could adversely affect growth (up to 4°C/day as indicated by the temperature record), by causing metabolic stress (Peck et al., 2009). The observed correlation time-lags (-10 and -12 days in bottom and suspended respectively) mirror the 6.3 days time-lag reported by Gosselin et al. (2013) between sclerochronological and the seawater temperature series at la Rinconada, Chile, which the authors attribute to a growth stop. Nevertheless temperature could potentially affect diverse metabolic processes simultaneously (Kooijman, 2010b) and growth consequences might not be observable instantaneously at a daily resolution. In this context, temperature increase can also affect gametogenesis and spawning (not included in this study) (Barber and Blake, 2006) compromising the energy available for scallop growth, since these processes demand high energy in bivalves (Sastry, 1979)

The methodology adopted to evaluate the influence of environmental parameters on growth, using deviations from VBGF, has been shown to correct for effects of age (Thébault et al., 2008). Similarly, cross-correlation analysis revealed correlations and allowed us to highlight time-lagged relationships. These time lags are presumably driven by metabolic smoothing and/or delaying of environmental variability impact on growth.

2.5 Conclusion

The stress generated by transport caused a visible mark on valves of *A. purpuratus*. This mark allowed us to demonstrate daily rhythm of striae formation in Peruvian scallop in Paracas Bay. This information allows precise age determination for stock evaluation and productivity and management studies. It also opens the possibility of using growth-increment information alongside stable isotope and microelement data for environmental reconstructions (e.g. for El Niño events).

Environmental variables affect growth in complex ways. Evaluation of food quality, composition (e.g. species of phytoplankton, detritus type) and form (e.g. degree of aggregation) is necessary since classical food descriptors cannot adequately growth differences between bottom and suspended scallops. Importantly, growth responses to changing environmental conditions are not always instantaneous, likely because of time-lags induced by metabolic processes (e.g. digestion, use/movements of reserves, growth, reproduction). Development of bio-energetic models might be particularly helpful in addressing these questions.

Aknowledgments

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Chapter 3

Croissance et reproduction dans un environnement limitant en oxygène

Chronic and severe hypoxic conditions in Paracas Bay, Peru: consequences on scallop growth and reproduction

Arturo AGUIRRE-VELARDE, Fred JEAN, Gérard THOUZEAU, Jaime MENDO, Midori KAWAZO-DELGADO, Jazmín VÁSQUEZ-SPENCER, Rosa CUETO-VEGA, Diego HERRERA-SANCHEZ, Alex VEGA-ESPINOZA, Jonathan FLYE-SAINTE-MARIE

Abstract

Paracas Bay is a traditional Peruvian aquaculture area for *A. purpuratus* (Peruvian scallop) which is characterized by an important primary productivity linked to the adjacent coastal upwelling. The present experiment was conducted in a 5-m depth commercial aquaculture area. Scallops growth and reproduction was monitored weekly over a 7-month period in two conditions: on the bottom and suspended 2m above the bottom. In addition, a high-frequency monitoring of environmental parameters was realized at both depths. Our results indicate that environmental conditions in the bay are highly variable and this especially during the summer: temperature fluctuations up to 8°C to were recorded in less than one day. Oxidic conditions sometimes ranged from oversaturation to anoxia. Milky turquoise waters discoloration were always related to anoxic conditions and accompanied by a sudden temperature drop. Increased stratification and upwelling favorable winds during the summer might be partly responsible for the observed environmental variability. Higher shell and somatic growth as well as gonadal mass were observed in scallops growing in suspended culture compare with on bottom. This pattern might be related to the different environmental conditions: turbidity was lower in suspended culture and hypoxic conditions represented only 18% of the study period versus 48% on the bottom. Gonadosomatic index varied according to an approx. 30-day cycle between winter and late spring and was synchronous in all scallop batches. During summer, when milky waters and anoxic events occurred frequently, cessation of reproduction, somatic weight losses and increased scallops mortality were observed. Exposure to hypoxia, and accompanying environmental conditions clearly affected scallops growth and reproduction. In addition, the occurrence of milky waters harmed the survival of the Peruvian scallops in culture.

Keywords: *Argopecten purpuratus*; high frequency monitoring; coastal upwelling; hypoxic/anoxic conditions; growth; reproduction; aquaculture; Peru.

3.1 Introduction

Peruvian scallop (*Argopecten purpuratus*) aquaculture kick-started in the 80s in Paracas Bay (Pisco, Ica) driven by favourable environmental conditions related to the 1982-83 El Niño event (Wolff, 1984). Since then scallop culture considerably developed and actually represents 54% of total Peruvian aquaculture production with annual harvests reaching more than 67 000 tonnes (PRODUCE - Peru, 2015). High growth rates of cultured populations are supported by the presence of a non-seasonal coastal upwelling that ensures high primary production all year round (Taylor et al., 2007). Nevertheless, scallop production in Paracas Bay is frequently affected by mass mortality events (Cabello et al., 2002; González-Hunt, 2010) and irregular recruitment (Mendo et al., 2008). Even though an important part of Peruvian scallop production has been transferred to the northern coast of Peru (Piura and Ancash) mainly because new cultivation areas were enabled and seed availability, the greater growth rates, higher gonadosomatic index and easiest handling (shallow waters and accessibility) make Paracas bay an interesting area for exploitations by fishermen and aquaculture companies.

In spite of their socioeconomic importance (aquaculture, fishing, tourism...), oceanographic characteristics of Peruvian coastal bays remain poorly known. Although these bays may present their proper oceanographic dynamics, they might be influenced by larger scale phenomena such as El Niño oscillations and the nearby upwelling system. In Paracas Bay, evidences for high fluctuations of environmental parameters (temperature, primary production and oxygen saturation) have been shown in relation to El Niño (Wolff, 1987, 1988). Sears (1954), also found strong temperature variations independently of El Niño and related it to local water heating due to the solar radiations. More recently high frequency monitoring under "normal" ENSO conditions allowed to record dramatic variations in temperature and dissolved oxygen concentration (Aguirre-Velarde et al., 2016). Paracas Bay is also affected by the occurrence of milky-turquoise water events, locally known as "aguas blancas", that are related to high scallops mortality. Such water discolorations have also been described in Namibian and Chilean coastal waters in relation with high sulphide (H_2S) concentrations. The upwelling of oxygen depleted and H_2S loaded deep waters could be behind the formation of elemental sulfur microgranules giving these characteristic discolorations (Ohde et al., 2007). High productivity, the presence of a nearby vast oxygen minimum zone and an important vertical transport could be the origin of "aguas blancas" in Paracas Bay. However, there are insufficient available data to validate this hypothesis.

Although the links between environmental variability and *A. purpuratus* daily shell microgrowth have been recently studied in Paracas Bay (Aguirre-Velarde et al., 2015), bioenergetic consequences and adaptations of this species to deal such a variability remain poorly known.

In order to capture the Paracas Bay dynamics a high frequency environmental monitoring and biological sampling of scallops were performed. Collected data were used to identify environmental effects on growth, reproduction and survival of *Argopecten purpuratus*. This knowledge is essential to ensure proper management and sustainability of the Peruvian scallop commercial farming. In addition, this work is a contribution to the understanding of the dynamics of coastal bays in the context of the Peruvian upwelling and their impact on benthic resources.

3.2 Material and methods

3.2.1 Scallops collection and experimental site

In late August 2012 two batches of 2500 wild scallops ranging between 60-70 mm (group 1, mean = 66.8 mm, CI = ± 0.97 mm) and 30-40 mm (group 2, mean = 36.5 mm, CI = ± 1.2 mm) shell height were collected off Lagunillas (7.3 km south of Paracas Bay, Fig. 6.1). Scallops were immediately transferred at Paracas Bay and placed in a 5-m depth aquaculture area with sandy-muddy bottom (13°49'35" S, 76°17'43" W, Fig. 6.1; tidal range ≈ 1 m). Individuals were acclimated on the bay's bottom without any cage for 10 days before the beginning of the experiment. A third batch of 1000 individuals ranging from 35 to 45 mm (group 3, mean = 41.5 mm, CI = ± 1.14 mm) was collected in late December 2012 following the same procedure.

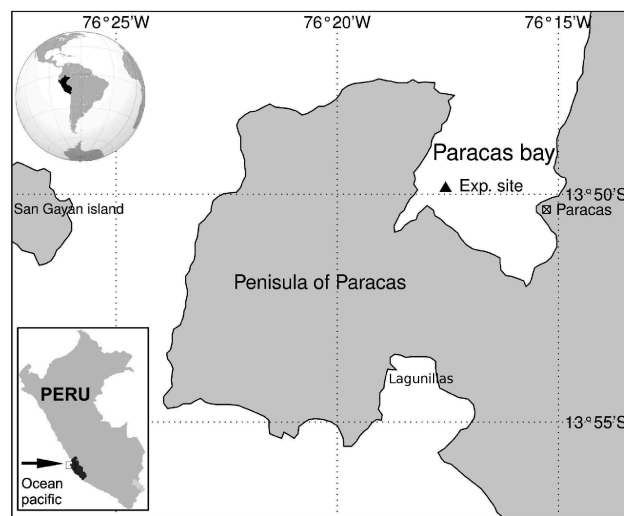


FIG. 3.1: Map of the experimental site in Paracas Bay (Peru; 13°49'35" S, 76°17'43" W). The experimental site was located in a 5-m depth area dedicated to the commercial farming of *Argopecten purpuratus*. Scallops used in the experiment were collected off Lagunillas.

3.2.2 Scallops culture set-up

After acclimatization, scallops of each batch were randomly placed in cylindrical cages constructed of plastic-coated metallic frame and monofilament mesh (diameter = 50 cm, height = 20 cm) with a density of 30 individuals per cage. For each batch, scallops were then placed into two growing conditions: half of the cages (25 for group 1 and 2 and 9 for group 3) were placed on the sea bottom, in contact with the sediment, and the other half were suspended in the water column at 2 m above the sediment. The experimental setup is shown in Fig. 6.2. A weekly monitoring of these cultures was conducted during a 7-months period between August 28, 2012 and Mars 10, 2013. This period included late winter, spring and summer in the Southern hemisphere.

Growth and reproduction monitoring

At the beginning of the experiment and then weekly (± 2 days), the scallops were sampled by removing one cage in each size group and culture depth. Shell height of live

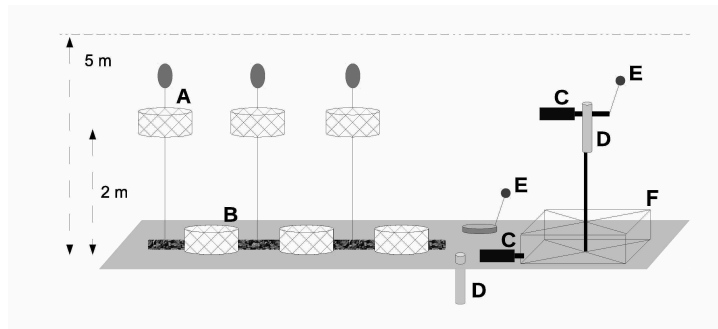


FIG. 3.2: Schematic representation of experimental set-up for scallop culture and environmental monitoring installed at Paracas Bay showing: suspended and bottom cages for scallop culture (respectively A and B), monitoring instruments (C), sediment traps (D), current meters (E) and the structure supporting the equipments (F).

scallops was measured at the nearest mm using a caliper. After dissection, wet-weight of gonads and somatic soft tissues was measured using a 0.01 g accuracy balance. For each sampled cage average shell height and somatic and gonadic wet weights with corresponding confidence intervals were calculated. A local polynomial regression (Cleveland et al., 1992) was used to assess the temporal trends of height and weight growth.

Reproduction (gametogenesis/spawning) was assessed in simple thought estimation of the gonadosomatic index (GSI). For each sample, GSI was calculated based on individual soft tissue wet weights as:

$$GSI = \frac{WW_{gonad}}{WW_{gonad} + WW_{somatic}}$$

where WW_{gonad} is the gonad wet weight and $WW_{somatic}$ is the somatic soft tissues wet weight. Average GSI and confidence intervals of each sample were calculated.

3.2.3 Environmental monitoring

Seawater environmental conditions were monitored at the two culture depths: (1) bottom, water-sediment interface and (2) Suspended, 2 m above the sea-floor on the water column. For this purpose, data-loggers and sampling equipment (Fig. 6.2) were placed on a metallic structure fixed to the bottom (Fig. 6.2 F) or directly on the sea-floor.

Physico-chemical descriptors

Autonomous data-loggers disposed at both monitoring depths (Fig. 6.2 C) allow recording temperature (HOBO U22-001), salinity (HOBO U24-002-C) and oxygen saturation (RBR TDO) with an hourly frequency. Oxygen and salinity probes were calibrated fortnightly. Current speed was estimated hourly using inclinometer current meters (Marchant et al., 2014) equipped with a three axes inclinometer data-logger (HOBO UA-004-64) placed at the two monitoring depths (Fig. 6.2 E). The relationships between current speed and inclination were tested into a hydraulic-test canal obtaining a calibration curve.

Wind speed and direction recorded at Pisco airport (13°44'42"S, 76°13'13"W, at 11.3 Km NE of the study site) were provided by Windfinder.com (2013). Because area upwelling is generated by Southeast trade winds in this (see Brink et al., 1983; Pauly

et al., 1989; Bakun and Weeks, 2008), positive meridional wind ($v+$) was used as a proxy to characterize the intensity of the upwelling-favorable wind.

Additionally, the occurrence of milky-turquoise water discolouration events (locally known as "aguas blancas" phenomenon) in Paracas Bay was recorded when visually observed.

Trophic resource characterization

At each culture depth, trophic resource was characterized by monitoring various food proxies. Phytoplanktonic cell determination and counting were realized weekly (± 2 days) on 1-L water samples collected at each depth using an horizontal Niskin bottle, and preserved in dark plastic bottles with Lugol. In-situ chlorophyll-*a* and turbidity were estimated using fluorescence/turbidity sensors (Trilux, Chelsea Technologies Group Ltd) fitted on autonomous digital dataloggers (Anticyclone Systems AntiLog). These sensor-logger assemblings were placed at each monitoring depth for 48h every weeks (Fig. 6.2 C). During deployment, chlorophyll-*a* concentration and turbidity data were recorded every hour. Sediment traps were deployed to estimate vertical fluxes of particulate matter (PM); one of them was placed in the water column and the other one was plugged into the sea-floor so that the apertures remained at the monitored depths (Fig. 6.2 D). The sedimented particulate matter was recovered weekly from both traps. Particulate organic and inorganic matter (POM and PIM, respectively) were quantified by drying (48h at 60°C) and calcining (3h at 500°C) the trapped material. Weight were measured using an 10^{-5} -g precision analytical balance. Particulate organic carbon and nitrogen (POC and PON, respectively) were quantified in aliquots of the captured material using a C-H-O-N elemental analyzer. Vertical fluxes for all PM descriptors were calculated using the following equation:

$$VF_x = \frac{W_x}{A_{trap} \cdot t}$$

where, VF_x (g or mg m^{-2} day $^{-1}$) is the vertical flux of the PM descriptor x , W_x (g or mg) is the total weight of the PM descriptor x captured in the sediment trap, A_{trap} (m^2) is the inlet area of the sediment trap and t is the time of trap deployment in the experimental area.

The C:N ratio (calculated as POC:PON) and PIM:PM ratio were computed from the measured particulate matter descriptors.

3.2.4 Data analysis

Environmental variables

Hypoxic conditions Continuous recording of oxygen saturation allowed calculating the daily and total monitoring cumulated hours that the scallops spent exposed to saturations lower than their oxygen critical point for respiration estimated at 24.4% (Aguirre-Velarde et al., 2016). These indices represent respectively the daily and global exposition to hypoxic conditions. A local polynomial regression (Cleveland et al., 1992) was used to assess the temporal trends of hypoxic conditions.

Stratification The degree of water column homogeneity between the two monitored depths was characterized by a stratification index calculated according to Li (2002) as:

$$SI = \frac{\Delta_{\sigma}}{\Delta_{depth}}$$

where, Δ_{σ} is the difference of density of the seawater between culture depths calculated from temperature and salinity using the IES80 equation and $\Delta_{depth} = 2m$ is the depth difference between the two culture conditions.

Statistics Because of the non-normal distribution of environmental descriptors, differences between the two culture conditions were tested using the nonparametric Wilcoxon test for each descriptor. Correlations between environmental descriptors were evaluated by cross-correlation analysis allowing identify lag-timed relationships between them. In addition, bottom and suspended culture conditions were characterized by they environmental descriptors using a principal component analysis (PCA). This allowed to identifying/summarize the variables that best characterized the culture conditions.

Environmental influence on growth and reproduction

Only environmental descriptors that showed significant correlations with the first component of the PCA (that explained the variance of bottom and suspended culture environmental conditions) were used to further study the relationships between environmental conditions and growth and reproduction.

Because biological sampling and environmental monitoring were performed with different times steps, data were linearly interpolated if necessary.

Analysis of the correlation between environmental conditions and growth was performed after removing the ontogenic reduction of growth rate (Gulland and Hold, 1959) according to the procedure described in Aguirre-Velarde et al. (2015). For this purpose, a weight-based von Bertalanffy growth function (VBGF) was fitted to the weight time series of groups 1 and 2 from bottom treatment (considered as a reference). Due to the strong environmental disturbances recorded during summer (hypoxic conditions, see Fig. 3), these fits were only performed during the winter-spring period (08/28/2012 and 12/01/2012). Growth rate deviations (E_{Growth}) between interpolated weight time series and expectations from the fitted VBGF were computed for each culture condition according to Aguirre-Velarde et al. (2015) as :

$$E_{Growth.t} = \overline{GR}_t^{obs} - GR_t^{calc.bottom}$$

where, $E_{Growth.t}$ ($g\ d^{-1}$) is the growth rate deviation at time t ; \overline{GR}_t^{obs} ($g\ d^{-1}$) is the interpolated average growth rate at time t ; and $GR_t^{calc.bottom}$ ($g\ d^{-1}$) is the predicted bottom growth rate at time t (from VBGF).

Gonadosomatic index temporal trend (GSI-trend) was evaluated at each culture condition using local regression models (Cleveland et al., 1992) in order to smooth the gametogenesis-spawning cycles and detect variations in reproductive activity. GSI-trend deviations (E_{GSI}) from a GSI reference (winter-spring average) were calculated.

A cross-correlation function analysis (CCF) was performed in order to highlight the eventually time-lagged relationships between E_{growth} and E_{GSI} and environmental descriptors (eight-day average). In addition, stepwise regression (Akaike information criterion - AIC) was used to identify environmental variables which better explain the E_{growth} variation. The relative importance in terms of contribution to the coefficient of determination (R^2) was also estimated for each environmental variable by calculating the bootstrap measures.

3.3 Results

3.3.1 Environmental dynamics

Physico-chemical conditions

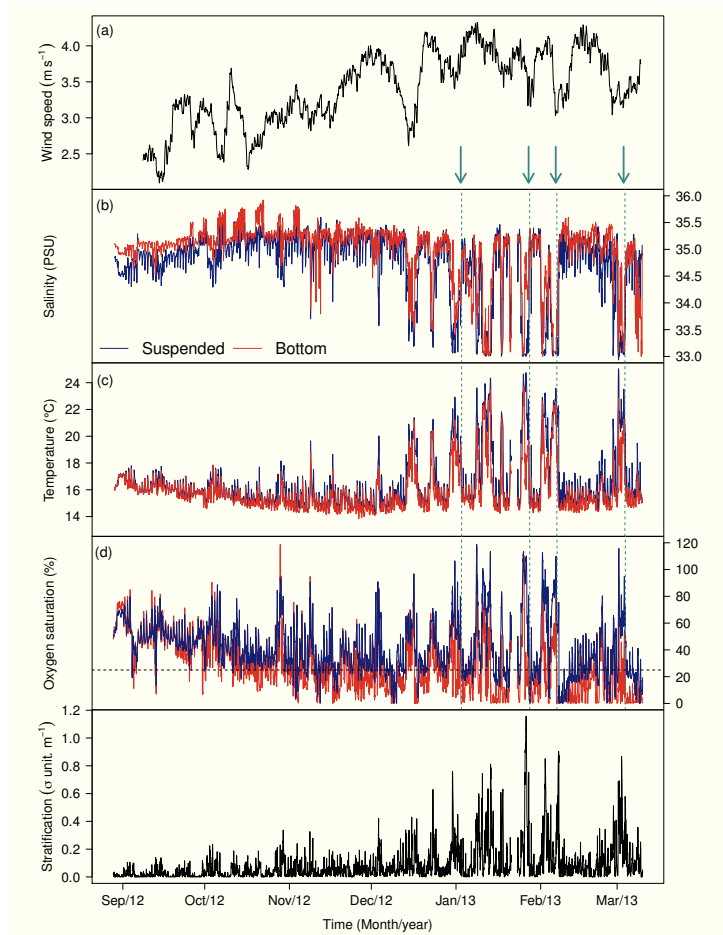


FIG. 3.3: Environmental descriptors recorded in Paracas bay on the bottom and in suspended culture: past seven-day moving average of upwelling favourable winds (a), salinity (b), temperature (c), oxygen saturation (d) and stratification index (e). The arrows and vertical dashed lines indicate the occurrence of milky-turquoise water discolorations in the bay.

Physico-chemical conditions of seawater were generally more stable between late winter and late spring (from August to November, Fig. 3.3). During summer, important and rapid environmental changes were observed on bottom as well as in suspended culture. Daily cycles with increases (day) and decreases (night) in temperature and oxygen saturation were identifiable all along the monitoring period (Fig. 3.3 c and d). Although the difference was low ($< 0.8^{\circ}\text{C}$), temperature was significantly higher in suspended culture than on the bottom (Wilcoxon test, $p < 0.001$). The minimum and maximum temperature recorded were 13.8°C and 23.7°C (mean = 15.8°C) respectively on the bottom, while the minimum and maximum values were 14.1°C and 25.0°C (mean = 16.5°C) respectively at suspended culture depth. Temperature (Fig. 3.3 c) exhibited a decreasing pattern at the beginning of the monitoring period (from late August to November) and was highly variable during summer (from late December to March). The median salinity throughout the monitoring period was 35.2 and 35.0 for bottom and suspended

culture, respectively. Salinity (Fig. 3.3 b) was significantly and negatively correlated to temperature in both bottom ($R^2 = 0.84$, $p < 0.001$) and suspended culture ($R^2 = 0.97$, $p < 0.001$). During this period, events of dramatic (positive or negative) variations of temperature (up to $\approx 10^\circ\text{C}$) occurred (Fig. 3.3 c) and were inversely related to variations of salinity (up to ≈ 2). Highest temperature variation rate reached $\approx 1^\circ\text{C}/\text{hour}$. The lowest temperatures observed during summer were similar to those found in winter-spring.

In spite of the low average difference in temperature between bottom and suspended cultures, strong stratification events of 3-4 days occurred during the summer: instantaneous difference up to 8°C between the bottom and suspended cultures were recorded.

The average oxygen saturation ($\text{O}_2\text{ sat}$) recorded on the bottom was significantly lower than in suspended culture during the monitoring period (Wilcoxon test, $p < 0.001$), the average difference between the two depths was 13.5%. Median $\text{O}_2\text{ sat}$ were 25.6% on the bottom and 39.4% in the suspended treatment. At both depths, seasonal average $\text{O}_2\text{ sat}$ was higher in winter (Wilcoxon test, $p < 0.001$). A decreasing trend in $\text{O}_2\text{ sat}$ was observed during spring, with a significantly lower average in summer than in winter and spring (Wilcoxon test, $p < 0.001$). Between December and March strong variations of $\text{O}_2\text{ sat}$ were observed: at both depths, $\text{O}_2\text{ sat}$ varied from oversaturation to anoxia. During summer, regular events of severe hypoxia and anoxia were observed at both depth although they were more marked on the bottom. The longest events of severe hypoxia and anoxia were recorded between January and March on the bottom when hypoxic conditions coincided with low temperatures. On the bottom treatment, $\text{O}_2\text{ sat}$ was more frequently below the P_cO_2 of *A. purpuratus* than in suspended culture. Over the whole monitoring period, bottom scallops were exposed to $\text{O}_2\text{ sat}$ below their P_cO_2 for 48% of the time as this proportion was only 18% for the suspended ones. It should be noted that those hypoxic/anoxic events were frequently concomitant with abrupt decreases in temperature and frequently associated with the occurrence of milky-turquoise water discolourations in the bay. These discolorations were visually observed four times during summer on Jan-03-13, Jan-28-13, Feb-07-13 and Mar-04-13 (Fig 3, turquoise arrows and vertical dotted lines). February was the coldest month during the 2013 summer season and also presented the lowest oxygen saturations during the monitoring period.

Temporal evolution of hypoxic conditions is showed in Fig. 3.4. Seasonal average of daily hours spent in hypoxic conditions was significantly lower in winter (Wilcoxon test, $p < 0.001$) with a marked tendency to increase during spring and reaching maximal values in summer. In suspended culture a large number of consecutive days with $\text{O}_2\text{ sat}$ above 24.4% (P_cO_2) was observed between late August and late October. An important increase in hours spend in hypoxic conditions was observed on early October on the bottom, while in suspended culture this increase was observed later in early November. From December (late winter) to summer, hypoxic conditions lasting for 24 hours were observed in both conditions although this was more frequent on bottom. During summer, up to four consecutive days under hypoxic conditions were observed on the bottom while the recorded maximum in the suspended treatment was two days. At both depths, most recurrent hypoxic conditions were observed in early March.

During all the monitoring period, median oxygen saturation exhibited clear daily cycles (Fig. 3.5) with low oxygen saturation around 6:00 while the maximum was recorded around 15:00 (at both depths). On the bottom, hourly median oxygen saturation did not exceed the P_cO_2 between 21:00 and 11:00 but in suspension the hourly median $\text{O}_2\text{ sat}$ exceeded the P_cO_2 the whole day long.

From winter to summer, the $v+$ moving average tended to increase (Fig. 3.3 a). A

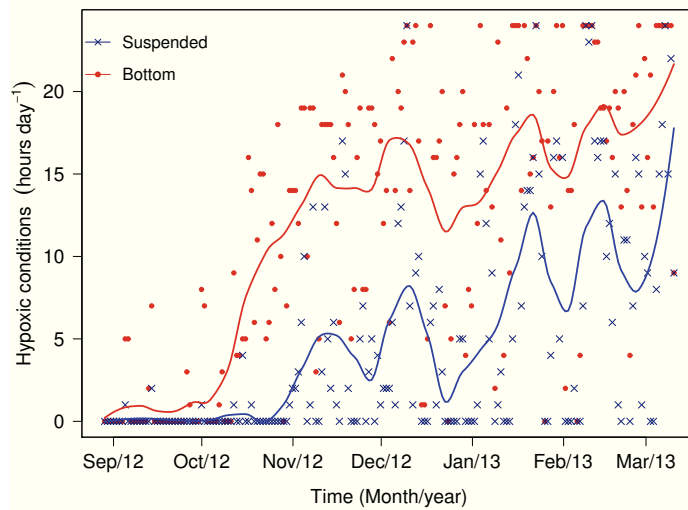


FIG. 3.4: Hypoxic conditions, daily counting of hours with oxygen saturation below *Argopecten purpuratus* critical oxygen point for respiration (24.4% estimated in Aguirre-Velarde et al., 2016), underwent by scallops on bottom and suspended cultures. Lines represent the trends of hypoxic conditions estimated from a local linear regression for each culture

relaxation period of $v+$ was observed on mid-December (late spring) while high values were recorded during summer.

Temperature, salinity and oxygen saturation were significantly correlated (ρ , $p < 0.001$). The cross-correlation analysis indicates that temperature, oxygen saturation and stratification time-series were inversely correlated ($p < 0.05$) to $v+$ (daily average) while a positive correlation ($p < 0.05$) was observed between salinity and $v+$ (Table 3.1). CCF highlighted a 1-day time-lag in the correlation between $v+$ and physico-chemical parameters. In addition, oxygen saturation was inversely correlated ($CCF_{max} = -0.42$, $p < 0.05$) to the stratification index while hypoxic conditions was positively correlated ($CCF_{max} = 0.44$, $p < 0.05$) and this with 5-days time-lag.

TAB. 3.1: Summary of the cross correlation analysis: maximum cross-correlation values (CCF) and corresponding time-lags between abiotic seawater descriptors registered on bottom and positive meridional winds ($v+$) speed time-series.

	Salinity	Temperature	Oxygen saturation	Stratification
	CCF (lag)	CCF (lag)	CCF (lag)	CCF (lag)
$v+$	0.31 (-1)	-0.50 (-1)	-0.40 (-1)	-0.37 (-1)

Anoxic conditions, often coinciding with the occurrence of milky-turquoise water discolourations, were associated with low temperatures (14°C-17°C) and salinities above 35 (Fig. 3.6). In suspended culture, $O_{2\text{ sat}}$ lower than 25% were observed only at temperatures lower than 17.5°C while on the bottom these conditions occurred at temperatures up to 20°C.

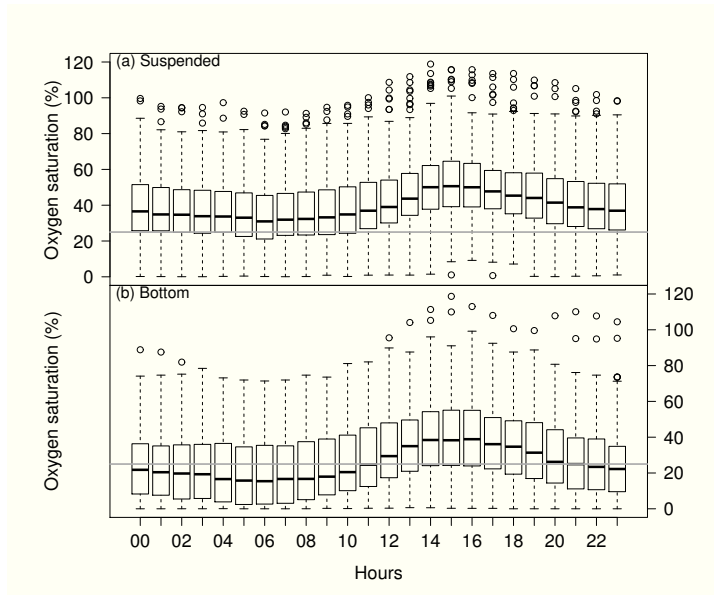


FIG. 3.5: Hourly distribution of oxygen saturation registered on scallops bottom (a) and suspended (b) cultures. The grey horizontal line represents the critical oxygen point for *Argopecten purpuratus* (24.4%, Aguirre-Velarde et al., 2016)

Trophic resource availability and quality

Phytoplankton cell concentration showed an increasing trend during the monitoring period at both depth (Fig. 3.7 a) and no significant differences over the all monitored period were observed (Kruskal-Wallis Test, $p > 0.05$). Maximum cell concentrations were observed between January and February at both depths, reaching up to 8×10^8 cells L^{-1} in suspended culture. In contrast the minimum cell densities were recorded in early September. Although chlorophyll-*a* weekly averages were significantly higher on bottom than in suspended culture during the summer period (Wilcoxon test, $p < 0.05$), the average chlorophyll-*a* concentration over the whole monitoring period was significantly higher in suspended culture than on the bottom (Wilcoxon test, $p < 0.05$). Vertical fluxes of POM, POC and PON were not significantly different (Kruskal-Wallis Test, $p > 0.05$) between culture conditions and remained relatively constant over the monitoring period. Only the POC flux was significantly higher on the bottom compared to the suspended condition (Wilcoxon test, $p < 0.05$). The C:N ratio was relatively stable and only exhibited variation from 4 to 9 but strong variations of PIM:PTM ratio were observed within a range of 0.04 and 0.74 and this at both monitoring depths (Fig. 3.8). No significant differences of PM quality descriptors were identified amongst culture conditions (Kruskal-Wallis Test, $p > 0.05$). In both culture conditions, turbidity was low at the beginning of the monitoring period and increased after mid-October. Turbidity was significantly higher (Wilcoxon test, $p < 0.001$) on the bottom than in suspended culture (Fig. 3.8 a), with average values 2.6 times higher and a turbidity peak up to approx. 10 NTU in late spring.

Characterization of cultures environments

Results of Wilcoxon rank test ($H_1: median_1 > median_0$) for each environmental descriptor indicating differences/similarities between bottom and suspended conditions are summarized in table 3.2. The most significant differences between the two cultivation depths are caused by the physico-chemical descriptors and turbidity. Although in

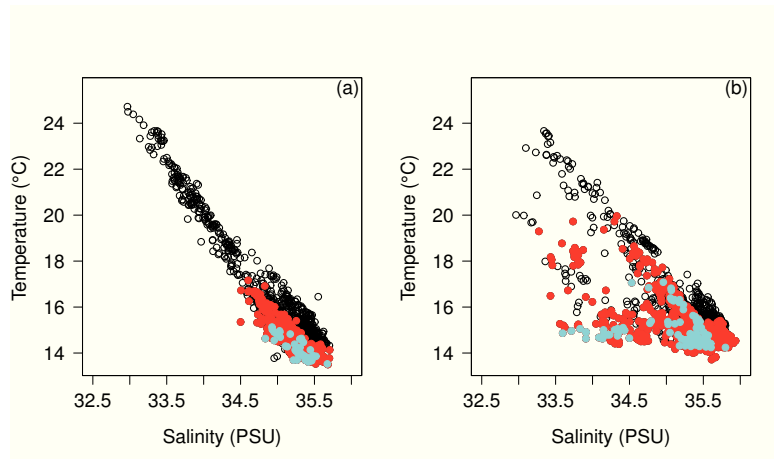


FIG. 3.6: Temperature vs salinity graphs for overall monitored period in scallop suspended (a) and bottom (b) cultures. Colour scale indicates corresponding oxygen saturation (red < 24.4%; cyan < 1%)

trophic terms, environmental conditions were more homogeneous, observations show a relatively greater concentration of chlorophyll-a in suspended culture compared to POC in bottom culture. In order to summarize scallops growing conditions and identify environmental variables with important effects, only descriptors exhibiting a significant differences between monitored depths ($p < 0.05$) were used for the principal component analysis. The first and second principal components that explain 39.3% and 26% of the variance, respectively, are plotted in Fig. 3.9. The variables (environmental descriptors) are show as vectors while samples (points) represent weeks during the monitoring period. Except for salinity, all physico-chemical descriptors showed a significant ($p < 0.01$) contribution to the first principal component unlike trophic resource descriptors ($p > 0.05$). Strong correlations between hypoxic conditions, turbidity and oxygen saturation as well as between temperature and salinity were observed. Bottom and suspended groups distributed throughout the first principal component can be distinguished. The bottom group is characterized by "unfavorable conditions" (hypoxia and turbidity) while the suspended one by "favorable conditions" (oxygen saturation). Only environmental descriptors exhibiting a high (> 0.50) and significant correlation ($p < 0.001$) with the first principal component (saturation = -0.96, hypoxic conditions = 0.84, turbidity = 0.79 and temperature = -0.54) were used to evaluate their effects on scallops growth and reproduction.

3.3.2 Scallops culture

Growth and reproduction

At the end of the monitoring, shell heights and somatic weights of scallops were significantly higher (t-test, $p < 0.001$) in suspended culture than on the bottom and this for all size groups (Fig. 3.10). During the whole monitoring inter-individual variability of these variables within cages remained relatively low. Shell growth in suspended cultures was almost constant while it seems to stop on bottom between December 2012 and January 2013 (Fig. 3.10 a). Somatic weight losses were observed in groups 1 and 2 (Fig. 3.10 b) in late spring (bottom) and summer (bottom and suspended). Scallops in group 1 were the most affected at both culture depths with weight losses up to 25% in suspended culture compared to 20% on the bottom. At the end of the monitoring

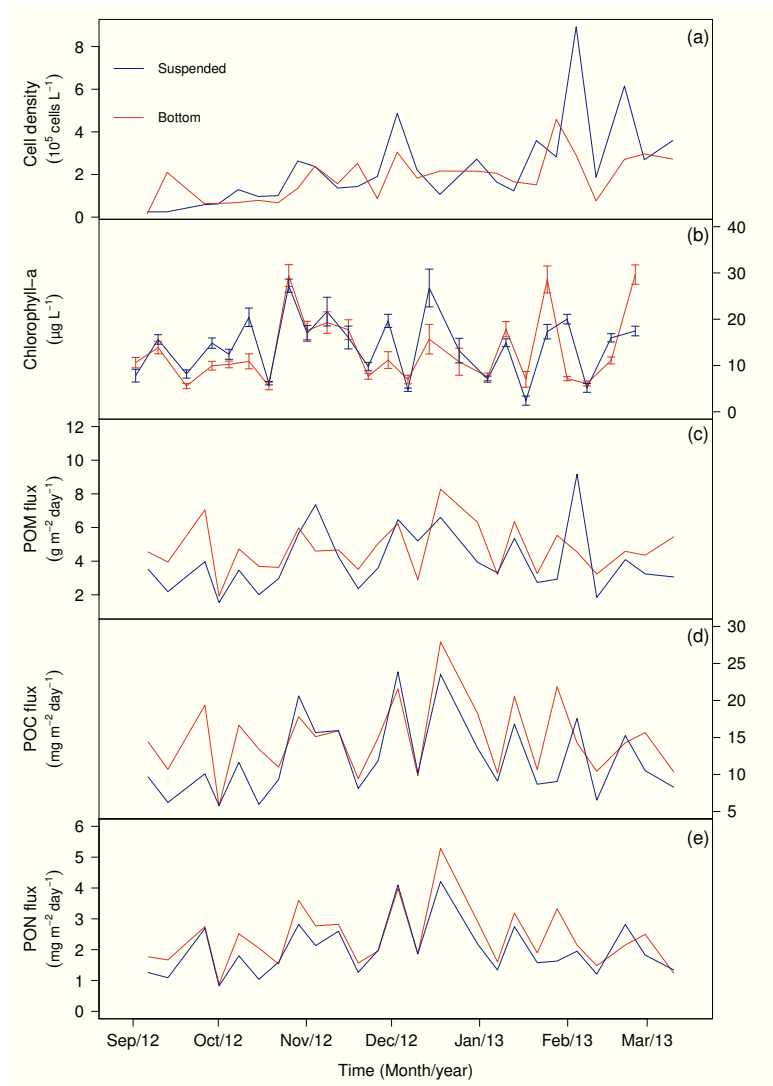


FIG. 3.7: Trophic descriptors recorded in Paracas Bay on the bottom (red lines) and in suspended cultures (blue lines): cell density (a), 48-hour chlorophyll-*a* mean with 95% confidence intervals (b), vertical fluxes of particulate organic Matter (c), Carbon (d) and Nitrogen (e).

period (early March), a recovery in somatic weights culture was observed in suspended. In group 3, for which the monitoring begun in early summer, somatic growth was not significant on the bottom (t-test, $p > 0.05$).

Average gonado-somatic indices (GSI) were significantly higher in suspended culture (24.7%, max= 33.4%, min= 12.8%) than on the bottom. (18.2%, max= 27.3%, min=9.2%). Three marked GSI cycles were observed between late August and late November (winter-spring) in size groups 1 and 2 in suspended culture (Fig. 3.10 c). In scallops reared on the bottom only two cycles between September and late October were observed. These GSI cycles, synchronous between the scallop batches, had approximately a 28-30 days period. During summer, after January, average GSI were significantly lower without distinguishable cycles in any scallop batch. During the last weeks of monitoring, GSI of suspended culture scallops re-increased. In group 3, only scallops in suspended culture showed a significant increase in GSI; scallops reared on the bottom exhibited the lowest GSI among all groups.

The somatic weight losses as well as reproductive cycle alteration with significant

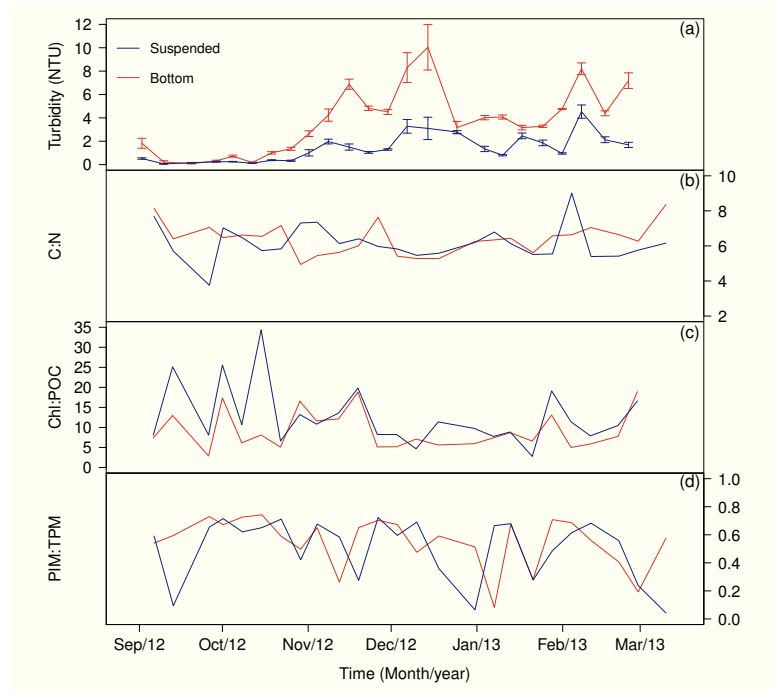


FIG. 3.8: Trophic resource quality descriptors recorded in Paracas Bay near bottom (red lines) and in suspended culture (blue lines): turbidity (a), C:N ratio (b), and PIM:TPM ratio.

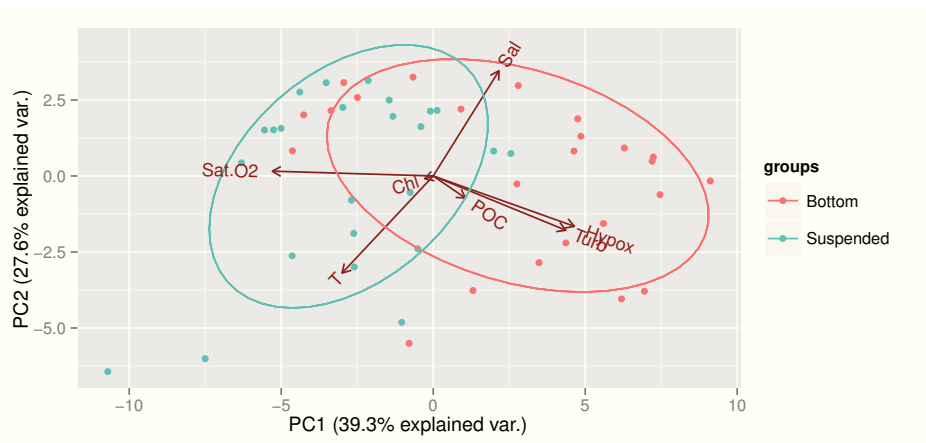


FIG. 3.9: Principal component analysis performed on environmental characteristics of scallop culture treatments. Biplot representing the two first principal components where variables are T: temperature; Sat.O2: oxygen saturation; Sal: salinity; Hypox: Hypoxic conditions; Turb: turbidity; Chl: chlorophyll-*a*; POC: Particulate Organic Carbon. Bottom culture is more related to hypoxic conditions and turbidity while suspended culture is associated with favourable oxygen saturation conditions.

GSI decreases coincided with hypoxic/anoxic events and milky-turquoise water discolourations during summer.

Survival

An initial decrease of survival was observed during the first three weeks of the monitoring in scallops groups 1 and 2 (Fig. 3.11 a and b). Then, survival stabilized until late spring then an important mortality occurred in scallops from both conditions in size

TAB. 3.2: Summary of environmental descriptors differences/similarities between bottom and suspended scallop culture conditions (Wilcoxon rank tested, $H_1: median_1 > median_0$). Significant ($p < 0.05$) higher median conditions are indicated with a plus sign (+). Highly significant differences ($p < 0.001$) are indicated with grey background

		Suspended	Bottom
Physico-chemicals	Temperature	+	
	Salinity		+
	Oxygen saturation	+	
	Hypoxic conditions		+
Trophic resource	Cell density		
	Chlorophyll-a	+	
	Availability		
	POM		
	PIM		
	POC		+
Quality	PON		
	Turbidity		+
	C:N		
	Chl:POC	+	
	PIM:TPM		

group 2. Scallops reared on the bottom were the most affected in terms of mortality: no survivors were found in cages at the end of the monitoring. In suspended culture, the highest survival was found in size group 3 (Fig. 3.11 c) followed by group 1 and finally by group 2 for which the cumulative mortality exceeded 50%. Important mortalities occurred in bottom culture during summer and coincided with the occurrence of milky-turquoise water discolourations.

3.3.3 Environmental effect on scallops growth and reproduction

Significant correlations ($p < 0.001$) between somatic growth rate deviations (all size groups confounded) and temperature ($r = -0.39$), hypoxic conditions ($r = -0.48$), and turbidity ($r = -0.48$) were found. The temporal trend of gonadosomatic index (GSI-trend) was significantly correlated ($p < 0.001$) to hypoxic condition ($r = -0.84$), oxygen saturation ($r = 0.71$), and turbidity ($r = -0.69$). Environmental variables were used to construct linear explicative models for growth rate deviations. Because of strong collinearity between hypoxia and turbidity ($r > 0.80$), the analysis of environmental contribution to E_{growth} and E_{GSI} variances explanation was conducted independently. The best models according to the AIC criterion for somatic growth rate deviations were:

$$E_{growth} = 1.645 - 0.100T - 0.013Hypox + 0.001T : Hypox \quad R^2 = 0.44, p < 0.001 \quad (3.1)$$

$$E_{growth} = 1.197 - 0.072T - 0.189Turb + 0.010T : Turb \quad R^2 = 0.44, p < 0.001 \quad (3.2)$$

In model 1 the greatest contribution to the R^2 was provided by the hypoxic conditions ($p < 0.001$) with 53%. In model 2, turbidity contributed 56% to R^2 ($p < 0.01$). In both models, interactions of hypoxic conditions and turbidity with temperature had a positive but small contribution (<15%).

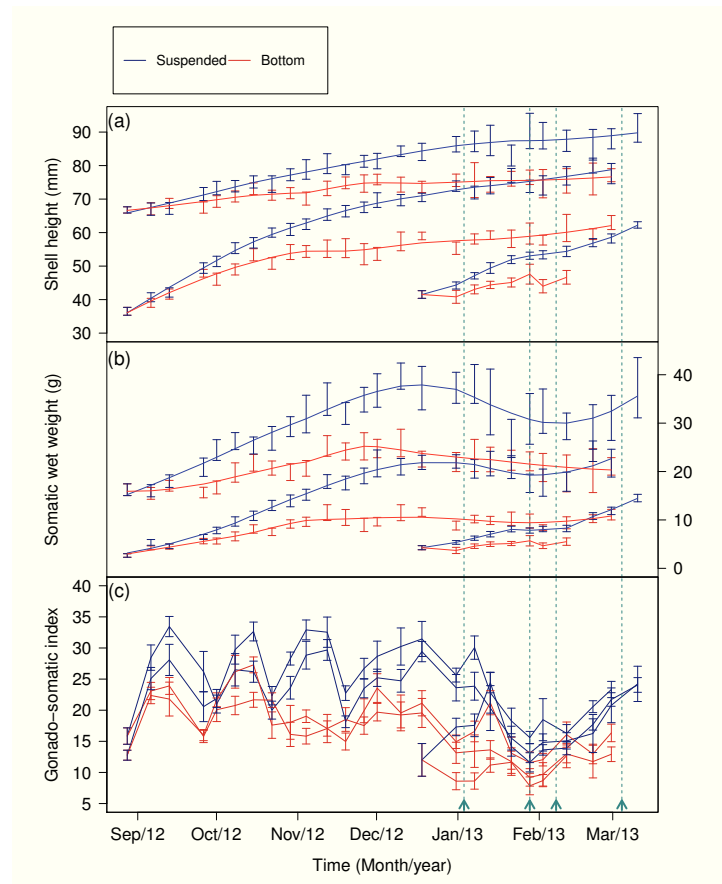


FIG. 3.10: Results of the growth and reproduction monitoring. Evolution of mean shell height (a) and somatic wet weight (b) and gonado-somatic index (c) of the three size groups of scallops cultured in bottom (red line) and suspended (blue line). The arrows and vertical dashed lines indicate the occurrence of milky-turquoise water discolorations in Paracas bay. Bars indicate 95% confidence intervals

The best model according to the AIC criterion for GSI-trend took into account only the contribution of the hypoxic conditions:

$$E_{GSI} = 4.136 - 0.071hypox \quad R^2 = 0.71, p < 0.001 \quad (3.3)$$

$$E_{GSI} = 2.721 - 1.208Turb \quad R^2 = 0.47, p < 0.001 \quad (3.4)$$

The results from models 1 and 2 show that temperature, hypoxia and turbidity had a negative effect on growth rate deviations. Relative important contributions (> 50%) to the R^2 highlights the effects of hypoxic conditions and turbidity on growth rate deviations variance in their respective models. On the other hand, GSI-trend deviations (models 3 and 4) were very dependent on hypoxia. Model 3 highlights a significant negative effect of daily hours under hypoxic conditions on reproductive condition.

3.4 Discussion

Environmental variability

Due to the presence of a wind-driven upwelling system, that up-wells cold deep waters toward the surface, the Peruvian coast is both a highly productive and dynamic

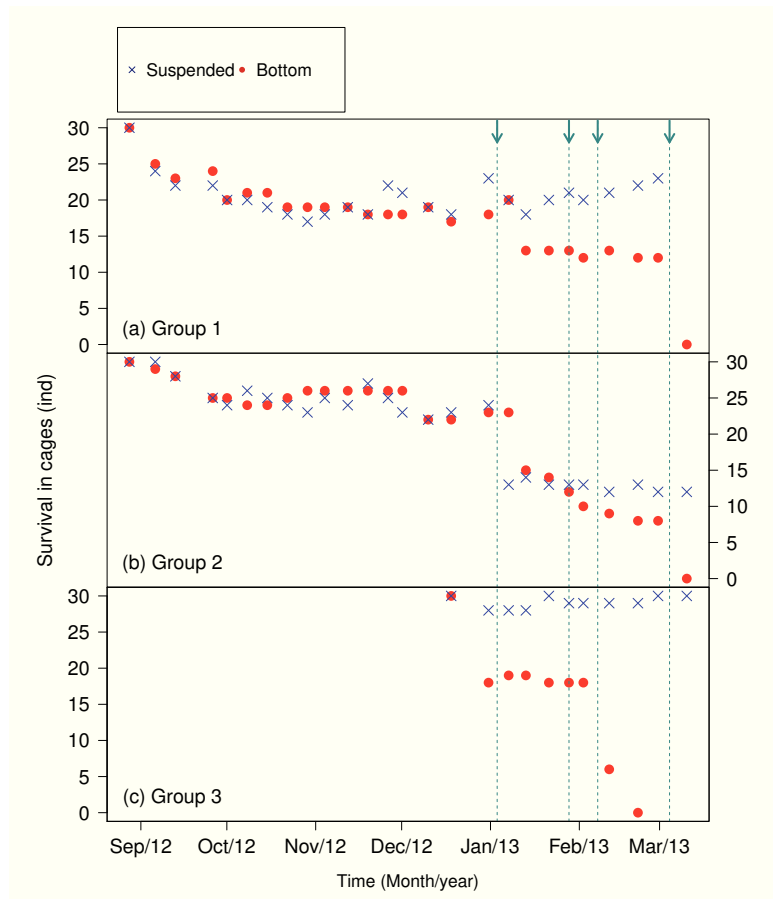


FIG. 3.11: Survival of scallops size groups 1 (a), 2 (b), and 3 (c) in bottom and suspended cultures. The arrows and vertical dashed lines indicate the occurrence of milky-turquoise water discolourations in Paracas Bay.

ecosystem exhibiting, for instance, remarkable temperature variations (Brink et al., 1983). Under El Niño conditions, warm waters invade the Peruvian coast (Wyrki, 1975). Although offshore temperature variability (ocean water masses) and winds patterns are well documented (see e.g. Burt et al., 1973; Pauly et al., 1989; Croquette, 2007), data on oceanographic dynamics inside Peruvian coastal bays are scarce. Until now, only Wolff (1987, 1988) documented $\approx 8-9^{\circ}\text{C}$ temperature variations between El Niño and post-event conditions (1983-1984 in Paracas Bay. The same pattern was observed in northern Chile (Rinconada bay, see Thébault et al., 2008) which also support a wind-driven upwelling system. Interestingly, our study emphasizes that strong variations in temperature up to approx. 8°C are frequently observed in Paracas even under ENSO conditions considered as normal (reports 2012-2013, NOAA, 2013). Similar observations have been done by Aguirre-Velarde et al. (2016). The question of temperature variability in Paracas Bay was addressed by Sears (1954), who hypothesized that the high temperatures was related to solar heating during a long upwelling relaxation period. Nevertheless, our high frequency data indicate positive and negative temperature variations within the range of few hours suggesting that this variability is due to changes in water masses location. The correlation of these temperature variations with $v+$ wind component as well as with other physico-chemical descriptors (salinity, oxygen and water column stratification) supports this explanation and emphasizes the importance of local wind on the hydrodynamics of this shallow bay. Although winds measured at Pisco airport station would not be relevant at the scale of the Peruvian upwelling system, they

could drive a cold water vertical transport into the bay locally. During summer, local southern wind is more intensive, but the offshore trade winds decrease and temperature increases (Pauly et al., 1989; Croquette, 2007; Gutiérrez et al., 2011). Local wind relaxation would allow the entrance of offshore warm water masses into the bay. During winter, an active offshore upwelling (Bakun and Mendelssohn, 1989) would cause more homogeneous conditions between the in- and offshore thus explaining the more stable conditions observed during winter. Decoupling of in-offshore winds was observed by Burt et al. (1973) on a daily scale; nevertheless, the interactions/dynamic between both inshore and offshore winds have been poorly studied.

Naturally highly productive coastal ecosystems, such as upwelling zones, are frequently characterized by low oxygen concentrations (see e.g. Helly and Levin, 2004). This phenomenon is due to the oxygen consumption in deep waters associated with the decomposition of the abundant organic matter originating from the superficial productive layer (Zhang et al., 2010; Gewin, 2010). The chronic and severe hypoxic/anoxic events observed in Paracas Bay are likely to be related to the local productivity-decomposition processes and the advection of oxygen-depleted deep waters within the bay. The last assumption is supported by the fact that severe hypoxic/anoxic events occur simultaneously with acute temperature diminution and salinity increase. Upwelled coastal waters are characterized by temperatures between 14-18°C and salinities between 34.9-35.0 PSU (Morón, 2000). As noted above, the wind is probably responsible for hydrodynamics in the bay and therefore the "motor" of the arrival of anoxic events. Although low oxygen saturation was observed all along the monitoring period, the strongest hypoxic/anoxic events were observed in summer. Their occurrence might be related to higher local southerly winds relaxation ($v+$) associated with the observed higher primary production (phytoplankton cell density) and increased stratification. Similar summer increases of coastal hypoxia have been reported in Oregon (Gewin, 2010) and Benguela (Monteiro et al., 2008) upwelling systems. The most severe anoxic events occurred after strong stratification event (Fig. 3.3) associated with southerly winds ($v+$) relaxation. This suggests that such events might worsen the situation by limiting oxygenation of bottom water layer within the bay. The present work shows that Paracas Bay can be exposed to severe and chronic hypoxic conditions.

In upwelling systems, the observation of milky-turquoise waters is generally associated with presence of elemental sulphur micro-particles in seawater (Weeks et al., 2002, 2004; Ohde et al., 2007). These micro-particles originate from the oxidation of upwelled hydrogen sulphide (H_2S) produced in oxygen-depleted deep waters by anaerobic microbial metabolism (Millero et al., 1987). Although we did not measure H_2S concentration neither the presence of colloidal sulfur in the water, we can hypothesize that the observation of the milky-turquoise waters, locally know as "aguas blancas" is due to this phenomenon. This hypothesis is supported by the fact that water discolorations were observed only in low temperature and anoxic waters that may originate from oxygen-depleted and H_2S deep upwelled water masses after a strong water column stratification. Such events have been reported near Paracas Bay in 2009 (Schunck et al., 2013) and similar events have been reported in Humboldt (Arntz et al., 2006; Gallardo and Espinoza, 2008) and Benguela (Weeks et al., 2004; Ohde et al., 2007; Brüchert et al., 2009) upwelling systems. Summer high productivity associated with higher stratification and likely greater local vertical transport (wind-driven) would increase the probability of occurrence of these events during this season. Sulfide toxicity was identified as the cause of aquatic populations mass mortality (see review of Bagarinao, 1992).

Environmental descriptors of bottom and suspended cultures

Most of the measured descriptors exhibited similar patterns between bottom and suspended culture overall except during strong summer stratification events. Nevertheless, although the depth difference between culture conditions was small, absolute values of the descriptors exhibited differences that might impact bio-energetics. Surprisingly, the culture conditions differed in terms of physico-chemical variables more than in food availability descriptors: oxic conditions as well as turbidity (both correlated) were the descriptors that exhibited the strongest differences between bottom and suspended culture. Although, the latter was also touched by hypoxia, severe and continuous low oxygen conditions were more pronounced on the bottom. These differences in exposure to hypoxia, in terms of intensity and duration, might induce differences in energetic of the scallops. Higher turbidity on the bottom due to resuspension and/or sedimentation might have some repercussion on the environmental/trophic quality.

Surprisingly, average chlorophyll-*a* cell concentration was higher in the suspended treatment than on the bottom while no difference was found in terms of cell concentration. This pattern might be explained by a higher chlorophyll-*a* content in the suspended treatment due to higher light conditions, or more probably by the difference in sampling frequency of both parameters. The average POC flux was higher on the bottom and was associated with a higher turbidity, thus this flux might be related to the deposition/resuspension of detritus. Strong PIM variability might be due to terrigenous atmospheric inputs, due to strong wind events so-called "Paracas winds".

During the whole monitoring, and in both treatments food availability was abundant and it is unlikely that it constituted a limitation in any of the treatments.

3.4.1 Consequences of hypoxic conditions on *A. purpuratus*

In bivalves, growth differences have been attributed to seston quantity and/or quality (Thouzeau et al., 1991; Grant, 1996; Lodeiros et al., 1996; Chauvaud et al., 1998; Lodeiros, 2000; Cantillán et al., 2007; Hunauld et al., 2005; Lodeiros et al., 2011). However our study tend to show that in Pacaras Bay ecosystem, influenced by the nearby upwelling system and thus very productive, there is little effect of trophic disponibility/quality on scallop growth. Other parameters such as oxic conditions and turbidity would control growth. The negative effect of hypoxia on growth has been reported in several aquatic species (Wu, 2002). Oxygen availability is susceptible to control bivalve bio-energetics and subsequently growth through various phenomena. Under hypoxic conditions, and beyond the oxyregulation ability, energetic yield is reduced due to the use of less efficient anaerobic pathways (Herreid, 1980; Pörtner and Grieshaber, 1993). Because metabolic costs of maintenance, including all processes that allow homeostasis, are payed in priority (Kooijman, 2010a), reducing energetic yield might impair allocation of energy to growth and reproduction. In addition, the accumulation of metabolic endproducts from anaerobic pathways may also modify the energy balance because of their toxicity (accumulation) and energy costs associated with their elimination (Herreid, 1980). This hypothesis is in accordance with our observations: growth rate deviations were negatively related to hypoxic conditions. In addition, growth was lower on the bottom where exposure to hypoxia was twice higher than in suspended culture. Hypoxic conditions increased during summer in both treatments and somatic weight loss was observed, especially in large size scallops groups. Although the Peruvian scallop exhibits a high regulation ability for oxygen uptake (Aguirre-Velarde et al., 2016), effective filtration and growth in oxygen-limiting conditions (Chapter 5), severe and chronic

hypoxia exposure might have important bioenergetic implications. During severe and prolonged hypoxic conditions if the energy available for maintenance from assimilation is insufficient, a mobilization of somatic tissues could occur and might explain the observed decrease of somatic weight. However, in smaller size groups, for which oxygen diffusion might be more efficient due to a higher surface to volume ratio, weight loss was less marked. Surprisingly, shell growth (calcification) was maintained even when weight loss was observed. This could be due to the low energetic cost of shell formation (Palmer, 1992), which can be maintained even under such unfavorable conditions (Chapter 5).

The synchronous gonado-somatic index cycles (gametogenesis-spawning) observed during winter and early spring appear to have a monthly (close to 28-day) periodicity in both culture conditions. This pattern might be related to environmental variability due to the 29.5-day describing the synodic month (Barber and Blake, 2006; Thébault et al., 2008) or to moon-related endogenous clocks (Takemura et al., 2010; Numata and Helm, 2015). In aquatic environments having low variability of photoperiod and water temperature as in tropical latitudes, moonlight intensity acts as a reliable zeitgeber that influences physiological activities (Takemura et al., 2010). To our knowledge, there is no previous study investigating the influence of lunar phase on Peruvian scallop gametogenesis. Nevertheless, there are some reports of reproductive activity apparently related to lunar cycles in the Pectinidae family (Amirthalingam, 1928; Tang, 1941; Sasstry, 1979; Mason, 1958; Parsons and Dadswell, 1992; Barber and Blake, 2006). The observed synchronism during the first months of monitoring was lost around November. The significant increase of hypoxic conditions between October and November on the bottom, and in both culture conditions during the summer might have impacted scallop reproduction. As for growth, negative effects of hypoxia on aquatic organisms have already been reported (Diaz and Rosenberg, 1995; Levin et al., 2009; Zhang et al., 2010; Kodama and Horiguchi, 2011). As for growth, oxygen limitation may impair reproduction thus compromising the GSI and gonadal development cycles. In addition, as for somatic weight decrease, the hypothesis of a mobilization of reproductive tissues to pay maintenance costs cannot be excluded. Similarly, a reduction in energy allocation to reproduction has been documented in the gastropod *Nassarius festivus* under decreasing oxygen concentration (Cheung et al., 2008). The strong relationship between oxic conditions and variations of the GSI would indicate that oxygen availability affects the reproductive capacity of *Argopecten purpuratus*.

The mortality observed during the first month of the monitoring might be associated with the initial handling stress. During summer, where hypoxic/anoxic conditions became recurrent, survival of scallops decreases dramatically. Although *A. purpuratus*, as other bivalves, is tolerant to oxygen-limiting conditions, prolonged and repeated exposures to severe hypoxia or anoxia may have negative consequences on survivorship as in other marine organisms (Wu, 2002; Levin et al., 2009). In this regard, lower survival of scallops cultivated on bottom could be explained by the highest exposure to severe hypoxia/anoxia (below P_cO_2) with respect to the suspended treatment. In addition, since hypoxia/anoxia events in nature do not occur isolated (e.g. with milky turquoise waters) we hypothesize that the combined effects of oxygen depletions and the presence of sulfide would increase the negative effects on energy balance with subsequently on growth, reproduction and survival.

3.5 Conclusion

This study emphasized an important environmental variability in Paracas Bay and particularly during summer. Warm/cold and normoxic/hypoxic/anoxic conditions alternated very rapidly in the bay highlighting the importance of high frequency monitoring to better understand how environmental variables influence the physiology of aquatic organisms. The scallops aquaculture zone is exposed to chronic hypoxia as well as anoxic events frequently accompanied by milky turquoise waters. The latter could result from the presence of toxic H_2S . The exposure to these conditions had a negative effect on growth and reproduction of *Argopecten purpuratus*. In addition, the anoxic events observed during the summer affected the survival of cultivated scallops. Interestingly, the high productivity of these ecosystems is counterbalanced by low oxygen availability. Studying the oceanographic dynamics of the area at fine spatial and temporal scales would be necessary to better understand the environmental dynamics in Paracas Bay. In addition, *ex situ* studies that allow to isolating the effect of low oxygen saturations on scallops physiology and metabolism would be useful to better understand the patterns observed for growth, reproduction and mortality.

Acknowledgements

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Part II

Ecophysiologie d'*A. purpuratus* en conditions hypoxiques

Chapter 4

Métabolisme et hypoxie

Effects of progressive hypoxia on oxygen uptake in juveniles of the Peruvian scallop, *Argopecten purpuratus* (Lamarck, 1819)

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Arturo AGUIRRE VELARDE, Fred JEAN, Gérard THOUZEAU,
Jonathan FLYE-SAINTE-MARIE.

Abstract

A field survey performed in Paracas Bay (Peru), a major scallop culture area, showed that the Peruvian scallop, *Argopecten purpuratus*, periodically faces severe hypoxic events. Oxygen uptake rate (VO_2) of *A. purpuratus* juveniles facing progressive decrease of environmental oxygen saturation (from 100% to 5%) was measured at two contrasting temperatures ("normal condition" = 16°C and "warm condition" = 25°C). In normoxia, (oxygen saturation >70%) average VO_2 was significantly ($p < 0.001$) higher in warm condition ($0.20 \pm 0.004 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$) than in normal condition ($0.12 \pm 0.007 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$). The shape of the VO_2 response curve during increasing hypoxic conditions was evaluated using a segmented linear regression. The break points between linear segments allowed estimating the oxygen critical points (P_cO_2 , oxygen saturation units), while the slopes of the various segments was used to assess the VO_2 regulatory capacity. In both temperature conditions at oxygen saturation lower than P_cO_2 , VO_2 was a fourth of the values recorded in normoxic condition. This trend was more pronounced in the warm condition. Paradoxically, the estimated P_cO_2 was lower in warm condition ($21.4\% \pm 0.7$) compared to the normal condition ($24.4\% \pm 1.9$). However, the study of the slopes at oxygen saturations higher than P_cO_2 revealed that *A. purpuratus* can regulate its respiratory rate similarly and efficiently at both 16 and 25°C. Moreover, for VO_2 above P_cO_2 , the estimated Q_{10} between normal and warm conditions was 1.78 (Arrhenius temperature = 4983 K), highlighting a moderate effect of temperature on VO_2 . These results reflect the adaptive capacity of this species to the changing environment along the Peruvian-Chilean coasts influenced by upwelling system and ENSO events. However, results from this study indicate that, at least during some periods, *A. purpuratus* spend more than 70% of its time exposed to hypoxic conditions below the estimated P_cO_2 . Such conditions could have negative consequences on the species metabolism and harm the performance of *A. purpuratus* culture.

Keywords: *Argopecten purpuratus* ; oxygen critical point ; oxyregulation; respiration aquaculture ; Peru .

4.1 Introduction

Peruvian coastal waters are characterized by an intense upwelling system. The associated high primary production supports a large biomass of filter feeders (Thiel, 1978). Among those, the Peruvian scallop, *Argopecten purpuratus*, is a major species for Peruvian aquaculture. In 2012, aquaculture production in Peru reached more than 67 000 tons and a value of about 159 millions USD (PRODUCE - Peru, 2015).

Massive mortality events, that affected production and subsequently local economy (Cabello et al., 2002; González-Hunt, 2010; Gonzales et al., 2012b), have been repeatedly observed in coastal bays. Environmental monitoring (e.g. dissolved oxygen, temperature and toxic blooms surveys) is scarce in coastal areas in Peru.

Aquatic organisms can be characterized by their ability to regulate their oxygen uptake when exposed to moderate and/or severe hypoxia (Le Moullac et al., 2007). Species exhibiting an oxygen uptake dependent on environmental oxygen concentration are called "oxyconformers". In contrast, those who are able to maintain their oxygen uptake independently of the external decrease in oxygen concentration, at least for a part of the oxygen decrease range, can be classified as "oxyregulators". Nevertheless, Mangum and Winkle (1973) stressed that this classification is no more than the two extreme ends of a range of gradual physiological responses. The oxygen critical point (P_cO_2) concept was introduced by Prosser (1973) to characterize the oxygen level below which an oxyregulator cannot keep its oxygen uptake independent of external concentration. The P_cO_2 would coincide with the initiation of anaerobic metabolic pathways (Herreid, 1980; Pörtner and Grieshaber, 1993). Switching from aerobic to anaerobic energy production leads to a lower ATP yield per unit glucose and generates accumulation of endproducts which might be metabolized when normoxic conditions resume. This phenomenon has been described as the oxygen debt (Herreid, 1980). Because metabolic pathways are affected by hypoxia, it can be hypothesized that energetics and subsequently growth and reproduction can also be affected.

Temperature also affects oxygen uptake regulation in marine bivalves by modifying P_cO_2 and/or shape of respiratory response against progressive hypoxia (e.g. Le Moullac et al., 2007; Artigaud et al., 2014). In scallops beds of the Peruvian coast, water temperature variations up to 8°C in a few hours can be observed presumably due to variation in the intensity of the adjacent upwelling system (Aguirre-Velarde et al., 2014). In addition, Peruvian-Chilean coastal waters frequently experience important temperature variations due to El Niño Southern Oscillation (ENSO). The latter can induce dramatic increases of water temperature (about 10°C) (Wolff, 1987, 1988; Cantillán et al., 2007; Avendaño et al., 2008a).

In order to better understand how physiology and energetics of *A. purpuratus* are affected by these fluctuating environmental conditions, this study was designed to focus on the metabolic response of this species to temperature and oxygen concentration. In this context, the present study aims at characterizing the respiratory response of *A. purpuratus* under progressive exposition to hypoxia at two contrasted temperatures (warm condition vs normal condition). A field survey was also performed in early 2013 in Paracas Bay, that is a main scallop culture area in Peru, to characterize the duration and magnitude of scallop exposition to hypoxic conditions.

4.2 Material and methods

4.2.1 Field monitoring

Field measurements of temperature and dissolved oxygen saturation of the near-bottom water (20 cm above the bottom) were performed in a *A. purpuratus* aquaculture bed located in Paracas Bay (Peru; 13°49'35" S, 76°17'43" W) using autonomous dataloggers (HOBO U22-001 and RBR TDO for temperature and oxygen, respectively) from the January 1st, to the March 10, 2013.

4.2.2 Laboratory experiment

Scallops ranging from 24 to 32mm in shell height were provided by La Arena hatchery (FONDEPES, Casma, Peru) and transferred to the Laboratorio de Investigaciones Acuicola of IMARPE (Callao, Peru) on the 27 of July 2013. After transfer to the laboratory, the scallops were acclimated into two thermoregulated 200-L tanks during 2 days with a constant 1µm-filtered seawater flow (8 L h⁻¹). No food was given during the whole experiment because (1) feeding rate is generally dependent on temperature and affects respiration rate and (2) the present experiment was performed over a short time period. One tank was maintained at 16°C ("normal condition") while the other one was progressively heated up to 25°C ("warm condition") in four days. Afterwards, the temperature was maintained constant.

Oxygen uptake measurements were performed in a third tank thermoregulated at the acclimation temperature (16 or 25°C). Temperature recordings within the tanks (15-minute intervals) showed that water thermoregulation for respiration measurements was accurate and stable. In the normal condition, the average temperature during the whole experiment was 16.0°C (max. = 16.2°C, min. = 15.9°C). In the warm condition, the average temperature during the experiment was 25.2°C (max. = 25.4°C, min. = 24.9°C). The experimental setting used was extensively described in Artigaud et al. (2014). Briefly, a computer-controlled system allowed to gradually decrease the concentration of oxygen within the experimental tank by the mean of injection of gaseous nitrogen (N₂) in the water. Gas exchanges with the atmosphere were limited by the mean of a floating PVC sheet placed on the water surface. The system allowed decreasing the dissolved oxygen percent saturation stepwise from 100% to 5% by steps of 10% to 5% every two hours. During the whole sequence of decrease of oxygen saturation, oxygen uptake rate by scallops was measured by repeated incubations in 0.59-L acrylic chambers. Six chambers were used in total, 5 chambers contained each four individuals, while the sixth one was used as a control and contained four empty scallop valves (which the external surface approximately equals the external surface of four individuals). Each incubation lasted 20 minutes; between two incubations, water within the chambers was automatically renewed by pumping water from the experimental tank for 5 minutes. At the end of each experimentation, scallop height and total volume were measured in each chamber.

For each temperature condition, the experimentation was repeated four times leading to a total of twenty replicates for each treatment. Between each experimentation, chambers were washed with a diluted hydrogen peroxide solution.

The individual oxygen uptake rate (VO_2 , mgO₂ ind⁻¹ h⁻¹), was calculated as:

$$VO_2 = \frac{O_2CR_{chamb} - O_2CR_{cont}}{n_{ind}}$$

with:

O_2CR_{chamb} : the oxygen consumption rate in chamber with scallops ($\text{mg O}_2 \text{ L}^{-1} \text{ h}^{-1}$)

O_2CR_{cont} : the oxygen consumption rate in control chamber ($\text{mg O}_2 \text{ L}^{-1} \text{ h}^{-1}$)

n_{ind} : the number of individuals into the chamber

Given the possible difference in scallop mean size between the chambers, estimated oxygen uptake rates were standardized to a 30–mm height individual using Bayne et al. (1987) formula:

$$VO_{2std} = VO_2 \cdot \left(\frac{H_{std}}{H_{mean}} \right)^b$$

with:

VO_{2std} : oxygen uptake ($\text{mg O}_2 \text{ ind}^{-1} \text{ h}^{-1}$) standardized for an arbitrary height H_{std} (fixed to 30mm)

VO_2 : measured individual oxygen uptake into the chamber ($\text{mg O}_2 \text{ ind}^{-1} \text{ h}^{-1}$)

H_{mean} : mean scallops height into the chamber (mm)

b : allometric relationship between size and oxygen uptake. In the review of Savina and Pouvreau (2004), the allometric coefficient that relates respiration rate to weight is close to 3/4 in bivalves. This coefficient was recalculated to 2.25 in this study in order to relate respiration rate to height (or length) based on the assumption that weight scales with cubic length (or height).

The oxygen critical point (abrupt decrease in respiration rate or break point) was calculated using a segmented linear regression method (Muggeo, 2003), as proposed by Artigaud et al. (2014), from measurements of oxygen uptake vs oxygen saturation. The capacity of oxygen uptake regulation under progressive hypoxia was evaluated through the "O₂ regulation percentage" of Hicks and McMahan (2002). This value corresponds to the ratio between (1) the area beneath the curve of oxygen uptake versus oxygen saturation (expressed as percentage of maximum oxygen uptake i.e saturation = 100%) and (2) the area achieved by a perfect oxyregulator (displaying a constant respiration rate whatever the level of oxygen saturation). All computations were performed using R software (R Development Core Team, 2011); segmented linear regressions were performed using the "segmented" R package (Muggeo, 2008).

The effect of temperature on *A. purpuratus* oxygen uptake was assessed through the Q_{10} temperature coefficient calculated as : $Q_{10} = (\dot{k}_1/\dot{k}_2)^{10/(T_2-T_1)}$, where \dot{k}_1 is the metabolic rate measured at temperature T_1 , \dot{k}_2 is the metabolic rate measured at temperature T_2 , and $T_1 < T_2$ using respiration rates in normoxia (VO_{2std} for oxygen saturation above 70%). The Arrhenius temperature (T_A , K) is frequently used to assess the effect of temperature on physiological rates in bioenergetic models within the thermal range tolerance of a species (Kooijman, 2010b). This parameter was estimated from Q_{10} using the relationship proposed by Kooijman (2010b) : $T_A = [\ln Q_{10} \cdot T \cdot (T + 10)]/10$, with T the reference temperature (i.e. 289 K)

4.3 Results

During the monitoring period, the oxygen saturation of the near bottom water varied from 0% to 112% (Fig. 4.1) and the average saturation was 18%. During the 69 days of monitoring, the aquaculture bed faced under saturation below 24% for 70%

of the time. Temperature varied between 14.2°C and 23.7°C and average was 16.3°C. Dramatic daily temperature changes were frequently observed: on March 1st 2013 temperature varied from 14.7°C to 22.9°C (increase of 8.2°C) within a few hours.

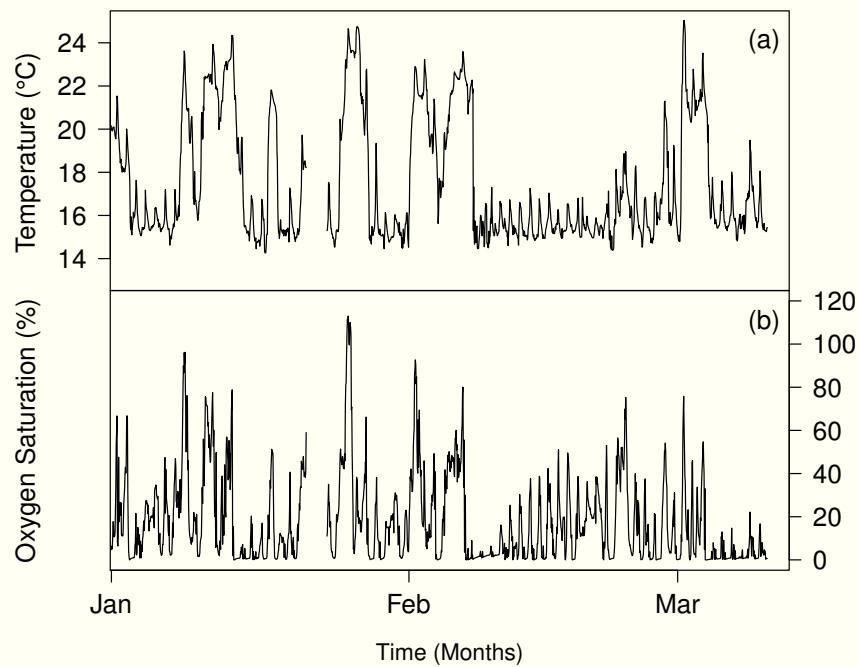


FIG. 4.1: Temperature and oxygen saturation of near-bottom water (20 cm above the bottom) of an *A. purpuratus* aquaculture bed located in Paracas Bay (Peru, 13°49'35" S, 76°17'43" W) measured between the January 1st, and the March 10, 2013.

Measured standardized oxygen uptake rate in normoxic conditions (O_2 saturation >70%) was $0.12 \pm 0.007 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$ at 16°C and $0.20 \pm 0.004 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$ at 25°C. Those data allowed to estimate the Q_{10} to 1.78 and the corresponding value of T_A was 4983 K. Under severe hypoxia (O_2 saturation close to 5.5%), VO_{2std} was $0.027 \pm 0.002 \text{ mgO}_2 \text{ ind}^{-1} \text{ h}^{-1}$ at 16°C and 0.050 ± 0.002 at 25°C, that is 22.5% and 25% of the values measured in normoxic conditions, respectively. In both normoxic and severe hypoxic conditions, VO_{2std} was significantly higher in warm than in normal condition ($p < 0.001$, Kruskal Wallis test).

The results of the segmented linear regression models fitted on the oxygen uptake rates as a function of oxygen saturation indicate a P_cO_2 (break point) at $24.4\% \pm 1.9$ in normal condition (16°C) and at $21.4\% \pm 0.7$ in warm condition (25°C) (fig. 4.2, tab. 4.1). In both conditions, a strong decrease of oxygen uptake rate is observed when oxygen saturation drops below the P_cO_2 (break point), segmented linear regressions indicating significant changes in the slopes of linear segments (Davies' test, $p < 0.001$). Likewise in both experimental temperature conditions, the regression slopes show that both P_cO_2 lower and higher segments depend significantly ($p < 0.001$) on oxygen saturation although in a different extent.

Comparison of the slopes of the segments above and below the P_cO_2 was assessed through analysis of covariance (ANCOVA); it allowed comparing the respiratory response of the scallops to progressive hypoxia between two temperature exposures. The comparison of the segments superior to P_cO_2 shows no significant interaction ($p > 0.05$) between temperature and oxygen saturation on oxygen uptake indicating no significant difference for slopes between the two temperature conditions. Thus for saturations

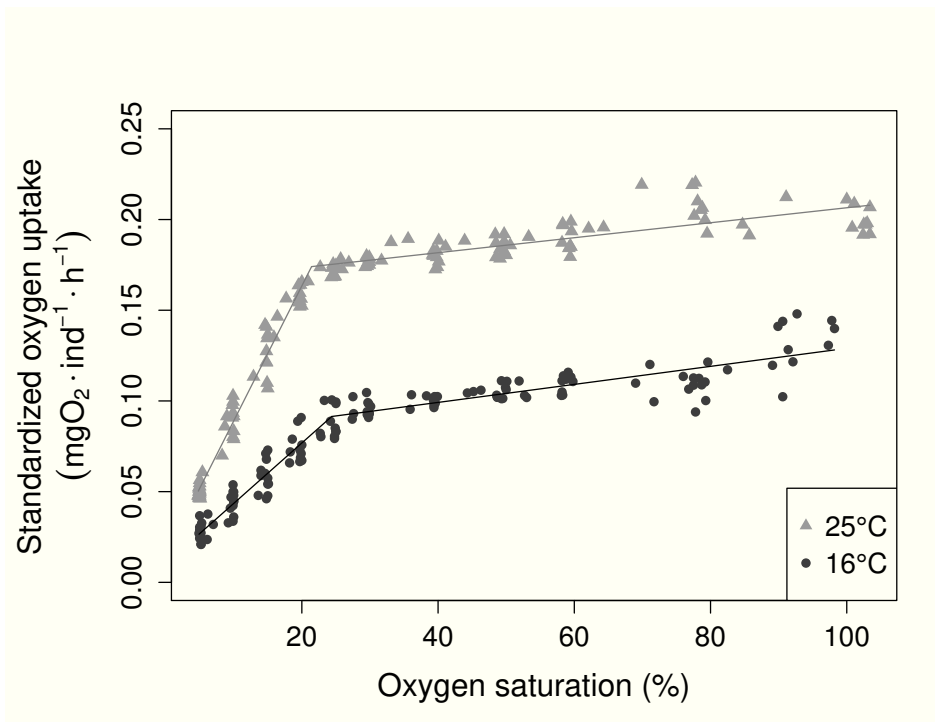


FIG. 4.2: Standardized (30mm shell height) individual oxygen uptake rate of *Argopecten purpuratus* facing progressive hypoxia at 16 and 25°C. Lines are the segmented linear models used to calculate the critical oxygen point at both temperatures. Estimated break points (P_cO_2) were 24.4% (CI=1.9) at 16°C and 21.4% (CI=0.7) at 25°C. No significant difference in the slopes of the linear segments above P_cO_2 was found between the two treatments, whereas slopes were significantly different for oxygen saturation below P_cO_2 .

above P_cO_2 , regulation of oxygen uptake in function of oxygen availability is identical. For saturations below P_cO_2 , interaction between temperature and oxygen saturation was significant ($p < 0.001$) indicating that the slopes are significantly different between treatments. Therefore, below P_cO_2 , the oxygen uptake regulation depends on oxygen saturation but also on temperature. At 25°C, respiration rate decrease is 2.2-fold higher than at 16°C when saturation falls below P_cO_2 . Finally, regulation capacity was slightly higher at 25°C (82%) than at 16°C (74%; see table 4.1).

4.4 Discussion

Traditional dichotomy between “oxyconformers” and “oxyregulators” has been criticized because of the varied responses of organisms facing progressive decrease of environmental oxygen saturation (Mangum and Winkle, 1973; Taylor and Brand, 1975). Herreid (1980) considers that “good regulators” have low P_cO_2 values and abrupt transitions and steep conformity slopes. “Poor regulators” are expected to have a more gradual transition from regulation to conformity. Bivalves species inhabiting periodically hypoxic habitats, are generally found to be better regulators when submitted to progressive hypoxia (Griffiths and Griffiths, 1987). This is the case in Peruvian coastal bays where the environmental monitoring presented in this study showed that *A. purpuratus* is frequently exposed to severe hypoxic conditions. The effects of environmental hypoxic events on marine natural (Llanso, 1992) or cultured (Brokordt et al., 2013) populations depend on the intensity and duration of these events. Brokordt et al. (2013) found that

TAB. 4.1: Oxygen critical points values (P_cO_2) and percentage of regulation estimated for *Argopecten purpuratus* at 16 and 25°C using segmented linear regression. The table indicates the slopes and confidence intervals of the linear segments below and above the break points (P_cO_2).

Temperature (°C)	P_cO_2 (% \pm CI)	Linear segment slopes		% regulation (%)
		segment $< P_cO_2$	segment $> P_cO_2$	
16	24.4 \pm 1.9	3.34 $10^{-3} \pm 3.3 \cdot 10^{-4}$	4.97 $10^{-3} \pm 7.6 \cdot 10^{-5}$	74
25	21.4 \pm 0.7	7.44 $10^{-3} \pm 3.4 \cdot 10^{-4}$	4.13 $10^{-3} \pm 6.7 \cdot 10^{-5}$	82

hypoxia exposition affects the escape capacity of *A. purpuratus* increasing vulnerability to predation and decreasing physiological capabilities to support other stress factors. To maintain oxygen uptake when oxygen availability decreases, bivalves can respond by increasing water pumping/ventilation (Tran et al., 2000) and cardiac activities (Grieshaber et al., 1994). This set of responses can be considered as a "oxyregulation effort", where P_cO_2 represents the limit of regulatory ability (Grieshaber et al., 1988). Although oxygen uptake is not completely independent of oxygen saturation for oxygen saturations higher than P_cO_2 ("regulated segment"), *A. purpuratus* exhibits relatively low P_cO_2 (fig. 4.2) and can thus be considered as a good regulator. Recently, Artigaud et al. (2014) estimated a similar P_cO_2 value (23.8% at 18°C) for *Pecten maximus* which is phylogenetically closely related. It can thus be hypothesized that morphology/anatomy plays a role in the physical oxyregulation ability (e.g. ventilation, oxygen perfusion). Nevertheless, results of Artigaud et al. (2014) indicate that in *P. maximus*, which is less naturally exposed to abrupt changes in temperature, regulation ability is more sensitive to temperature.

Generally the P_cO_2 increases with temperature (Herreid, 1980), this relationship resting upon the temperature-dependence of oxygen solubility in seawater (Le Moulac et al., 2007). Interestingly, the difference of estimated P_cO_2 was very low between both temperature exposures in this study, and was associated with a regulation ability slightly higher at 25°C than at 16°C. This pattern might be associated with an increased metabolic capacity for ciliary ventilation and/or hemolymph perfusion of the gills (Alexander and McMahan, 2004). This can explain also the significantly higher oxygen uptake in warm conditions under severe hypoxia (O_2 saturation near 5.5%) compared to normal (16°C) condition. Such a positive relationship between temperature and oxygen uptake regulation has also been found in the fresh water bivalves *Sphaerium simile* (Waite and Neufeld, 1977) and *Dreissena polymorpha* (Alexander and McMahan, 2004). On the other hand, in upwelling zones, as along the Peruvian coast, hypoxia can occur at low temperatures. Under low temperature conditions, the reduced efficiency of regulation strategies may cause a early decrease of oxyregulation effort and consequently of oxygen uptake rate. Increased metabolic rate (higher energetic demand) at elevated temperatures may need extending oxyregulation effort to maintain aerobic metabolism. Indeed, the latter is more efficient in terms of ATP production.

Respiration rates generally increase with body temperature until a threshold temperature is reached (Hand and Hardewig, 1996). The Q_{10} value of 1.78 calculated from oxygen uptake data in normoxia is close to values characteristic of temperature-dependent physiological response (Q_{10} ranging between 2 and 3; Willmer et al., 2005). This Q_{10} value is slightly lower than the lower limit of this range, which reflects a moderate effect of temperature on physiological rate. The latter may favor the main-

tenance of homeostasis in an environment presenting high temperature fluctuations. Comparisons of subtidal (relatively stable temperature) and intertidal (highly fluctuating temperature) mollusk species show that species experiencing high temperature fluctuations (intertidal) present lower Q_{10} (e.g. Sokolova and Pörtner, 2003; Dunphy et al., 2006). *A. purpuratus* displays a ability to adapt/acclimate to both high temperature, i.e. during El Niño events ($\approx 24^{\circ}\text{C}$ in Peru, Wolff, 1987), and low temperatures ($\approx 12^{\circ}\text{C}$ in Southern Chile, González et al., 2002; $13\text{-}14^{\circ}\text{C}$ in Northern Chile during la Niña events, Cantillán et al., 2007). In addition, similarly to intertidal species, temperature changes higher than 8°C , combined with dramatic changes in oxygen concentration, were recorded in few hours in Paracas Bay, Peru. Wolff (1987) suggested that *A. purpuratus* was a relict form of the subtropical fauna which once inhabited Chile and Peru during Miocene. Adaptations to warm conditions, including hypoxia handling, may have preserved after the general cooling of the oceans at the end of the Miocene due to periodical El Niño occurrence on the Peruvian coastal zones. This relative low effect of temperature on physiological rates combined with a good regulation of oxygen uptake under hypoxia might explain the ability of this species to adapt/acclimate to such conditions. In an environment where trophic resource is poorly limiting, *A. purpuratus* is well adapted to cope with temperature changes and to deal with frequent hypoxia events under both cold and warm conditions. Such a strategy would allow maintaining aerobic metabolic pathways and efficiently using food resources (e.g. for growth and reproduction) under low oxygen concentration. The success of *A. purpuratus* aquaculture can be related to its ability to acclimate to this very dynamic environment, while displaying important growth rates in comparison to other scallops species. It is clear from this study however that *A. purpuratus* aquaculture could be optimized by selecting culture areas (bottom and suspended cultures) presenting the best fit between temperature and oxygen fluctuations, and metabolic rates.

Several studies showed that temperature strongly impacts the organisms ability to cope with hypoxia (Newell, 1978; McMahon and Wilson, 1981; Hicks and McMahon, 2002; Jansen et al., 2009; Alexander and McMahon, 2004; Le Moullac et al., 2007; Pörtner, 2012; Artigaud et al., 2014). Artigaud et al. (2014) found an inverse relationship between the temperature and percentage of regulation in *P. maximus*, while Hicks and McMahon (2002) found a direct relationship in *Perna perna*. In the present study, the calculated percentage of regulation was slightly greater at 25°C than at 16°C . However, two phases can be considered in the response to hypoxia: a highly regulated segment (above $P_c\text{O}_2$) and a poorly regulated segment (below $P_c\text{O}_2$). The slopes of the highly regulated segments seems as a pertinent criteria to assess oxyregulation ability. This study showed close $P_c\text{O}_2$ values (21.4 and 24.4%) and no significant difference in the slopes of the highly regulated segments between the two temperature conditions. The combination of these two observations indicates that *A. purpuratus* oxyregulation ability is only slightly affected by temperature. This physiological acclimation ability displayed between these two widely remote temperatures may be linked to an adaptive response to a highly variable environment in terms of temperature and oxygen concentration (e.g. ENSO and high frequency events) and may contribute to explain the wide geographical distribution range displayed by this species.

In the poorly regulated segments, the decrease of oxygen uptake is more abrupt at 25°C than at 16°C (fig. 4.2). This difference can be explained by the higher metabolic rate observed at 25°C (that might include oxyregulation effort), causing a more pronounced energetic decrease when oxygen saturation drops near zero. The inability to maintain the oxygen consumption rate below the $P_c\text{O}_2$ marks the beginning of energetic

anaerobic pathways (Grieshaber et al., 1988; Pörtner and Grieshaber, 1993). While many bivalves are adapted to survive periodic hypoxia (Le Moullac et al., 2007), less efficient energy production under anaerobic conditions can affect their energetics. The synthesis of endproducts to be metabolized when normoxic conditions resume can generate oxygen debt (Herreid, 1980). Chronic exposure to severe and prolonged hypoxic conditions, as in the Peruvian coastal waters, might affect the *A. purpuratus* energy budget by reducing the energy available for the major metabolic functions, thus affecting growth, reproduction and immune response with consequences for culture performances.

4.5 Conclusion

The Peruvian-Chilean coastal marine area presents an environment highly variable in terms of temperature and oxygen saturation. The results of this study highlight *A. purpuratus* ability to efficiently regulate its oxygen uptake in a wide temperature range. The observed low oxygen critical points indicate an important regulation capacity of oxygen uptake at both normal and warm conditions. Although oxyregulation decreases considerably for oxygen saturations lower than the critical point, the oxygen uptake under severe hypoxic conditions is not null. The ability of *A. purpuratus* to deal with oxygen limiting conditions might provide an adaptive advantage to acclimate to environmental conditions along its distribution range. Further studies must focus on the anaerobic metabolic capacity and the effect of hypoxia on the energy balance of this scallop species.

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Chapitre 5

Effets de la limitation en oxygène sur la filtration et la croissance

Feeding behaviour and growth of the Peruvian scallop (*Argopecten purpuratus*) under daily cyclic hypoxia conditions

Arturo AGUIRRE VELARDE, Fred JEAN, Gérard THOUZEAU, Jonathan FLYE-SAINTE-MARIE

Abstract

As a secondary consequence of the high productivity of the upwelling system, organisms inhabiting Peruvian coastal bays are frequently exposed to hypoxic conditions. The aim of the present paper was to investigate the effects of daily-cyclic-severe hypoxia on energetics of a species presenting little escape ability when facing to hypoxia. For this purpose, juveniles Peruvian scallops (*Argopecten purpuratus*) were exposed to four experimental conditions: fed and starved, combined or not to nightly severe hypoxia (5% oxygen saturation) for \approx 12 hours over a 21-days experiment. In both fed conditions, clearance rate was measured by the mean of an open-flow system. Surprisingly, our results indicate that the Peruvian scallop is able to maintain an active filtration even at low oxygen saturations, at least during expositions up to 12 hours. During the first phase of exposition to hypoxia, clearance rate decreased abruptly when oxygen saturation dropped below 10%, but rapidly recovered to values close to those found under normoxia. As a consequence of this ability to feed during hypoxia, no difference in soft tissues dry weight (digestive gland not included) was observed at the end of the experimental period between oxic conditions among fed scallops. However, shell growth was negatively affected by hypoxic condition. Starved individuals exhibited similar weight loss between hypoxic and normoxic conditions indicating no or little effect of oxic condition on maintenance costs. Considering the observed responses for feeding, growth and maintenance, we can hypothesize that this species presents metabolic/bioenergetic efficient adaptations to deal with hypoxic conditions that are recurrent in Peruvian coastal bays. We hypothesize that the small observed effects might be modeled in the context of the Dynamic Energy Budget theory as a restriction of reserve mobilization under hypoxic conditions.

Keywords: Pectinidae ; hypoxia; growth; clearance rate; feeding behaviour; bioenergetics; *Argopecten purpuratus*.

5.1 Introduction

The Peruvian scallop (*Argopecten purpuratus*) inhabits a wide geographic range along the Peruvian and Chilean coasts. The non-seasonal upwelling system that occurs in this region is responsible for a high primary production favouring continuous food availability (Walsh, 1981; Levin, 2003; Zhang et al., 2010) for large populations of filter feeders. The sinking and degradation of this particulate organic matter in the offshore zone causes high oxygen consumption inducing the occurrence of the oxygen minimum zone (OMZ) in mid-depth waters (Diaz and Rosenberg, 1995; Bakun and Weeks, 2008; Diaz and Rosenberg, 2008; Gewin, 2010). These oxygen-depleted waters can be upwelled into shallower coastal areas (Grantham et al., 2004; Diaz and Rosenberg, 2008; Chan et al., 2008; Monteiro et al., 2008; Gewin, 2010; Stramma et al., 2010) thus affecting benthic communities (Carruthers et al., 1959; Grantham et al., 2004; Zhang et al., 2010; Villnäs et al., 2012). When facing these hypoxic conditions organisms with no or limited mobility such as bivalves are particularly vulnerable. Recent environmental monitoring in Paracas Bay (where important wild and cultured biomasses of *A. purpuratus* can be found) has revealed strong diurnal variations in oxygen saturation: during the day conditions are generally close to normoxia while severe hypoxic conditions are observed during the night (Aguirre-Velarde et al., 2016). The critical oxygen saturation point below which *A. purpuratus* is unable to regulated oxygen uptake (P_cO_2) is $\approx 24\%$ at 16 °C (Aguirre-Velarde et al., 2016). Field observations in Paracas bay showed that *A. purpuratus* populations are frequently exposed several hours per day to oxygen saturations lower than this P_cO_2 value.

Bivalves are generally considered as tolerant to low oxygen concentration, and particularly species that are naturally exposed to environmental hypoxia (Bayne, 1973; Hammen, 1980; de Zwaan et al., 1991; Wang and Widdows, 1993b; Taylor et al., 1995; Matthews and McMahon, 1999; de Zwaan et al., 2002; Le Moullac et al., 2007). Nevertheless, exposition to severe hypoxia (oxygen saturations lower than P_cO_2) may induce the use of anaerobic metabolic pathways (Herreid, 1980) that are less efficient than aerobic pathways in terms of ATP production. The former pathways may significantly limit the energy available for the organism's functions and generate endproducts (e.g. lactate, octopine. . . ; Enomoto et al., 2000) which must be metabolized when oxygen availability resumes possibly generating an oxygen debt (von Brand, 1946; Herreid, 1980). Lower energy yield under anaerobic metabolism may alter reserves dynamics. Nevertheless the effects of hypoxia on the dynamics of reserves in bivalves remain poorly known. Wang and Widdows (1993b) observed under hypoxic conditions a highest anaerobic rate on starved vs. fed individuals of *Mytilus edulis*. During hypoxic events, organisms may adopt different energetic strategies modifying also their behaviour to attempt to reduce negatives consequences of anaerobic metabolism and increase survival probability (Burnett and Stickle, 2001). It has been reported that hypoxia decreases the escape response in juveniles of *A. purpuratus*, where carbohydrates stored in the abductor muscle would be used for anaerobic energy supply, thus limiting motor capacities (Brokordt et al., 2013). A decrease in feeding rate has been reported for several invertebrate species exposed to hypoxic conditions (see reviews in Burnett and Stickle, 2001; Wu, 2002), including marine bivalves (Sobral and Widdows, 1997; Wang et al., 2011). As a consequence of these metabolic and behavioural modifications, it can be hypothesized that a chronic exposition to hypoxia would affect the overall energy balance of the organisms, by modifying the use of reserves but also the energy intake with potential negative consequences on growth. Nevertheless, such modifications remain poorly documented.

In the context of ongoing climate changes, it is expected that coastal areas will be more frequently exposed to major hypoxic events (Bakun et al., 2010; Stramma et al., 2010). The Peruvian scallop represents an economically valuable species in Peru and Chili; it is thus necessary to evaluate the possible energetic consequences of chronic exposition to hypoxia in this species. In this context, the present study aims at evaluating experimentally the effects of a cyclic, non-lethal and chronic exposition to hypoxia on scallop growth, use of reserves under starvation and feeding behaviour. This study focuses on better understanding the environmental control of energy budget in a species inhabiting coastal waters influenced by the adjacent oxygen-limited upwelling system. We finally discuss how to include these effects in individual bio-energetics models based on Dynamic Energy Budget theory (Kooijman, 2010a).

5.2 Material and methods

5.2.1 Biological material and acclimation conditions

Argopecten purpuratus spat presenting undifferentiated gonad and shell height between 24 and 32 mm (mean = 28.2 mm) were provided by the hatchery of La Arena (FONDEPES, Casma, Peru). After transfer to the Laboratorio de Investigaciones Acuicola de IMARPE (Callao, Peru) on 27 July 2013, scallops were acclimated during three days into four 200-L tanks (200 individuals/tank) at the experimental temperature (16°C, close to *in situ* temperature) and 100% oxygen saturation. Water tanks renewal rate was 100% each 24 hours with a continuous open flow.

5.2.2 Experimental conditions

After the acclimation period, scallops were redistributed randomly in four 200-L, thermoregulated (16°C) tanks with a density of 120 scallops per tank. Each tank was continuously supplied with 1µm-filtered seawater; the water flow rate allowed 100% renewal per day. Photoperiod was subject to the natural light. Tanks were cleaned daily. One of the following experimental conditions was attributed to each tank: ad libitum food and normoxia (F-N), ad libitum food and cyclic hypoxia (F-H), no food and normoxia (S-N) and no food and hypoxia (S-H). Fed tanks were provided continuously with a phytoplankton mixture composed of *Isochrysis galbana* and *Chaetoceros calcitrans* (in cells proportion of 3:2 respectively) by the mean of a peristaltic pump. Particle concentration within the tanks was monitored daily using a PAMAS S4031 GO particle counter (PAMAS GmbH, Germany). The flowrate of the peristaltic pump was adjusted in order to maintain an average concentration of 9200 cells/ml within the tanks, estimated as the number of particles counted in the 2-10µm size class.

Each tank was equipped with a 1200 L h⁻¹ aquarium homogenization pump that allowed maintaining normoxia (oxygen saturation near 100%) in the two normoxic tanks (F-N and S-N). F-H and S-H tanks were exposed to non-lethal daily cycles of hypoxia (12h:12h normoxia:hypoxia). Water oxygen saturation within the F-H and S-H tanks was lowered every night to 5% (in the span of three hours) by regulated bubbling of gaseous nitrogen using the computer-controlled system described in Artigaud et al. (2014) for a period of ≈ 12h. Oxygen saturation within the four tanks was automatically recorded every 30-seconds using two WTW Multi 3430 Multiparameter each fitted with a FDO 925-3 optical oxygen probe (WTW, Oberhayern, Germany). Water temperature

into the tanks was recorded every 15 minutes with Water-Temp-Pro v2 (HOBO-Onset) loggers.

5.2.3 Growth survey and biometric data treatment

At the beginning of the experiment, and then weekly, 30 scallops were randomly sampled in each treatment. For each individual, shell was removed, then digestive gland and remaining soft tissues were dissected and wet-weighted. Both digestive gland and remaining soft tissues were then dried for 96 h in an oven at 60°C and weighted. Shell height (H , mm) was measured using a numeric caliper (to the nearest 0.01 mm). The Johnstone (1912) condition index ($DWCI$, g cm^{-3}) was calculated for the remaining dried soft tissues according to the formula:

$$DWCI = \frac{1000 DW}{H^3}$$

where DW is the remaining soft tissues dry weight (g) and H the shell height (mm). Means and confidence intervals (95%) of shell height, digestive gland and remaining soft tissues dry weights, as well as water contents were estimated at each sampling time. Possible effect of treatments on growth/shrinking and scallop water content were evaluated at the end of the experimentation period using a 2-way (feeding regime and oxygen % saturation) analysis of variance test (ANOVA) for each scallop biometric descriptor. In addition, the Tukey's rank test was used for multiple comparisons between treatments. Normality and homoscedasticity of the data were previously checked with Shapiro and Bartlett tests, respectively. All statistical treatments were performed using the R software (R Development Core Team, 2013).

5.2.4 Feeding behaviour assessment

Clearance rate measurement system

Feeding behaviour was assessed by measuring clearance rates in F-N and F-H treatments. Phytoplankton supply and water temperature control were performed as described in section 2.2. Clearance rate measurements were performed for 24 hours in constant normoxia (F-N treatment) and during cyclic normoxia-hypoxia (F-H treatment).

The clearance rate measurements were performed with the COSA system which is similar to the ones described in Savina and Pouvreau (2004) and Flye-Sainte-Marie et al. (2007). The system (Fig. 5.1) is composed of a total of eight 0.94-L open-flow acrylic chambers (Fig. 5.1 C_0 to C_7) located in the experimental tank (Fig. 5.1 E). Seven chambers (C_1 to C_7) contained each 3 individuals while the control chamber (C_0) contained only empty valves. Chamber flowrate ranged from 5.1 to 6.5 L h^{-1} ; it was controlled by a 8-lines peristaltic pump (Fig. 5.1P, Masterflex L/S 7551, Cole Parmer, USA) and was manually measured at the beginning and the end of each experiment. A computer controlled device (Fig. 5.1A) drove a set of eight solenoid valves that redirected the outflowing water either from a chamber to a fluorometer (Fig. 5.1F, red arrow) or directly back to the experimental tank (Fig. 5.1, green arrow). The fluorometer (WETstar chlorophyll, WETLABS, Philomat, USA) allowed quantifying the chlorophyll- a and subsequently the microalgae concentrations in terms of arbitrary units (arb. units) in the water outflowing from the selected chamber. Water outflowing from chambers with scallops (C_1 to C_7) was alternately monitored for 10 min. Between two measurements with scallops, the control (containing only empty valves) was monitored for 5 min. A

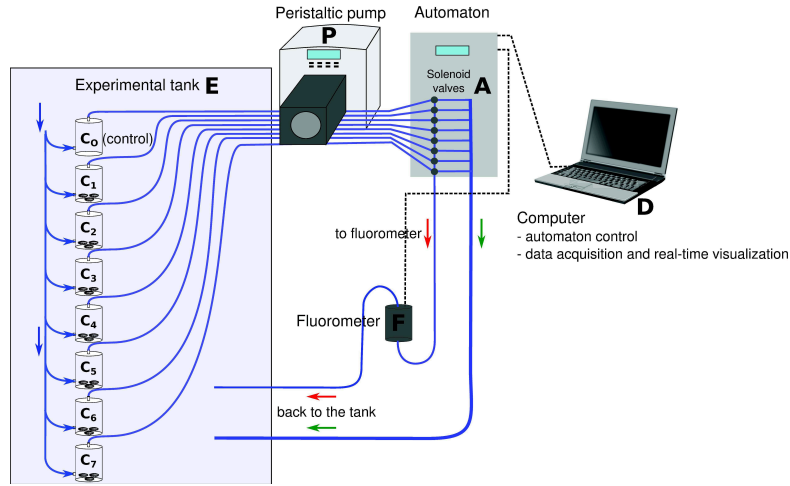


FIG. 5.1: The COSA clearance rate measurement system. Blue lines indicate the hydraulic circuit, black dotted lines indicate data connections. The chamber C_0 was used as a control as the chambers were located in the experimental tank (E). A peristaltic pump (P) allows to control the water flow within the chambers. The computer-controlled automaton (A) allow to drive solenoid valves and to select if the water from a chamber goes to measurement on the fluorometer (F) or directly back to the experimental tank. The computer (D) allows to control the automaton, to log and real-time visualize acquired data.

graphical user-interface designed for the COSA system allowed controlling the automaton and real-time visualizing as well as saving data (every 20s) of the fluorometer.

Between each set of experiment, acrylic chambers and hydraulic circuit were washed with a diluted hydrogen peroxide solution and rinsed with freshwater.

Clearance rate data treatment

Fluorescence measurements were first corrected from the baseline of the fluorometer (determined from fluorometer calibration). For each measurement, the 100 first seconds of data (five first values) were excluded due to the time needed for a full replacement of the water within the hose and the fluorometer. Mean fluorescence ($Fluo_{scal}$, arb. units) was calculated for each measurement in a chamber with scallops. The corresponding mean fluorescence in the control ($Fluo_{cont}$, arb. units) was calculated as the average of the values measured in the control before and after the measurement in the chamber with scallops. The individual clearance rate (CR , $L h^{-1} ind^{-1}$) was then calculated according to Hildreth and Crisp (1976) formula:

$$CR = F_R \frac{Fluo_{cont} - Fluo_{scal}}{Fluo_{scal}} \frac{1}{n_{ind}}$$

where, F_R is the water flowrate through the chamber ($L h^{-1}$) and n_{ind} is the number of individuals into the chamber.

After each 24-h clearance rate measurement experiment, scallops were processed according to the procedure described in section 5.2.3. Shell height (H), wet weight (WW) and dry weight (DW) were measured. In order to correct the clearance rates from potential variations in mean individual size between chambers/experiments, clearance rates were standardized to a 30 mm shell height individual using Bayne et al. (1987) formula:

$$CR_{std} = CR \cdot \left(\frac{H_{std}}{H_{mean}} \right)^b$$

where CR_{std} is the standardized clearance rate for an individual of shell height H_{std} (30 mm), CR is the estimated clearance rate and H_{mean} the mean scallops height in the chamber, and b is the allometric coefficient relating size and clearance rate. This coefficient was taken equal to 2 (according to review of Pouvreau et al., 1999, recalculated for length).

Mean CR_{std} temporal evolution during day-night cycles was compared between F-N and F-H treatments; For a better visualization means over 30-minutes intervals were estimated. Mean CR_{std} under hypoxia and normoxia conditions were compared in/between treatments using a the non parametric Kruskal-Wallis test.

Critical points (breakpoints) and trends in clearance rate during daily cycles were assessed by the means of segmented linear regression using the "segmented" R library (Muggeo, 2003, 2008).

5.3 Results

5.3.1 Experimental conditions

Water temperature within the tanks was stable in all treatments during the 21-days experiment, with average values ranging between 16.0 and 16.2 °C. Temperature only deviated punctually (less than 1.5°C) from the average conditions (less than 6 hours). A significant difference in temperature between treatments was registered. Nevertheless, differences between both did not exceed 0.2°C during the experimental period.

In both normoxic treatments (F-N and S-N), oxygen saturation was maintained between 93% and 100% and only dropped occasionally to 83% for less than 6 hours during the experiment. In both tanks exposed to cyclic hypoxia, saturation was maintained above 93% during normoxic periods and close to 5% during approx. 10.5 hypoxic periods. Transition periods between normoxia and hypoxia represented approximately 2 hours per day.

5.3.2 Effect of chronic hypoxia and food conditions on biometric parameters

After 21 days of experimentation, the average shell height was significantly higher ($p < 0.001$) in scallops fed under constant normoxia treatment (F-N) relative to all other treatments (F-H, S-N and S-H; Fig. 5.2a). Average shell height increase of fed scallops was 3.27 mm in normoxia and 2.13 mm under cyclic hypoxia during the study period. Shell growth was not significantly different from 0 ($p > 0.05$) in both unfed treatments (S-N and S-H).

At the end of the experiment marked differences were also observed for soft tissues between fed and starved scallops (Fig. 5.2). The digestive gland DW was significantly ($p < 0.001$) higher in fed scallops than in starved ones (Fig. 5.2b). Among fed scallops (F-N and F-H), final digestive gland DW was significantly higher in scallops exposed to cyclic hypoxia. Remaining soft tissue DW was significantly ($p < 0.001$) higher in fed scallops than in starved ones (Fig. 5.2c); however, in both fed and starved scallops no

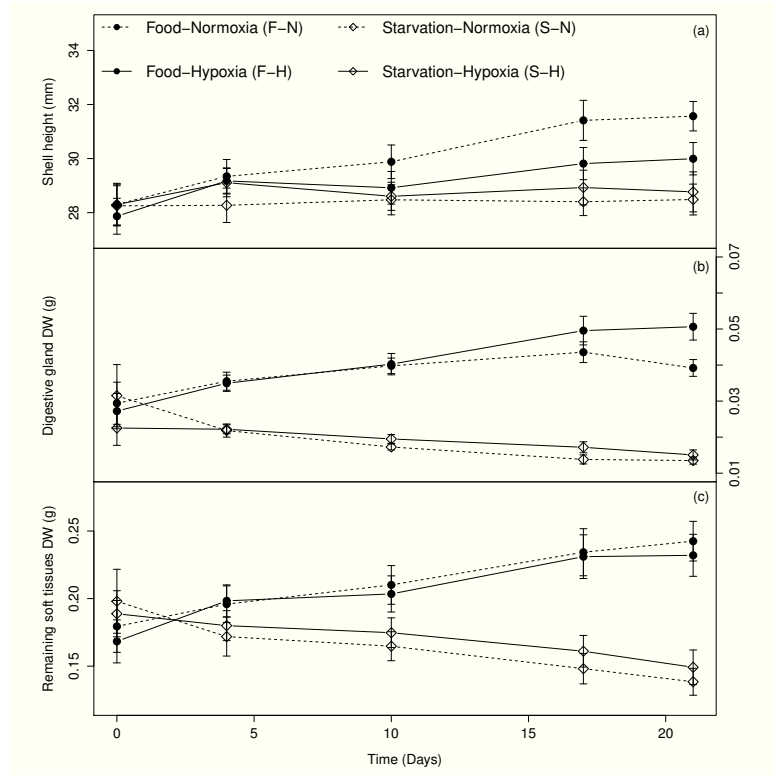


FIG. 5.2: Evolution of shell height (a), digestive gland dry weight (b) and remaining soft tissues dry weight (c) during the 21-days experimental period and for the four treatments. Bars indicate 95% confidence intervals.

significant differences were observed between the two oxic treatments ($p > 0.05$). Under starvation, soft tissue dry weights decreased regularly over the experimental period with a similar rates (ANCOVA slope comparison, $p > 0.05$), although important DW losses (up to 60%) were registered in S-N treatment during the first week (Fig. 5.2b,c).

The final condition index, $DWCI$ (Fig. 5.3), calculated from remaining soft tissues DW , was significantly higher in fed than in starved scallops. The highest mean $DWCI$ after 21 days was observed for individuals of the F-H treatment. In starved scallops, water content of remaining soft tissues increased regularly during the experiment, while a trend was hardly distinguishable in fed scallops. At the end of the experiment, the starved scallops showed significantly higher water contents compared with fed scallops ($p < 0.001$). Scallops of the F-H treatment exhibited the lowest percentage of water at the end of the study period compared with the other treatments.

Results of the two-way ANOVA (Table 5.1) showed that feeding had a significant and positive effect on final shell height, dry weight and condition index. The effect of food on water content of remaining soft tissues was significantly negative. Constant normoxia had a significant positive effect on shell height and water content of remaining soft tissues but a significant negative effect on digestive gland DW and $DWCI$. Food and constant normoxia interaction had a positive effect on shell height and a negative effect on digestive gland DW and $DWCI$. By contrast, this interaction did not show any significant trend on remaining soft tissues dry weight and water content.

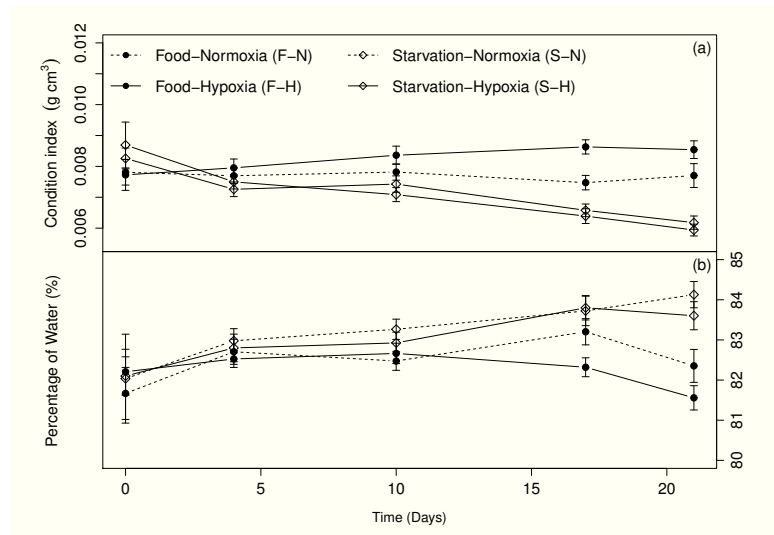


FIG. 5.3: Temporal evolution of condition index (a) and percentage of water (b) during the 21-days experimental period in the four treatments. Bars indicate 95% confidence intervals.

TAB. 5.1: Positive (+) and negative (-) effects of the experimental treatments on shell height, digestive gland dry weight, remaining soft tissues dry weight, condition index and water content assessed by a two-way ANOVA comparing average values obtained at the end of the experiment. Significance codes for p -values are : * * * : p -value < 0.001, ** : p -value < 0.01 and * : p -value < 0.05.

	Shell height	Digestive gland DW	Remaining tissues DW	Condition index	Water content
Food	+***	+***	+***	+***	-***
Normoxia	+*	-***		-***	+***
Food:Normoxia	+**	-***		-*	

5.3.3 Scallop feeding behaviour in response to hypoxia

Under constant normoxia mean daily (taking the day/night cycle into account) clearance rate was 1.96 ($CI = \pm 0.07$) $L h^{-1} ind^{-1}$ (Fig. 5.4 a). The average daylight clearance rate was 2.08 ($CI = \pm 0.06$) $L h^{-1} ind^{-1}$ while clearance rate decreased slightly overnight (between hours 10 to 22) to 1.84 ($CI = \pm 0.07$) $L h^{-1} ind^{-1}$ in constant normoxia treatment. Although this day-night difference in clearance rate was small, it was significant (Kruskal-Wallis test, $p < 0.001$). In the cyclic normoxia-hypoxia treatment, clearance rate during normoxia (oxygen saturation $\geq 90\%$) was 1.92 ($CI = \pm 0.16$) $L h^{-1} ind^{-1}$, and it was not significantly different (Kruskal-Wallis test, $p > 0.05$) from the clearance rate in constant normoxia. During the beginning of nocturnal hypoxia (starting approximately at 20:00) one abrupt decrease in clearance rate down to a $0.28 L h^{-1} ind^{-1}$ was observed. Filtration was maintained until an oxygen critical point of 11.2% ($SE = \pm 1.4$) was reached and then collapsed for lower oxygen saturation (Fig. 5.5). After 3.30 hours ($SE = 0.29$) under severe hypoxia (oxygen saturation $\leq 5\%$), clearance rate recovered to values comparable to those observed under normoxia. Then a gradual decrease in clearance rate was observed. At the end of the hypoxic conditions an instantaneous increase in clearance rate above average normoxic values was observed. This maximum occurred as soon as 75% oxygen saturation was reached. Then, the clearance

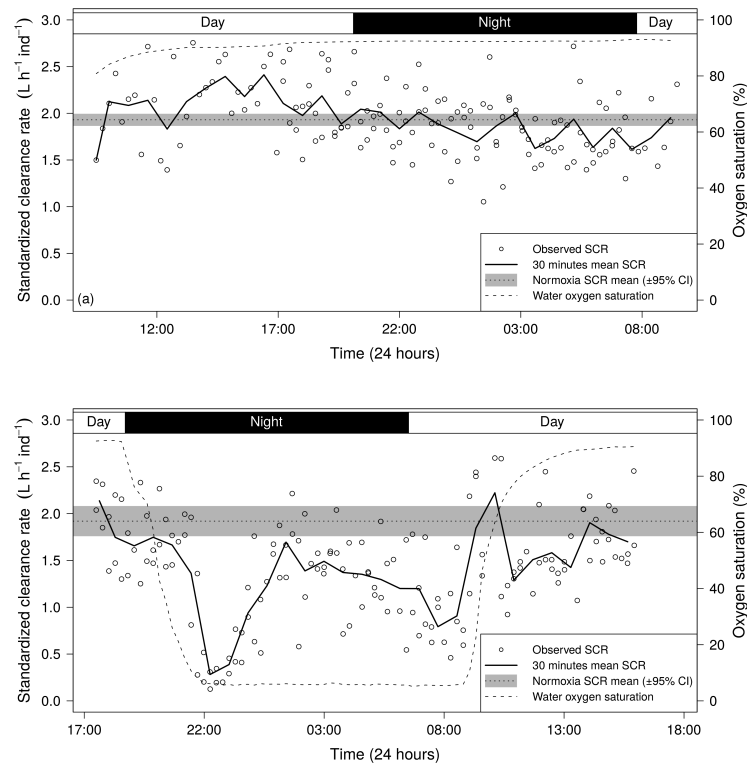


FIG. 5.4: Evolution over time of standardized (30mm-height individual) clearance rate under constant normoxia (a) and under cyclic normoxia-hypoxia (b). Empty circles indicates clearance rate observations, continuous black lines indicate 30-minutes clearance rate average. Horizontal dotted line and gray stripe represent the average clearance rate and 95% confidence interval under normoxic conditions for each treatment. Dashed lines indicate oxygen saturations in experimental tanks.

rate decreased and fluctuated before returning to values close to mean normoxic values. Over a 24-h cycle, significant difference ($p < 0.05$) between constant normoxia and cyclic normoxia-hypoxia treatments was observed for clearance rate. Mean clearance rate during cyclic normoxia-hypoxia treatment was about 70% of the value measured during constant normoxia treatment.

5.4 Discussion

5.4.1 Feeding behaviour under cyclic hypoxia

Under constant normoxia, average clearance rate standardized for a 1-g flesh dry weight individual was 5.05 L h^{-1} . This value is close to the value obtained by Zhou et al. (2006) for *Chlamys ferrari* at a similar temperature (5.95 L h^{-1} at $15.4 \text{ }^{\circ}\text{C}$) and is within the range observed for other pectinid species, taking into account that clearance rate scales with temperature: 1.13 L h^{-1} at $12.2 \text{ }^{\circ}\text{C}$ for *Placopecten magellanicus* (MacDonald and Thompson, 1986) and 6.2 L h^{-1} at $18 \text{ }^{\circ}\text{C}$ for *Argopecten irradians* (Riisgard et al., 1988). This indicates that the methodology used for the measurements of clearance rate is appropriate.

Various behavioural studies showed that marine bivalves can exhibit circadian activity rhythms in terms of feeding activity, shell gapping or respiration (e.g. Reid et al.,

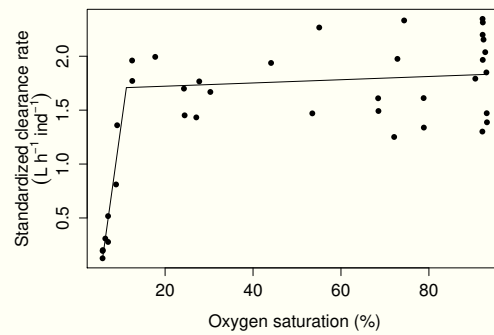


FIG. 5.5: Standardized clearance rate (30mm-height individuals) as function of oxygen saturation during transition between normoxia and severe hypoxia (≈ 4 hours). Note that this graphic has been constructed using only data from the progressive diminution of oxygen saturation within the experimental tank. Lines indicate the segmented linear model used to estimate the critical point for clearance rate. The estimated breakpoint was at 11.2 (± 1.4 SE) % oxygen saturation.

1984; Beentjes and Williams, 1986; Ameyaw-akumfi and Naylor, 1987; Kim et al., 1999; García-March et al., 2007; Gnyubkin, 2011) that might be related to daily environmental cycles or internal rhythms. A small but significant nightly decrease in clearance rate under constant normoxia (-9% compared with daytime activity) was observed indicating that *A. purpuratus* exhibits circadian rhythm in its feeding activity. Such a periodicity is in accordance with the daily rhythm in shell microstriae formation observed in the field in Peru (Paracas Bay, Aguirre-Velarde et al., 2015) and tends to indicate that laboratory condition of this study did not perturb the species natural rhythm. It is likely that such a daily rhythm is controlled by photoperiod and/or internal mechanisms since the other environmental parameters were kept constant in the experimental tank (F-N). Despite of this slight nocturnal decrease, *A. purpuratus* exhibits an active feeding behaviour during both day and night under constant normoxia.

Modifications of energy acquisition (i.e. feeding and/or assimilation) might affect the energy balance of an individual (Kooijman, 2010a). In this context, one of the aims of this study was to quantify the effect of cyclic hypoxia on feeding activity. We found that such conditions induce a 30% decrease in the daily average clearance rate compared to constant normoxia. Such a result is in accordance with other studies on bivalves that also showed a decrease in clearance rate under hypoxia (Wang and Widdows, 1993b; Sobral and Widdows, 1997; Hicks and McMahon, 2002; Wu, 2002; Norkko et al., 2005; Le Moullac et al., 2007; Wang et al., 2011). However, the dramatic decrease of clearance rate was only observed in the first hours of exposition to severe hypoxia, then scallops rapidly resumed feeding activity. The methodology used in our study allowed to assess the immediate response of scallops in terms of feeding behaviour to strong variations in oxygen availability, comparable to those observed in the natural habitat (see environmental data in Aguirre-Velarde et al., 2016). Our results (Fig. 5.4) allowed emphasizing the different phases in scallops response to such variations of oxygen saturation :

1. Initiation of hypoxia (between 100 and 11.2% O_2 sat, upper segment of Fig. 5.5): clearance rate remains unchanged. This can be related to high oxyregulation capacity down to 20-25% O_2 sat (Aguirre-Velarde et al., 2015). Such ability would allow *A. purpuratus* to maintain most of its physiological functions independent of ambient oxygen saturation. A lowest critical point for feeding activity than

respiration may indicate a decoupling of these physiological rates enabling food filtering even under low oxygen saturations.

2. First phase of severe hypoxia (below 11.2% $O_{2\text{ sat}}$): drop in the clearance rate. Below this oxygen threshold, we can hypothesize that the aerobic energy production decreases considerably and the energy demand might then be supplied by reserves such as phosphagens (Grieshaber et al., 1994) providing energy to maintain ciliary activity necessary for filtration. However, these energetic reserves are limited and are quickly consumed under severe hypoxic conditions (Ellington, 1989; Grieshaber et al., 1994). This, combined with the relatively fast decrease in oxygen saturation could explain the fast drop of clearance rate below 11.2% $O_{2\text{ sat}}$.
3. Second phase of severe hypoxia (first 3.30 hours at $\approx 5\%$ $O_{2\text{ sat}}$): recovery of the filtration activity. Under severe hypoxia and after a first phase of strong reduction of clearance rate, a partial recovery of feeding activity is observed. Such a recovery might be explained by the low energetic cost of bivalves gills ciliary activity (Jorgensen and Riisgard, 1988; Widdows and Place, 1989; Jorgensen, 1996) that would allow to maintain an active filtration at low oxygen levels (Sobral and Widdows, 1997). Nevertheless, if energy reserves such as phosphagens are exhausted it is likely that anaerobic metabolic pathways such as the Embden-Meyerhof-Parnas can be activated and supply energy. Such a pathway is used for anaerobic energy provision by invertebrates, but generally it does not last longer than 3-6 h under severe hypoxia (Grieshaber et al., 1994). Similarly to our results, Wang and Widdows (1993b) found that the bivalve *Abra tenuis* is able to maintain a pumping/feeding activity representing 83% of the normoxic feeding rate in anoxic conditions. Continuous feeding would allow maintaining anaerobic metabolism as long as the accumulation of metabolic endproducts allows it. Although feeding, digestion and assimilation are considered as costly functions, easily digestible food would be the key to successful adaptation of organisms in the oxygen minimum zones (Rosenberg et al., 1983; Mullins et al., 1985; Forbes and Lopez, 1990; Levin et al., 1991; Diaz and Rosenberg, 1995). Under such conditions it would be possible and perhaps energetically interesting for *Argopecten purpuratus* to continue feeding, at least for the first hours after the installation of severe hypoxia, to maintain its metabolic requirements. On the other hand, a decoupling between filtration (all-day) and digestion (under oxygen availability) would allow taking advantage of the trophic resource available by maintaining high assimilation.
4. Third phase of severe hypoxia (beyond 3 hours at $\approx 5\%$ $O_{2\text{ sat}}$): gradual re-decrease of the filtration activity. This behaviour has been documented in the hypoxia-tolerant bivalve *Ruditapes decussatus* that reduces, but not inhibits, its feeding and digestion activities to survive hypoxic or anoxic stress events (Sobral and Widdows, 1997). The maintenance of a consistent feeding activity might result in the accumulation of anaerobic endproducts and induce a change in the energetic strategy. A switch towards a metabolic depression (Wu, 2002), which is reflected by a gradual decrease in filtration rates, might be an efficient mechanism to survive to long-lasting severe hypoxic crisis. However, other explanation is that highest oxygen demand for digestion/assimilation processes would decrease under low oxygen conditions. The consequences would be the saturation of the digestive tract and the diminution of nutrition activity.
5. Resume of oxygen availability and recovery of feeding activity. A rapid recovery

of clearance rate associated with the increase in oxygen saturation after a severe hypoxic period highlights the ability of *A. purpuratus* to adjust its physiological/behavioural activities to environmental conditions that are naturally highly variable (at diurnal, seasonal and interannual scales). Interestingly, such a daily 12-h exposure to severe hypoxia does not seem to affect feeding activity in an extended way. However, more prolonged and cumulative hypoxic/anoxic conditions might induce metabolic damages with more negative consequences. Kozuki et al. (2013) showed that filtration ability and survival of the bivalve *Ruditapes philippinarum* were dramatically affected after a 3-days exposition to severe hypoxic conditions ($< 7\% O_{2\text{ sat}}$). The effects of severe hypoxia on metabolic damages have been shown to vary according to oxygen level, duration of exposure to hypoxia and species (Wang et al., 2009).

5.4.2 Growth under cyclic hypoxia

Several studies agree that chronic exposure to hypoxic conditions negatively affects growth of aquatic organisms (Brett and Blackburn, 1981; Cech et al., 1984; Pedersen, 1987; Diaz and Rosenberg, 1995; Thetmeyer et al., 1999; Pichavant et al., 2000, 2001; Wu, 2002; Brante et al., 2009; Mustafa et al., 2011; Rees et al., 2012). Exposition to hypoxia has been shown to be associated with a decrease of scope for growth in bivalves (Sobral and Widdows, 1997; Norkko et al., 2005; Wang et al., 2011). Although, scallops in F-N conditions had a mean shell height significantly higher than those in F-H condition at the end of the experiment, the remaining soft tissues dry weights were comparable between these two fed treatments. Shell-calcification might be compromised due to the use of carbonates to cope with metabolic acidification induced by anaerobiosis (Cameron, 1986, 1990; Cancino et al., 2003). As a result, a lag between the growth of the shell and soft tissues would be observed. Such a decrease in shell growth but not in soft tissues dry weight during exposure to hypoxia might explain the paradoxical higher condition index observed in the F-H treatment. The effects of hypoxia on bivalves condition are controversial in literature: Norkko et al. (2005) found a negative effect of hypoxia on *Paphies australis* condition index under abundant food supply, while no effect could be detected when food was limiting. Sandberg et al. (1996) did not find any effect of a 21-day exposure to hypoxia on *Macoma balthica* condition index. Greater digestive gland dry weight observed in the F-H treatment could result from the time of dissections: the latter were made at the end of the hypoxia periods (return to normoxia), after the clearance rate increased above average (see Fig. 5.3b). Thus, it is possible that at the time of dissection the digestive glands of F-H scallops were well filled compared to the scallops fed under constant normoxia.

The difference in water content between F-N and F-H treatments can be attributed to the distinct water balance between aerobic and anaerobic catalytic reactions (Hochachka et al., 1993). Water is produced under aerobic respiration while it is consumed under anaerobic respiration. An alternative explanation would be that oxic condition modifies the dynamics of reserves and thus the reserve to structure ratio. Because reserves might contain more water than structure components (Kooijman, 2010a) the overall water content of the organism might be modified.

5.4.3 Starvation, reserves and energetic strategies

The increased water content during starvation in this experiment is consistent with other studies on bivalves (Ansell and Sivadas, 1973; Whyte et al., 1990; Liu et al., 2010). However the reason for this strategy is still unknown (Navarro and Thomson, 1995). One possible explanation is that increased water content in the tissues would result from increased osmotic pressure linked to increased metabolite levels (Carbohydrates, lipids, proteins) during exposure to starvation (McCue, 2010). More likely, cells would replace the lost organic matter with water in order to maintain their size (volume), internal turgidity and ultimately their functionality during starvation (McCue, 2010; Liu et al., 2010).

Numerous studies have addressed the energetic strategies of bivalves (inhabiting different habitats: intertidal, subtidal, estuarine) facing oxygen-limiting conditions. However, comparisons between data sets are often difficult in terms of specific energetic adaptations due to the variety of experimental set-ups (hypoxia intensity, exposure and duration of hypoxia/anoxia, temperature, food supply, etc.) and study approaches (ecophysiological, calorimetric and molecular). In the field, energetic adaptations may also vary as a function of the environmental constraints (intensity, frequency and duration of hypoxic events).

Under oxygen-limiting conditions the energy production (ATP) by aerobic pathways (Krebs cycle + electron transport chain) is affected and the energetic contribution of anaerobic metabolic pathways with low ATP yield per glucose unit (Shick et al., 1986; de Zwaan et al., 1991) is controversial. On one hand, it is known that bivalves are able to exploit a variety of anaerobic biochemical pathways (Grieshaber et al., 1994; Isani et al., 1995). Simultaneous calorimetry-respirometry studies showed that the anaerobic contribution to the total dissipated energy can be important in bivalves (Wang and Widdows, 1993b,a). Biochemical studies reported a high potential for anaerobic metabolism (Le Moullac et al., 2007) as well as the presence of anaerobic endproducts in bivalves (Le Moullac et al., 2007; Tuffnail et al., 2008). Concentrations of the latter are dependent on the intensity (Grieshaber et al., 1994) and duration (Isani et al., 1995) of exposure to hypoxia. On another hand and from a thermodynamic point of view, the use of anaerobic pathways to supply the energy deficit of aerobic metabolism (i.e. Pasteur effect) is unlikely since it may cause a rapid depletion of reserves (de Zwaan, 1977, 1983; Shick et al., 1986; Gnaiger et al., 1989). Face to this "energetic dilemma", aquatic organisms would be able to adapt/acclimate by reducing their metabolic rate thus decreasing the ATP turnover (Isani et al., 1995; Wu, 2002; David et al., 2005; Sussarellu et al., 2013). Although the present study did not include metabolites analysis, energy available during starvation only depends on the amount of reserves. This allows to do assumptions about the energetic strategy of *A. purpuratus* dealing with cyclic hypoxia. If a massive consumption of reserve to fuel anaerobic pathways would occur, it would induce a faster weight loss in the S-H than in the S-N treatment. Such an hypothesis is unlikely because weight loss was similar in both treatments. This result tends to indicate that *A. purpuratus* has an important ability to regulate its metabolic rate in oxygen-depleted environments presumably by reducing its energy demand. Such a strategy would consist in decreasing the energy demand to achieve a low balance between energy supply and demand (Hochachka and Buck, 1996; Le Moullac et al., 2007) As a consequence, energy production by anaerobic pathways would only feed a reduced ATP turnover rather than supplying the deficiencies of aerobic metabolism (Hochachka and Buck, 1996). This metabolic depression under hypoxic conditions has been described for several bivalve species (Widdows and M., 1985; Shick et al., 1986; Widdows and

Place, 1989; Storey and Storey, 1990; Wang and Widdows, 1993b; Isani et al., 1995; Sobral and Widdows, 1997; Wu, 2002; Le Moullac et al., 2007; Wang et al., 2011). Under depressed metabolic conditions, it is likely that functions such as growth and reproduction, that represent important energy expenditures, are significantly reduced (Wang and Widdows, 1993b). According to this hypothesis, the observed weight gain in the F-H treatment could result of an accumulation of reserves due to the metabolic depression since somatic growth is reduced. This explanation is consistent with lower length growth and higher condition index in the F-H treatment compared with the F-N treatment.

5.5 Conclusions and modelling perspectives

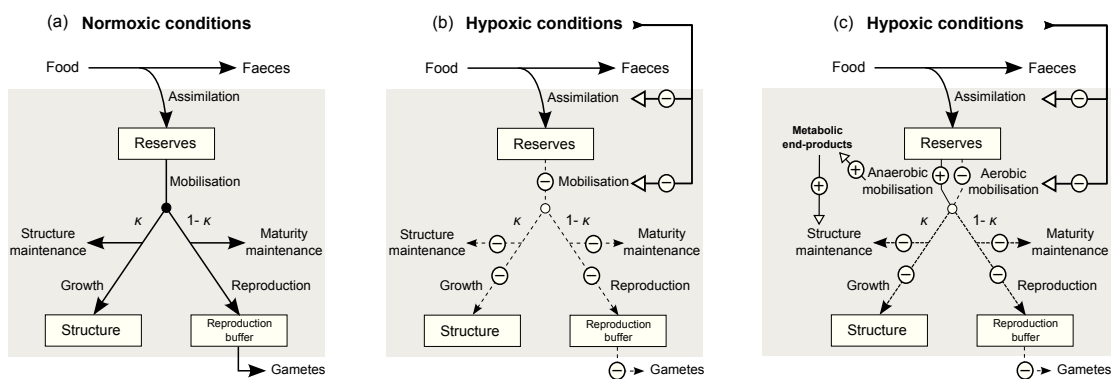


FIG. 5.6: Schematic representation of energy fluxes in the standard Dynamic Energy Budget (see Kooijman, 2010a) (a). Possible direct effect of hypoxia on reserves mobilisation and indirect on assimilation (b). Hypothetical representation of aerobic and anaerobic mobilisation of reserves under hypoxic conditions (c). Plus and minus signs indicate respectively positive and negative effects of hypoxic conditions on energy fluxes.

Models based on dynamic energy budget theory (DEB) are used to describe the energetic processes of an individual organism (Fig. 5.6 a) and have been widely used to study bivalves energetics (see e.g. Cardoso et al., 2006; Vanderveer et al., 2006; Pouvreau et al., 2006; Flye-Sainte-Marie et al., 2009; Rosland et al., 2009; Saraiva et al., 2011; Lavaud et al., 2014). Briefly, assimilated energy is incorporated into a reserve pool. Reserve pool is mobilized and a fixed fraction κ is used for maintenance (priority) and growth, while a fraction $1 - \kappa$ is used for maturity maintenance (priority), development and reproduction. See Kooijman (2010a) for an extensive explanation of the theory and for description of the parameters of DEB-based models.

In this context, we can hypothesize that low oxygen conditions might modify reserve mobilization (\dot{p}_e) because ATP production yield is reduced in those conditions (Shick et al., 1986; de Zwaan et al., 1991) (Fig. 5.6 b). Under the assumption that the reserve mobilization flux is affected, energy available for growth and reproduction might be compromised considering that the costs of maintenance are fulfilled in priority (Kooijman, 2010a). Nevertheless, we observed comparable weight growth in both normoxia (F-N) and cyclic hypoxia (F-H) fed treatments. This result suggests that physiological/metabolic mechanisms allowing the regulation of oxygen consumption e.g. increased ventilation, heart rhythm and/or oxygen transport efficiency (Wu, 2002) in relation with the high oxyregulation capacity of *A. purpuratus* (Aguirre-Velarde et al., 2016), might reduce the effect of low oxygen conditions on reserve mobilization flow.

In the DEB framework, this effect could be modeled relating positively oxygen saturation with the energy conductance parameter (v) that controls the reserve mobilization rate, using a rule that reflects the organism oxyregulation capacity such as the one used in Aguirre-Velarde et al. (2016). Low oxygen conditions might also affect assimilation since it is an oxygen-demanding activity, and a common strategy under hypoxia is to reduce food intake (Wu, 2002). However, our observations suggest a decoupling strategy between food intake and assimilation that might limit the effect of hypoxia on energy intake.

The inclusion of those effects of hypoxia in dynamic energy budget models will help to better predict the consequences of oxygen limitation on growth patterns of benthic aquatic organisms submitted to hypoxic events.

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Troisième partie

Modélisation de la bioénergétique d'*Argopecten purpuratus* et conséquences métaboliques de l'hypoxie

Chapitre 6

Un modèle bioénergétique pour *A. purpuratus* prenant compte de l'hypoxie

Including the effects of hypoxia on the dynamic energy budget of the Peruvian scallop (*Argopecten purpuratus* Lamarck, 1819)

Arturo AGUIRRE-VELARDE, Frederic JEAN, Gérard THOUZEAU, Laure PECQUERIE, Jonathan FLYE-SAINTE-MARIE

Abstract

Recent monitoring reveal that scallops cultures in Paracas Bay are exposed to chronic hypoxic conditions. In order to assess bioenergetic consequences of oxygen limitation on this important socio-economic bivalve, we first modeled the energy balance of the Peruvian scallop under the context of the Dynamic Energy Budget (DEB) theory. Then, following hypoxia related restrictions on respiration physiology/metabolism, oxygen availability was included into the model DEB as forcing variable. The model was tested using high frequency environmental observations recorded in Paracas bay at two depths of scallop cultivation: suspended in the water column and on the bottom. According to the simulation experiments, the negative effects of hypoxia can be explained by a restriction on assimilation and reserve mobilization fluxes. Exposure to chronic and severe hypoxic conditions in the Bay of Paracas therefore have a negative effect on flows allocated to growth and reproduction which are dependent of the mobilization of reserve. These effects are more evident in scallops cultured on bottom where exposure to hypoxia is more important. Besides the increased maintenance costs during anoxic events (often accompanied by milky turquoise water discolourations) would explain the lost in somatic weight tissues and reproductive cessation observed during the summer.

Keywords: DEB theory; bioenergetics; low oxygen; growth; reproduction; Peru.

6.1 Introduction

Highly productive areas like the Peruvian coastal upwelling system are naturally exposed to hypoxic conditions (Rabalais et al., 2010). On the one hand, important phytoplankton concentrations have favored the development of the Peruvian scallop (*Argopecten purpuratus*) culture in coastal bays of Peru. In commercial production of this bivalve, suspended cages in the water column and bottom farming systems are used. Production reached today 65000t/year (average of the last three years, PRODUCE). On the other hand, degradative processes of organic matter that settles consume oxygen in deep waters and bottom (Gewin, 2010). Environmental monitoring has revealed that coastal bays, where cultivation of Peruvian scallop is practised are affected by chronic hypoxic conditions. In Paracas bay there has been measured an important environmental variability where oxygen saturation can be, for long periods, below the oxygen uptake of regulation capacity of *A. purpuratus* (Aguirre-Velarde et al., 2016). Despite the moderate tolerance showed by bivalves against hypoxia (Vaquer-Sunyer and Duarte, 2008), chronic exposure to hypoxic conditions may have negative consequences on Peruvian scallop cultures (Chapter 3). Numerous studies agree on the negative effects of hypoxia on growth, reproduction and survival of aquatic organisms. The decrease of food intake rate (Wu, 2002) and aerobic metabolism (Hochachka and Buck, 1996) accompanied by the generation/cumulation of anaerobic metabolites (Grieshaber et al., 1994) are commonly observed negative consequences during exposure to hypoxia. In this regard, it is pertinent to explore the effects of physiological/metabolic consequences of oxygen limitation on the energy flows balance, especially a commercially important and socially sensitive species as the Peruvian scallop.

Kooijman (2010a) provides a bioenergetic model based on his theory of Dynamic Energy Budget (DEB) that provides an organization of metabolism and energy fluxes structuration. DEB theory assumes that assimilates from ingested food get into a reserved compartment. Feeding/digestion cost are paid directly from the food. A fixed fraction of energy κ from reserve is assigned to the growth and somatic maintenance, the remaining $1 - \kappa$ is assigned to development and reproduction. Priority is always given to somatic maintenance, if the rate of energy flux from reserves is not enough to pay the somatic maintenance cost, the individual dies in consequence of the use structure as energy source. The feeding rate is proportional to the organism's surface while maintenance is proportional to the volume of its structure. DEB theory uses the equation Van't Hoff-Arrhenius to describe the temperature dependence of physiological rates. The "standard" version of the DEB model has 12 parameters. The estimation of these parameters requires numerous data life cycle of the species (Kooijman, 2010a). A DEB model allows quantitative predictions of growth, reproduction as well as a variety of physiological rates and energy fluxes in a dynamic environment.

As a result of the industrialization of human activities and climate change frequency of hypoxia events increases globally (Levin et al., 2009; Rabalais et al., 2010). In this context, we need to better understand the impact of a decreasing oxygen concentration on individual performance and ultimately on population dynamics. Present paper aims, first, to model the energy balance of *A. purpuratus* (benthic phase) using DEB theory. Secondly, we describe the first study considering oxygen concentration as a forcing variable of a Dynamic Energy Budget model. The resulting model is tested against observations of scallops exposed to hypoxic conditions in a culture area Paracas Bay.

6.2 Material and methods

6.2.1 Data

A data set from a monitoring conducted in Paracas bay ($13^{\circ}49'35''$ S, $76^{\circ}17'43''$ W, Fig. 6.1), between August 28, 2012 and March 10, 2013 (late austral winter to summer) on two groups of scallops was used: a group experiencing the environmental conditions of the water column in suspended cages (3 m depth) and a group located on the bottom (Fig. 6.2). Data includes monitored shell height, dry weight, and fecundity (number of eggs) together with temperature, oxygen saturation and Chlorophyll-a concentration both at 3 m depth and on the bottom, and occurrence of milky turquoise waters. Environmental data shows relative stability between early-winter and spring while summer variability was relatively high (Fig. 6.3). Although there is a significant difference between the average between depths, this difference is small ($\approx 0.7^{\circ}\text{C}$). However, it should be noticed that abrupt temperature variations were observed ($\pm 8^{\circ}\text{C}$), especially between January and March. A decreasing oxygen saturation trend was observed between (austral) winter and (austral) summer, where prolonged periods of severe hypoxia and anoxia were recorded, particularly on the bottom. The time spent at oxygen saturations lower than 20% by scallops growing on the bottom is about two times higher than in the suspended culture. Chlorophyll-a concentration (as proxy of trophic resource) did not present a marked seasonality nor significant differences between depths. The recorded values of chlorophyll-a range from 4 to $55 \mu\text{g}\cdot\text{L}^{-1}$. Additionally observations of milky turquoise water discoloration events were recorded in 2013: Jan. 03, Jan. 28, Feb. 07 and Mar. 04. We observed that these events were accompanied by anoxic conditions.

Environmental conditions surrounding the suspended cages allowed a much higher growth and gonadal investment than conditions at the bottom (Fig. 6.8, data points). In early summer (mid-December), shell growth stopped in bottom-cultured scallops and was highly reduced in suspended-culture scallops after mid-January. More detail on monitoring data sets are available in chapter 3.

6.2.2 Description of the standard DEB model

DEB theory (Kooijman, 2010a) describes energetic processes of an individual organism using three state variables: structural volume (V), reserve (E) and reproductive buffer (E_R). It assumes that energy uptake from the environment is incorporated into a reserve pool from which it is used for maintenance, growth, development and reproduction following the so-called κ allocation rule. A fixed proportion κ of the energy from reserve goes to maintenance and growth, where maintenance has priority over growth. The remaining fraction $1 - \kappa$ is spent on development and reproduction. If the energy mobilized from reserve is less than the maintenance requirements, growth stops and maintenance needs are met by reducing the reproduction buffer. It is also assumed that energy allocated to development during the embryo and juvenile stage is allocated to reproduction during the adult stage, once the individual reaches (V_p). Details of DEB equations are shown in Table 6.1.

The dynamics of the reserve is the difference between assimilation (\dot{p}_A) and energy mobilization for physiological processes (\dot{p}_C). During starvation, no energy enters into the reserve pool, thus, the dynamic of the reserves a function of energy utilisation rate. The uptake rate (e.g. filtration rate) is proportional to structural surface area of the organism, while maintenance rate depends on structural volume. Maturity maintenance

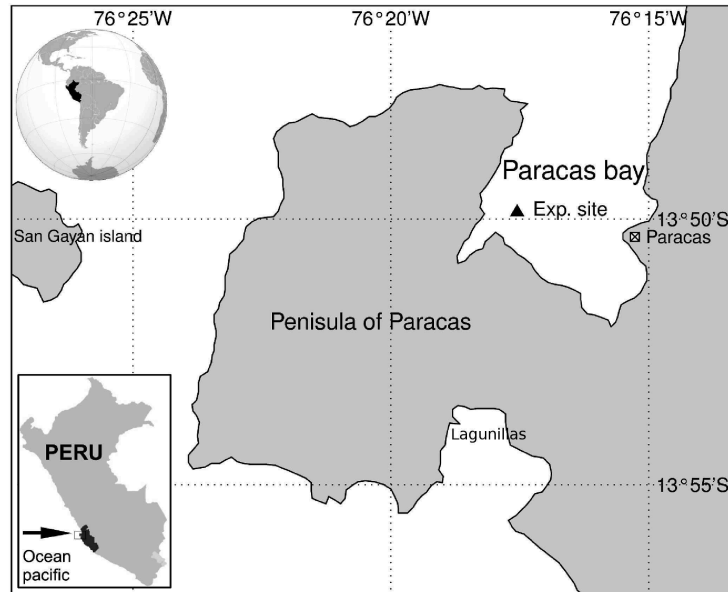


FIG. 6.1: Map of the monitoring site in Paracas Bay (Peru; $13^{\circ}49'35''$ S, $76^{\circ}17'43''$ W). The experimental site was located in a 5-m depth area dedicated to the commercial farming of *Argopecten purpuratus*. Scallops used in the experiment were collected off Lagunillas.

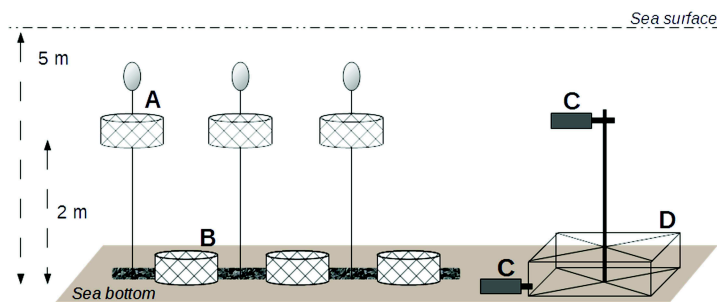


FIG. 6.2: Schematic representation of monitoring set-up for scallops culture and environmental monitoring installed at Paracas bay showing: suspended and bottom cages for scallops culture (respectively A and B), position of monitoring instruments (C) and the structure allowing the fixation of environmental equipments (D).

increases with structural size till it is fully developed (at size V_p). In adults, energy for reproduction is allocated to a reproduction buffer and emptied at each spawning event. Physiological rates depend on temperature within a species-specific tolerance range of temperatures, following an Arrhenius relationship (see Table 6.1). Further details regarding DEB theory can be found in Kooijman (2010a), Sousa et al. (2010), and Nisbet et al. (2012)

6.2.3 Application to Peruvian scallop

Observable variables

The model variables that will be compared to field experimental and literature data are defined in Table 6.2: Shell height, Somatic dry and wet weight, monthly fecundity, and gonadal wet weight are computed from the standard DEB variables and weight-specific oxygen consumption rate and clearance rate are defined from DEB energy

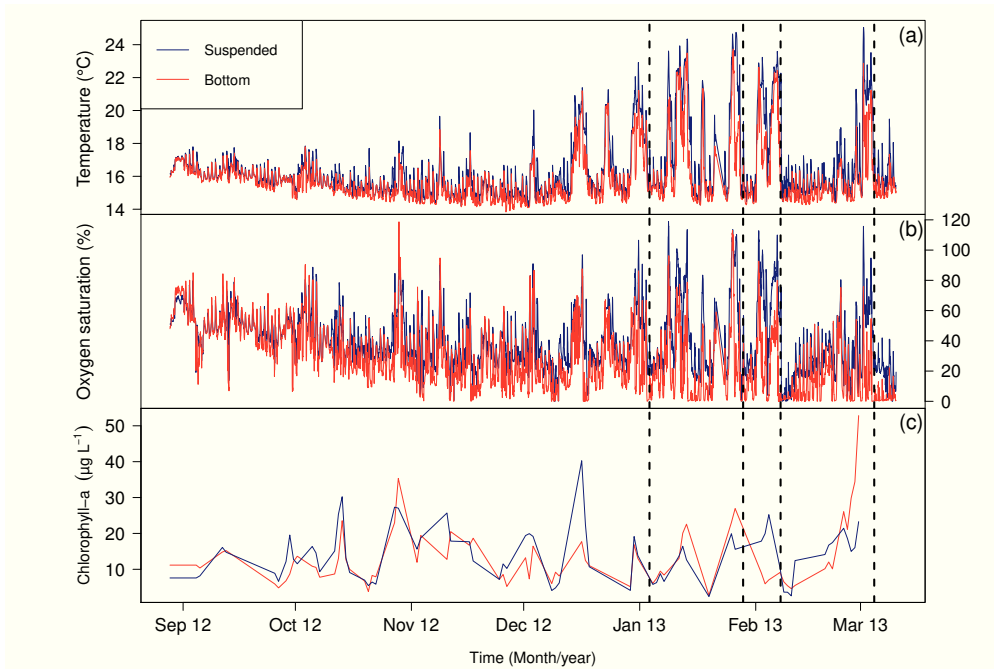


FIG. 6.3: Environmental variables collected between August 2012 and March 2013 in Paracas Bay at 5 m depth (suspended cages) and on the bottom: a) Temperature, b) Oxygen saturation, c) Chlorophyll-a concentration

fluxes. The reproduction (gametogenesis-spawning) of the scallops was modelled in cycles of 28 days according to the observations made by Cueto-Vega (2016) in Paracas Bay.

Data used for parameter estimation

Parameterisation of a DEB model requires information and datasets about the biology and physiology of the studied organism. A review of Peruvian scallop life-history traits from literature data was first performed. Data and sources are summarized in Table 6.3. We then considered the suspended scallop (groups 1 and 2 concatenated) dataset obtained from the monitoring in Paracas Bay during the late winter to autumn, described in the Data section to better constrain parameter values, as these scallops did not present a significant incidence of hypoxia during this period. In addition, data from physiological measurements under normoxic conditions was used: respiration rate (at 16°C and 25°C; for more details see Aguirre-Velarde et al., 2016) and clearance rate of standardized 30 mm individuals at 16°C (more details on Chapter 5). The covariation method for estimation of DEB parameters was used (details in Lika et al., 2011). A single-step procedure including all the different above-mentioned datasets, based on the minimization of a weighted sum of squared deviations between observations and predictions, produced parameter estimates presented in Table 6.4.

6.2.4 Including the effect of hypoxia in a DEB model

The effect of hypoxia on organisms is complex and involves molecular and physiological as well as behavioural responses (Wu, 2002). These responses will depend on the intensity, exposure time and frequency of hypoxic events as well as species-specific tolerance and acclimation capabilities. Under hypoxic conditions, energy production

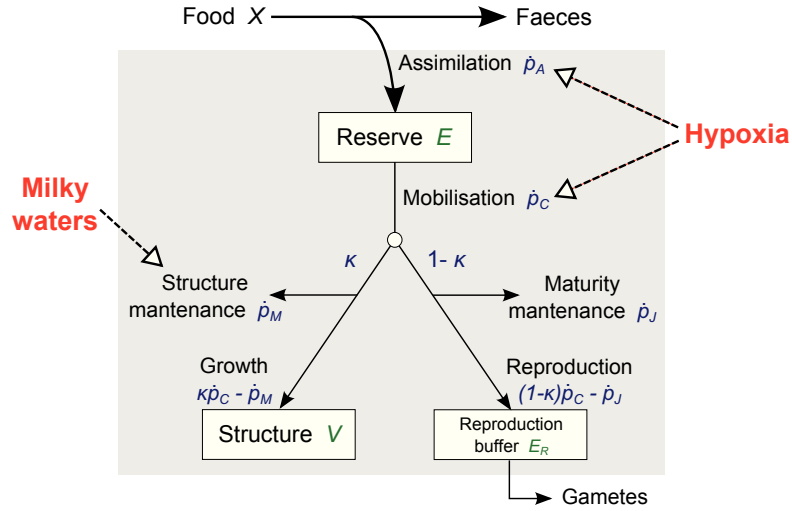


FIG. 6.4: Schematic representation of the scallop DEB model including the effects of hypoxia and toxicity related to the occurrence of milky turquoise waters

through aerobic metabolic pathways (i.e. Krebs cycle and electron transport chain) is impaired. Anaerobic metabolic pathways may supply energy, but the production yield of ATP is about 15 times lower per glucose molecule compared to the aerobic pathways. In the present work, we considered the resulting impact of *i*) impaired aerobic and *ii*) contributions of anaerobic pathways but did not consider them separately. We therefore first assumed that, overall, an organism under hypoxic conditions will be limited in its ability to "mobilize" energy required for metabolic activities (maintenance, growth, and reproduction). Consequently, an oxygen correction function was imposed on the reserve mobilization flux \dot{p}_C (Fig. 6.4; Eq. 6.2). More specifically, we assumed that hypoxic conditions would impact the energy conductance parameter (\dot{v}), regulating the reserve compartment output. Similarly, it is commonly observed a decrease or cessation of food intake under hypoxic conditions (Wu, 2002), probably due to the high energy cost of digestive/assimilation processes (see Kramer, 1987; Willows, 1992). It is thus likely that the resulting assimilation flux (\dot{p}_A) is also affected by limiting oxygen conditions. We assumed the same oxygen correction function $h(O_2)$ on (\dot{p}_A) for simplicity's sake (Eq. 6.1):

$$\dot{p}_A = c(T) h(O_2) \{ \dot{p}_{Am} \} f V^{2/3} \quad (6.1)$$

$$\dot{p}_C = c(T) \frac{[E]}{[E_G] + \kappa[E]} (h(O_2) \dot{v} [E_G] V^{2/3} + \dot{p}_M) \quad (6.2)$$

$$\text{with } h(O_2) = \begin{cases} \frac{P_{O_2}}{P_c} & \text{if } P_{O_2} < P_c \\ 1 & \text{otherwise} \end{cases} \quad (6.3)$$

where $h(O_2)$ varies between 1 and 0 following an oxyregulator type law (see Herreid, 1980): an organism is able to regulate its oxygen consumption until a critical point (P_c). Below this point, the organism is no longer able to maintain its oxygen consumption, which decreases linearly with the oxygen saturation of the surrounding water P_{O_2} . Under hypoxic conditions, below the organism regulatory capacities, the simultaneous decrease in the assimilation and mobilization fluxes restrict both reserve entry and output.

TAB. 6.1: Equations of the Dynamic Energy Budget model

Equations	Definition
$c(T) = \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)$	temperature dependence
$f = \frac{X}{X + K}$	functional response
$\dot{p}_A = c(T) \cdot \{\dot{p}_{Am}\} \cdot f \cdot V^{2/3}$	assimilation rate
$\dot{p}_M = c(T) \cdot [\dot{p}_M] \cdot V$	maintenance rate
$\dot{p}_C = c(T) \cdot \frac{[E]}{[E_G] + \kappa[E]} \cdot ([E_G] \dot{V}^{2/3} + \dot{p}_M)$	mobilization
$\dot{p}_J = c(T) \cdot \min(V, V_p) \cdot [\dot{p}_M] \cdot \frac{1 - \kappa}{\kappa}$	maturity maintenance rate
$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$	reserve dynamics
$\frac{dV}{dt} = \frac{1}{[E_G]} \cdot (\kappa \dot{p}_C - \dot{p}_M)$	Structural growth
$\frac{dE_R}{dt} = 0$ if $E_H < E_H^p$	reproductive reserve dynamics
$= (1 - \kappa) \cdot \dot{p}_C - \dot{p}_J$ otherwise	

Additionally, we assumed an increase in maintenance costs (\dot{p}_M) during the occurrence of milky waters. These seawater discolorations caused by toxic H_2S have been associated with scallops mortality events in different bays along the Peruvian coast in the recent years (Cabello et al., 2002; González-Hunt, 2010). Following Muller et al. (2010), we considered that the damages induced by the toxic agent required some repairs and thus increased maintenance costs.

6.2.5 Model simulations

After parametrization of the *A. purpuratus* DEB model, we performed four simulations to study the impact on growth and reproduction of environmental conditions at two different depths and for two groups with different initial size. We considered temperature, chlorophyll-a and oxygen saturation, monitored in Paracas Bay between August 2012 and March 2013 (Fig. 6.3) as forcing variables: suspended (Simulations 1 and 3) and bottom (Simulations 2 and 4) conditions were considered.

To simulate growth and reproduction of scallops using data series from Paracas bay, P_c , the critical oxygen saturation below which the organism cannot maintain its respiration rate, was fixed at 40% (best fit). During the occurrence of milky waters \dot{p}_M was increased by a factor 7 (best fit) for three consecutive days (average observed duration of these events). Model outputs were compared to observations on shell growth, somatic and gonadal wet weight from two size groups of scallops: group 1 with a 36.5 cm initial size (Simulations 1 and 2) and group 2 with a 66.8 cm initial size (Simulations 3 and 4).

TAB. 6.2: Equations of the observables computed from the DEB state variables and energy fluxes

Equations	Units	Definition
$L_w = \frac{V^{(1/3)}}{\delta_M}$	cm	Shell height
$W_d = d_{Vd} \cdot V \cdot (1 + \omega_d \cdot e)$	g	somatic dry weight
$W_w = d_{Vw} \cdot V \cdot (1 + \omega_d \cdot e)$	g	somatic wet weight
$N = \frac{E_R}{E_0}$	#	monthly fecundity (eggs per spawn)
$W_{ER} = \frac{(E_R \cdot \kappa_R) / \mu_E}{d_{Rw}}$	g	gonad wet weight
$\dot{J}_O / W_d = (\eta_{OA} \dot{p}A + \eta_{OD} \dot{p}D + \eta_{OG} \dot{p}G) / W_d$	mol O ₂ ·g ⁻¹ ·d ⁻¹	weight-specific O ₂ flux (respiration)
$CR = c(T) \cdot \{\dot{F}_m\} \cdot L_w^2$	mL·d ⁻¹	clearance rate

TAB. 6.3: Comparison between life-cycle data from the literature, used to estimate model parameters, and values predicted by the DEB model. Relative errors ((predicted value - observed value) / observed value) are reported.

Data	Literature value	Model value	Relative error
age at puberty	100 d	61.38 d	0.386
physical length at puberty	3 cm	3.3 cm	0.100
ultimate physical length	11 cm	11.28 cm	0.025
somatic dry weight at puberty	0.31 g	0.3554 g	0.146
ultimate somatic dry weight	16.8 g	16.65 g	0.009
maximum reprod rate (# eggs per spawning)	$3.8 \cdot 10^6$	$1.4 \cdot 10^6$	0.632
Gonadosomatic index	0.38	0.3803	0.001

6.3 Results

6.3.1 DEB model parameters and goodness-of-fit

The DEB parameters estimated for *A. purpuratus* using the covariation method are presented in Table 6.4. This set of parameter was estimated for a functional response of 1 and a reference temperature of 21°C. Overall, the goodness-of-fit obtained for scallops life history traits is good (mean relative error = 0.186; Table 6.3). However, age at puberty was underestimated by 38% and the maximum reproduction rate was 63% lower than the observed value. Model fit on growth (weight and shell height) and reproduction datasets used for calibration are shown in Figure 6.5. Model adjustment on physiological rates (oxygen consumption and clearance) are shown in Figure 6.6. In all three cases (growth, reproduction and physiological rates) model appears to satisfactorily predict our observations in normoxic conditions.

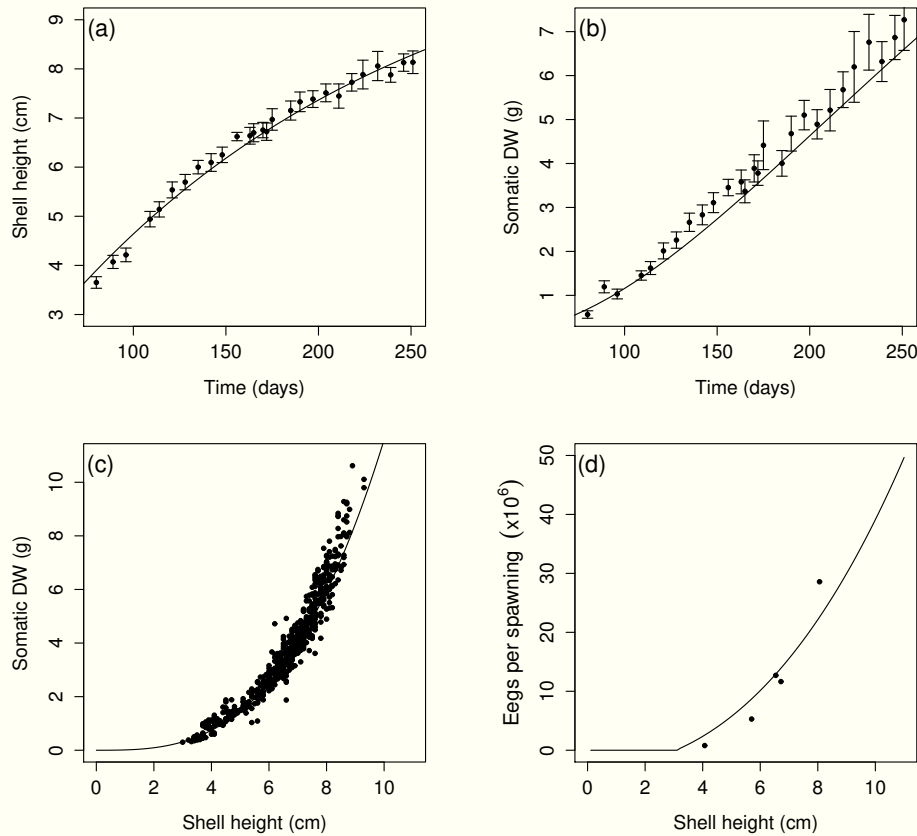


FIG. 6.5: Fitting of *A. purpuratus* DEB model on field experimental data collected in Paracas bay (suspended cages): (a) shell height and (b) somatic dry weight (DW) growth, (c) size-weight relationship, and (d) number of eggs per spawning as a function of shell height.

6.3.2 Simulation experiments

The average $h(O_2)$ values that are considered are significantly lower on the bottom with respect to suspended culture (Fig 6.7, $p < 0.01$). At both depths, relatively low $h(O_2)$ values (<0.5) occurred between November and March, with a particularly critical period between January and March (austral summer). Oxygen saturation values close or equal to zero were recorded repeatedly, particularly at the bottom. Note also that during the first half of February, considerably low P_{O_2} values were observed for consecutive days both at the bottom and at the suspended culture depth.

Model simulations including oxygen saturation correction and increased \dot{p}_M during milky waters events are presented in Figure 6.8. The overall growth and reproduction differences between bottom and suspended cultures is very well captured by the model: Suspended scallops grew faster and had higher gonadal weights than bottom-cultured scallops till the first milky waters occurred. Model simulations fit data better for scallops of size group 1. For the bottom-group-2, predicted weights were overestimated for the September - December 2012 period.

The weight loss that occurred during the January-March period, after the start of milky waters events, is well represented. The model also adequately represent observed trends in gonadal weight, corresponding to a sharp decline in reproductive activity. A 28-day spawning cycle appeared also to satisfactorily adjust gonadal weight decrease before the beginning of environmental summer disturbances.

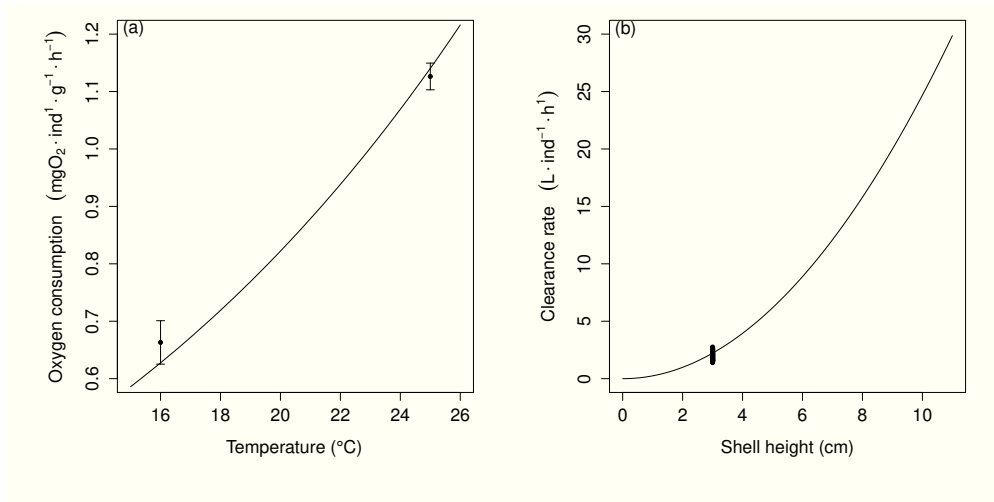


FIG. 6.6: Fitting of *A. purpuratus* DEB model on oxygen consumption of 3 cm standardized individuals as function of temperature (a) and clearance rate by size (b).

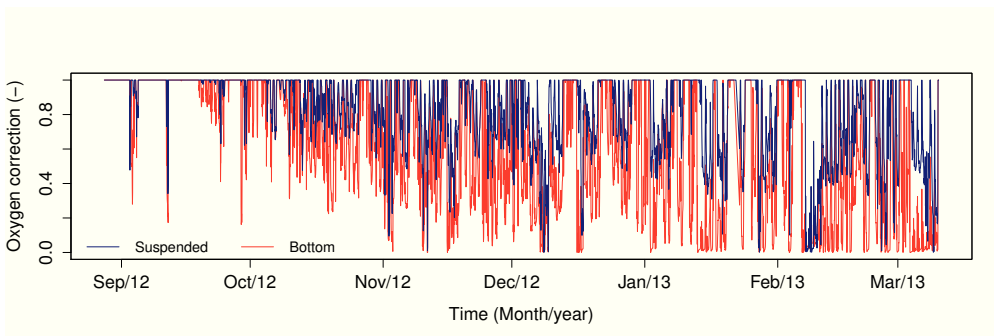


FIG. 6.7: Temporal evolution of the oxygen correction function $h(O_2)$ obtained from environmental monitoring in Paracas bay (Fig. 6.3b) used for the four model simulations presented in Fig. 6.8 (two depths and two different initial sizes).

6.4 Discussion

6.4.1 Parameterization of *A. purpuratus* DEB model

The standard DEB describes the interconnections among the metabolic processes of assimilation, maintenance, development, growth and reproduction of an organism throughout its life cycle, in dynamic food and temperature conditions (Kooijman, 2010a). In the present work, we provide the first DEB application taking into account the impact of hypoxic conditions on metabolism. Doing so, we successfully reproduced the differences in growth and reproductive patterns of Peruvian scallops experimentally cultured in suspended cages and at the bottom for a 7-month period in Paracas bay.

The predicted DEB model values for *A. purpuratus* life history traits were overall accurate. Nevertheless, the age at puberty and maximum reproduction rate were underestimated. Although, in this study the age at puberty is set at 100 days (corresponding to a 3-cm shell height, pers. obs.) Mendo et al. (1989) and (Disalvo et al., 1984) report first maturity for the Peruvian scallops at 2.5 and 1.3 cm respectively. In addition, the aforementioned references are based on the presence of differentiated gonad, however the onset of puberty should be started certainly before the first maturity (Kooijman, 2010a). On the other hand, the model was parametrized only for to the benthic life stage of the Peruvian scallop. The inclusion of the larval stage could potentially

TAB. 6.4: List of parameters for the *A. purpuratus* DEB model. All rate parameters are expressed at $T_1 = 291$ K (= 18 °C)

Parameters	Symbol	Value	Units
Primary parameters:			
Specific searching rate	$\{\dot{E}_m\}$	57.58	mL.cm ² .d ⁻¹
Digestion efficiency	κ_X	0.8	–
Maximum surface-area-specific assimilation rate	$\{\dot{p}_{Am}\}$	750.83	J.cm ⁻² .d ⁻¹
Volume-specific somatic maintenance rate	$[\dot{p}_M]$	93.98	J.cm ⁻³
Volume-specific cost for structure	$[E_G]$	3323	J.cm ⁻³
Energy conductance	\dot{v}	0.1961	cm.d ⁻¹
Fraction of utilized reserve to growth + maintenance	κ	0.4849	–
Maturity maintenance rate coefficient	\dot{k}_J	0.7405	d ⁻¹
Maturity threshold at birth	E_H^b	0.000839	J
Maturity threshold at puberty	E_H^p	427.3	J
Fraction of the reproduction buffer fixed into eggs	κ_R	0.95	–
Auxiliary and compound parameters:			
Arrhenius temperature	T_A	5715	K
Zoom factor	z	3.874	–
Shape coefficient	$\delta_{\mathcal{M}}$	0.3433	–
Structure density	d_{Vd}	0.12	–
Molecular weight of reserve	w_{Ed}	23.9	g.mol ⁻¹
Chemical potential of reserve	$\bar{\mu}_E$	550000	J.mol ⁻¹
Half-saturation coefficient	K	0.5	J.cm ⁻³
Maximum reserve density	$[E_m]$	$\frac{\dot{p}_{Am}}{\dot{v}}$	J.cm ⁻³
Fraction of reserve to total weight (without reproduction)	ω_d	$\frac{[E_m] \dot{v}}{d_{Vd} \bar{\mu}_E}$	–

modify the model predictions. Concerning the maximum reproduction rate, the model parametrization only took into account the female gonad (oocytes). The lower reproduction rate predicted by the model would include sperm production since the obtained value for gonadosomatic index is correct. A more precise estimate of reproduction rate must include the production of both oocytes and sperm. However, *A. purpuratus* has a high reproduction rate. A relative low investment on soma (κ) and rather high energy conductance (\dot{v}) would allow simulate the observed gamete production in cycles of 28 days.

Datasets of growth and reproduction used for parametrization were well predicted by the DEB model. It is worth noting that *A. purpuratus* is a species with relatively fast growth. Recently, Lavaud et al. (2014) conducted a DEB model parametrization for *Pecten maximus*, a Pectinidae with similar maximum length but slower growth. Comparatively, *A. purpuratus* and *P. maximus* have similar shapes. However, *A. purpuratus* has a lower kappa while a considerably higher energy conductance. This combination of parameters reflects the high energy investment in reproduction and fastest growing of *A. purpuratus* against *P. maximus*.

The Arrhenius relationship explains quite well the variation of oxygen consumption as a function of the observed temperature data. However, the upper and lower physiological critical are not available for this species for a most complete temperature correction. Although the clearance rate observations were available only for one size of scallops, it is expected that the feeding rate was proportional to the square of individual length (Kooijman, 2010a).

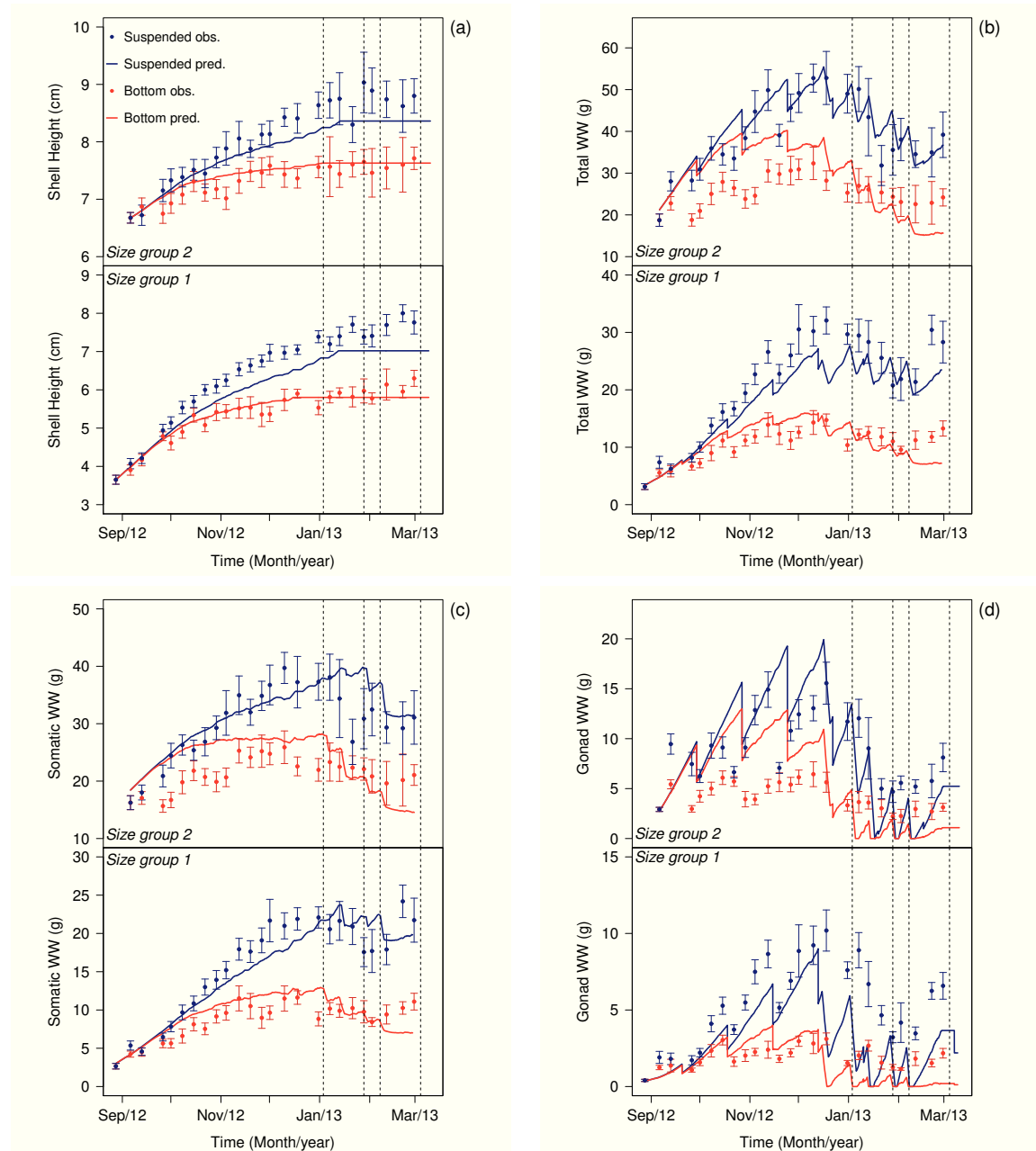


FIG. 6.8: Simulations (lines) of shell height (a), total wet weight (WW) (b), somatic WW (c) and gonad WW (d) for two size groups (initial shell height of 3.8 and 6.6 cm for group 1 and 2, respectively) of *A. purpuratus* scallops cultivated on the bottom and in suspended cages in Paracas Bay between August 2012 and March 2013. Points represent observed means and bars the respective confidence intervals ($\alpha = 0.05$). Dotted vertical lines correspond to the different milky water events observed in Paracas bay.

6.4.2 Effects of Hypoxia

The aim of this study was to include the effect of hypoxia on the energy budget of *A. purpuratus*, in a simplest way. We demonstrated that the effects of hypoxia on growth and reproduction could be well captured by our approach. Indeed, the two other environmental datasets used as forcing variables, chlorophyll-a and temperature, showed no significant differences between depths of scallops culture. That is, without the inclusion of the oxygen saturation correction, the simulations would show no differences. Here,

modelling the energetic consequences of environmental oxygen saturations below P_c , the critical oxygen saturation below which the organism is unable to regulate its oxygen uptake, allowed us to reproduce the observations. At the bottom, where exposure to hypoxia was frequent and sometimes prolonged, growth (shell height and weight) and reproduction (gonadal mass) of scallops was highly impacted. Declining of assimilation and mobilization fluxes below P_c restrict both the energy input and output from reserve towards metabolic functions (maintenance, growth, reproduction). The decrease of clearance rate under hypoxic conditions has been observed in *A. purpuratus* (Chapter 5), and generally in aquatic organisms (Wu, 2002). While the effect on the mobilization is based on the fact that energy restriction in aerobic metabolic pathways. In that sense, it seems appropriate to use a law according to the organism ability to regulate their oxygen consumption to condition the mobilization and assimilation fluxes.

In the simulations, a P_c of 40% was used, although Aguirre-Velarde et al. (2016) observed that in laboratory experiments, P_c would be around 24%. It is likely that the critical oxygen point varies depending on the organism size since respiration would be depends on a surface-volume relationship (Kooijman, 2010a). In natural environment hypoxia is accompanied by other potential environmental factors stressors (e.g. hypercapnia, pH, H_2S , POM...). The interaction of physiological stressor factors would potentially increase P_c . Despite the complexity of environmental hypoxic conditions, the simple inclusion of a correction on assimilation and mobilization fluxes using a oxyregulation law was satisfactory.

6.4.3 Effect of Milky waters

Milky turquoise waters events in Paracas Bay have been associated with the presence of hydrogen sulphide H_2S (Schunck et al., 2013). The degradation of organic matter under anoxic conditions generates H_2S , which under certain environmental conditions can be oxidized to elemental sulfur giving the milky turquoise discolouration (Ohde et al., 2007). The toxicity of H_2S and anoxic events have been responsible for marine organisms mass mortalities. However, the metabolic consequences of H_2S and/or elemental sulfur presence on filter feeders have been poorly studied (see example in Laudien et al., 2002). The conjunction of H_2S and anoxia would have dramatic consequences on maintenance costs. To reproduce the observed weight loss and the reproductive activity cessation, it was necessary to increase maintenance costs seven times during milky waters events (for 3 days). Under these conditions, reserve mobilization is near zero (anoxia or severe hypoxia), increased maintenance needs must be paid from the structure and reproduction buffer. It is necessary to design experiments to correctly model the effect of H_2S in interaction with hypoxia/anoxia and increase our knowledge on the toxicity of H_2S and its effects on organisms energy budget.

6.5 Conclusion and perspectives

Hypoxia has important energetic implications reflected in the decline in growth and reproduction of the Peruvian scallop. Although physiological adaptations allow to deal with oxygen limitation (i.e. regulation of respiration) of these are exceeded bioenergetic consequences can be dramatic. According to the simulation experiments performed in the context of the Dynamic Energy Budget theory, the negative effects of hypoxia can be explained by a restriction in the assimilation and reserves mobilization fluxes. Exposure to chronic and severe hypoxic conditions observed in Paracas Bay therefore have

a negative effect on allocated fluxes to growth and reproduction. Besides interactions with other stress factors could increase maintenance costs.

Although we show that it is possible to simply include the effect of hypoxia incorporating oxygen nuptake regulation, it is appropriate to explore the elemental balance of the DEB model. In order to deeper explore the oxygen limitation on the elemental balance of energy fluxes. It is also necessary to explore the anaerobic metabolic pathways and energy consequences that these could have on the bioenergetic budget.

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Quatrième partie

Synthèse

Chapitre 7

Synthèse

7.1 La côte péruvienne : variabilité environnementale et disponibilité en oxygène

L'écosystème côtier péruvien compte parmi les plus surveillés au monde du fait de son importante production halieutique pélagique. Cependant, ces efforts d'observation et de surveillance environnementale sont réalisés principalement par le biais d'images satellites et de croisières océanographiques et ce avec une résolution spatio-temporelle limitée. En outre, les zones très côtières telles que les baies sont rarement incluses dans ce type d'observations. Jusqu'à présent, le suivi environnemental à haute fréquence le long des côtes péruviennes à l'aide d'enregistreurs autonomes (data-loggers) a rarement été implémenté du fait d'un manque de financement mais aussi d'expertise pour l'installation et l'entretien de ce type d'équipements. De ce fait, les baies côtières sont généralement peu suivies alors qu'elles constituent des zones très importantes en terme de production aquacole et halieutique destinée à la consommation humaine. Elles constituent pourtant un enjeu majeur sur le plan à la sécurité alimentaire (possibilité physique, sociale et économique de se procurer une nourriture suffisante, saine et nutritive). Dans la baie de Paracas, zone traditionnelle de culture du pétoncle, le suivi haute fréquence des variables physico-chimiques dans la colonne d'eau et à l'approche du fond a démontré que les variations des conditions environnementales peuvent y être drastiques (voir Chapitre 3, p. 33) : en été, des variations de la saturation en oxygène allant de la sursaturation à l'anoxie accompagnées de changements de température de l'ordre de 8°C ont été observées à l'échelle d'une demi-journée. Lors de ces chutes de température, les eaux peuvent atteindre une température plus basse que le minimum hivernal (<15°C). Par contre, au cours de l'hiver et du début du printemps les conditions environnementales sont plus stables. La saisonnalité serait donc plus marquée par l'amplitude et la fréquence de la variabilité que par les valeurs moyennes de température, salinité et de saturation en oxygène. On observe également des cycles diurnes bien marqués *a priori* contrôlés par le rayonnement solaire (température) et l'activité photosynthétique (oxygène). Bien que dans la région de Paracas les marées soient de faible amplitude (maximum 1m) elle pourraient tout de même avoir un effet sur les conditions environnementales du fait de la faible profondeur de la baie (max. 14m pour une moyenne d' \approx 5m). Le suivi réalisé au cours de ce travail n'ayant duré que quelques mois (3 mois en 2007 et 6 mois entre 2012 et 2013), il est difficile de déterminer les tendances annuelles. Cependant, les deux suivis confirment l'importante variabilité thermique de l'écosystème. Dans les années à venir, il sera nécessaire de mettre en place une stratégie de suivi à long terme afin de mettre en place une climatologie de la région côtière

et mieux comprendre cette variabilité aux échelles saisonnière et inter-annuelles ainsi que les tendances à des échelles de temps plus longues et ce dans la baie de Paracas mais également dans d'autres zones d'importance halieutique/aquacole. Au cours de ce travail, seul un point a été suivi en Baie de Paracas, toutefois des observations à haute fréquence dans différents points de la baie sont en cours (données non publiées) et montrent que cette forte variabilité environnementale est observable à l'échelle de l'ensemble de la baie. Un suivi mené en baie de Sechura (5°34' S, profondeur moyenne = 12m), actuellement zone majeure de production de aquacole du pétoncle péruvien, montrent également une variabilité environnementale importante et des périodes d'hypoxie se prolongeant pendant des durées de l'ordre d'un mois (données non publiées). Une variabilité thermique similaire à celle enregistrée à Paracas a été observées plus au Sud, dans d'autres baies côtières peuplées d' *A. purpuratus*, à La Rinconada (Avendaño et Cantillánez, 2005; Cantillánez *et al.*, 2007; Thébault *et al.*, 2008; Avendaño D *et al.*, 2007, 23°34' S.), alors qu'à Tongoy (30°15' S) il existe une saisonnalité plus marquée avec occurrence d'hypoxie (2.0-1.5 mg O₂ l⁻¹ Uribe et Blanco, 2001). L'ensemble de ces résultats montrent que, tout au long de son aire de distribution, *A. purpuratus* est confronté à une forte variabilité thermique, trophique et oxygène.

Alors que, classiquement, la variabilité environnementale sur la côte péruvienne est attribuée au phénomène ENSO, l'observation à haute fréquence a révélé que dans les baies côtières, et au cours de périodes dites "normales" (hors conditions el Niño/la Niña) les conditions environnementales peuvent varier avec une amplitude similaire à celle observées au cours d'un événement El Niño, et ce sur périodes de temps extrêmement courtes (voir Chapitre 2 p.19 et 3 p.33). Ces enregistrements à haute fréquence sont les premiers à être publiés dans les baies côtières Péruviennes. Sears (1954) a observé également une variabilité importante de la température durant des années "normales" et attribue ce réchauffement aux effets du rayonnement solaire. Cependant, il est clair que la vitesse à laquelle les changements de température se produisent nous amène à croire que ces changements sont en fait dus aux mouvements des masses d'eau. Sous une telle hypothèse, les masses d'eaux chaude et froide pourraient alterner rapidement dans la baie, avec une plus grande intensité pendant l'été. Les masses d'eau chaude semblent correspondre à des eaux subtropicales de surface qui peuvent pénétrer dans la zone de Pisco (Quispe *et al.*, 2010), tandis que les eaux froides proviendraient de la remontée d'eaux profondes par l'upwelling. Cette alternance de masses d'eau dans la baie répondrait aux variations de conditions océanographiques et atmosphériques (présence de différents masses d'eaux, intensité et la direction des vents, transport vertical de l'upwelling, dynamique des courants et des marées ...). En raison des activités de production aquacole réalisées dans la baie de Paracas, il nous a semblé nécessaire d'approfondir la compréhension des causes de la variabilité environnementale observée dans ce secteur. En outre, il a été constaté que les différences de température entre le fond et la "colonne d'eau" (à 2m au dessus du fond) peuvent également être très importantes et atteindre jusqu'à 8°C de différence instantanée mesuré induisant une stratification importante (voir Chapitre 3). La surveillance environnementale haute fréquence menée au cours de cette étude donc à la fois révélé une variabilité thermique temporelle et verticale extrêmement importante.

La côte péruvienne constitue l'un des écosystèmes marins les plus productifs au monde du fait de la présence d'un upwelling côtier de forte intensité. Ce mécanisme généré par les vents côtiers de secteur sud-ouest provoque un transport vertical des eaux profondes (venues du large) vers la surface à l'approche de la côte. Les eaux de fond atteignant la surface fournissent des nutriments permettant une forte production primaire



FIG. 7.1: Vue de la baie de Paracas en conditions océanographiques "normales" (A). Événement d'eaux blanches ("Aguas blancas") dans la baie de Paracas le 18 avril 2015 (B). Source des photos : Edgart Flores Rafael

phytoplancton à l'origine d'une importante production dans les maillons trophique supérieurs. Cependant, une partie de la matière organique produite dans la colonne d'eau sédimente et consomme l'oxygène dissous dans l'eau par des processus de dégradation aérobie dans les eaux profondes, là où la photosynthèse et les échanges gazeux avec l'atmosphère ne sont plus possibles ce phénomène étant observé en dessous de 20m. Dans ces conditions de faibles concentration en oxygène, la matière organique est dégradée en anaérobiose par des microorganismes sulfato-réducteurs et une production de sulfures entre en jeu. Ces processus peut avoir lieu tant dans l'eau que dans le sédiment. Les eaux profondes, hypoxiques voire anoxiques et chargées en sulfures peuvent, par ce même mécanisme d'upwelling, être transportées à la surface. Bien qu'il soit montré que la zone de minimum d'oxygène le long de la côte péruvienne soit à la fois très étendue et peu profonde (en dessous de 50m ; Morales *et al.*, 1999), nos observations montrent que la disponibilité en oxygène peut également être limitée dans des zones peu profondes (quelques mètres) telles que les baies côtières. Ainsi, la baie de Paracas présente une exposition chronique et sévère à l'hypoxie. Pendant la période de suivi dans cette baie (août 2012- mars 2013 : fin de l'hiver et été), nous avons observé que les conditions sont hypoxiques (<25 % de saturation) jusqu'à environ 48% du temps d'observation dans l'eau proche du fond. Dans la colonne d'eau l'hypoxie est également importante puisqu'elle représentait 25% du temps au cours de la période de suivi. En outre, pendant la période estivale, des épisodes anoxiques (saturation en oxygène proche de zéro) ont été observés de façon récurrente et ce principalement au niveau du fond. Ces événements anoxiques se produisent simultanément à des chutes abruptes de température après un

épisode de forte stratification et sont souvent associés à la présence d'eaux de couleur turquoise et d'aspect laiteux (nommées localement "aguas blancas" illustrées dans la Fig. 7.1). Les chutes simultanées d'oxygène et de température semblent indiquer une entrée, voire un upwelling soudain, des eaux profondes froides et anoxiques, la couleur turquoise semble indiquer que ces masses d'eau sont chargées en sulfure d'hydrogène (H_2S). En effet, il semble que couleur soit caractéristique de l'oxydation du H_2S en soufre élémentaire (Ohde *et al.*, 2007). En outre, cette réaction chimique expliquerait l'anoxie presque totale observée lors de ces événements malgré la faible profondeur de la baie et la turbulence générée par les vents car cette réaction d'oxydation ferait réagir l'oxygène pouvant éventuellement diffuser de la surface. Au cours du suivi environnemental, nous n'avons pas effectué de mesures de la concentration en H_2S ; cependant, un panache d'eaux blanches de grandes dimensions attribué à une concentration importante en H_2S a été détectée dans les environs de la baie de Paracas en mai 2008 (Schunck *et al.*, 2013) à l'aide d'images satellite (couleur de la mer). Cette observation montre que dans la zone de Paracas (Pisco), des concentrations importantes en H_2S peuvent apparaître et conforte donc notre hypothèse concernant l'origine de ces eaux blanches. Notons que dans la région sud-ouest africaine, également caractérisée aussi par une importante productivité primaire liée à un upwelling, des événements d'eaux blanches liés aux fortes concentrations en H_2S avec des conséquences écologiques dramatiques ont été décrits (Lavik *et al.*, 2009).

Les vents dominants locaux, de direction Sud-Ouest et favorables à l'upwelling, sont susceptibles d'être impliqués dans la variabilité thermique et oxique observée car ils participeraient au transport vertical des eaux froides pauvres en oxygène vers la baie. Il serait intéressant d'étudier la dynamique existante entre les vents côtiers et océaniques car il existe apparemment un décalage entre eux. Curieusement, nos données montrent une intensification des vents dans la baie de Paracas pendant l'été alors que les vents océaniques qui génèrent l'upwelling sont généralement plus faibles à cette période de l'année (Correa *et al.*, 2014). Il est probable que les vents locaux de secteur sud en conjonction avec la géographie de la baie favorisent un transport vertical important qui y provoque l'entrée des eaux froides ($< 16^\circ C$) pendant les périodes chaudes de l'année. Les fortes stratifications observées en été pourraient favoriser la production de H_2S en dessous de la thermocline près du fond et dans les sédiments de la baie (Fig. 7.2). Bien qu'il soit probable qu'il y ait une production locale de sulfures, le fait que les événements d'eaux blanches soient associés à de brusques diminutions de température tends à indiquer que le H_2S qui s'oxyde dans la baie proviens des masses d'eaux froides et anoxiques qui entrent dans la baie par advection. Il semble donc nécessaire d'étudier la circulation dans la baie de Paracas et l'effet des vents locaux/océaniques sur la dynamique environnementale afin de mieux comprendre ces phénomènes. L'installation de bouées océanographiques permettant d'obtenir des profils de haute fréquence de température, de saturation en oxygène, de pH, des courants... le long de transects allant de l'intérieur vers l'extérieur de la baie pourraient aider à mieux comprendre cette dynamique. Les marées pourrait également jouer un rôle dans ces événements puisqu'elles peuvent favoriser l'entrée ou la sortie des masses d'eaux dans la baie. En outre, dans l'optique de mieux comprendre la formation des eaux blanches, un suivi de la concentration d' H_2S dans l'eau ainsi que des flux de sulfures à partir du sédiment et plus généralement une meilleure compréhension du cycle du soufre dans la baie semble nécessaire. L'utilisation d'imagerie pourrait aider à décrire et caractériser ces événements (étendue, distribution, périodes d'occurrence, durée...) qui induisent des mortalités importantes dans le élevages de pétoncle. Bien que les images satellites pourraient être utilisées, le

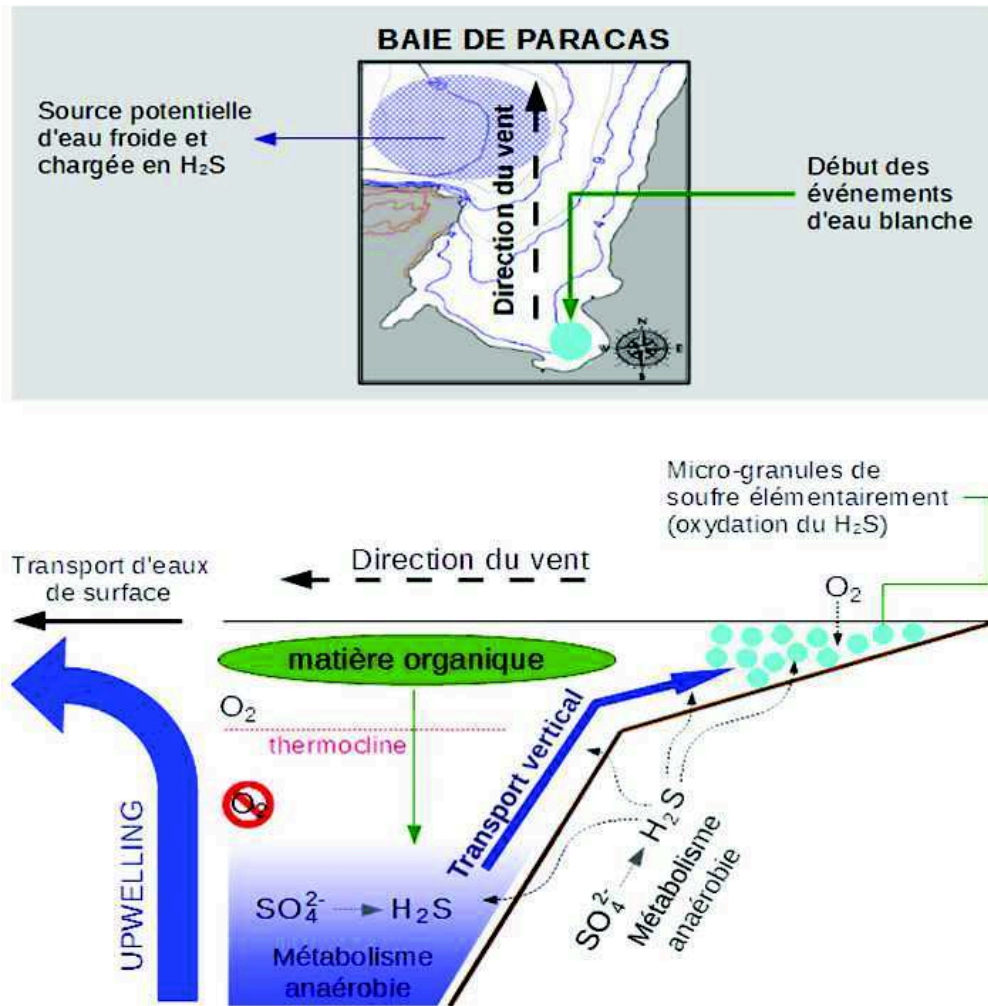


FIG. 7.2: Représentation schématique des possibles mécanismes physiques et biogéochimiques expliquant les phénomènes d'eaux blanches (localement nommés "aguas blancas") en Baie de Paracas : la dégradation de la matière organique qui sédimente vers le fond épuise l'oxygène dissous, en conditions anaérobie des bactéries sulfato-réductrices produisent de l'H₂S. Les vents de secteur sud induisent un transport vertical de eaux chargées en sulfure vers la surface où l'oxydation de l'H₂S produit des micro-particules de soufre qui donnent la couleur "blanche-turquoise" des eaux

couvert nuageux extrêmement fréquent est limitante, en revanche l'utilisation des caméras serait mieux adapté pour l'observation de la couleur de la mer.

Ce travail montre clairement que la variabilité environnementale réelle des baies côtières adjacentes le système d'upwelling Humboldt ne peut être appréhendée que grâce à de l'observation haute fréquence (temps ou à des intervalles ne dépassant pas les 4 heures). La mise en œuvre de mesures à une fréquence quotidienne signifierait déjà la perte d'informations pertinentes en raison de la vitesse à laquelle les conditions environnementales sont susceptibles de changer (ex. température et oxygène, voir chapitres 2 et 3). En conséquence, l'étude de l'effet des variables environnementales sur la biologie des organismes vivant dans ces zones devrait prendre en compte cet ordre de variabilité afin de mieux comprendre les défis adaptatifs (physiologiques, métaboliques ...) auxquels ils sont confrontés.

7.2 Défis énergétiques pour vivre dans un environnement pauvre en oxygène et très variable

Le suivi mené dans la baie de Paracas a montré que les organismes qui y vivent sont soumis à une forte variabilité environnementale. Des transitions rapides entre des températures chaudes et froides ainsi que des conditions oxiques allant de la sursaturation à l'anoxie ont été enregistrées, ces conditions se produisant particulièrement fréquemment en été. La validation du rythme de formation des stries sur les valves de *A. purpuratus* (1 strie/jour) dans cette baie permet d'étudier les effets de l'environnement sur sa croissance à une échelle de temps très fine (jour). Toutefois, ces effets sur la croissance ne sont pas nécessairement instantanés et simultanés au stress environnemental subi : ils peuvent être observés avec un décalage temporel du fait du temps nécessaire pour leur intégration par les processus métaboliques (la digestion, l'utilisation des réserves, la croissance, la reproduction...). En ce sens, la modélisation de la croissance (i.e. modèle de von Bertalanffy) qui permet d'analyser les écarts de taux de croissance par rapport à un modèle de croissance de référence s'avère efficace pour distinguer les signaux liés à l'ontogénèse de l'organisme et des effets dus aux stress environnementaux. D'autre part, la validation de la formation journalière des stries de croissance ouvre la possibilité d'utiliser les micro-éléments ou isotopes stables "capturés" dans les valves comme proxys environnementaux permettant ainsi l'utilisation d'*A. purpuratus* comme un enregistreur de la variabilité du milieu. La fine résolution temporelle que permet ce genre de technique permettrait d'appréhender la variabilité environnementale à haute fréquence des baies abritant des populations/cultures de pétoncles et de la relier par exemple à la croissance. Étant donné que notre capacité à prédire les événements El Niño est limitée, des reconstructions environnementales rétrospectives pour évaluer ces impacts sur les zones côtières du Pérou et du Chili pourraient être envisageables pour aider à une meilleure gestion de la ressource et des activités aquacoles. L'utilisation, par exemple, du rapport des isotopes d'oxygène ($^{18}O/^{16}O$) mesurée dans les valves qui permet de reconstruire la température de l'eau de mer (Chauvaud, 2005) peut être utilisé pour identifier des périodes chaudes et froides. En se servant de large distribution latitudinale d'*A. purpuratus*, l'intensité et la durée du phénomène El Niño et La Niña dans le Pacifique oriental pourrait être évalué ainsi que les relier aux impacts sur les populations naturelles et aquacoles. Cette information pourrait aider les décideurs et producteurs à mieux gérer les risques liés à la variabilité environnementale qui caractérisent cette région du monde.

Le suivi à haute fréquence de la température et de la saturation en oxygène a montré que la baie de Paracas était exposée à une hypoxie intense et chronique. Les zones de culture de pétoncle de cette baie sont donc soumises à des conditions de faible teneur en oxygène et ce de façon récurrente. Cependant, les organismes aquatiques sont capables, dans une certaine mesure, de tolérer les faibles saturations en oxygène. Il est généralement admis que le seuil en deçà duquel on considère un milieu comme hypoxique correspond à 30% de saturation (Rabalais *et al.*, 2010). Nos expériences ont montré qu'au-dessus de 24% de saturation le taux de respiration d'*A. purpuratus* est quasiment indépendant de la saturation en oxygène. On peut donc considérer qu'en dessous de ce seuil le pétoncle est donc soumis à un stress hypoxique. Les enregistrements en baie de Paracas indiquent que des sous-saturations allant en dessous de cette valeur se produisent de façon fréquente et prolongée au niveau du fond. Lorsque les organismes aérobies se trouvent en conditions limitantes en oxygène, leur efficacité à produire de l'ATP (énergie pour le métabolisme) est affectée. En effet, l'oxygène est l'accepteur final d'élec-

trons dans la production aérobie d'ATP. En absence d'oxygène, des voies métaboliques anaérobiques peuvent participer à la production d'ATP mais elles sont environ 15 fois moins efficaces que les voies aérobies si on considère que du glucose est métabolisé (Herreid, 1980). On peut donc s'attendre à ce que la limitation en oxygène affecte le rendement énergétique de l'organisme et sa capacité à assurer ses différentes fonctions métaboliques (maintenance, croissance, reproduction). Pour faire face à des conditions environnementales pauvres en oxygène, les organismes ont développé des adaptations physiologiques (ex. augmentation de la ventilation et de la fréquence cardiaque) afin de maintenir un apport constant (ou presque) en oxygène. Cependant, les mécanismes de régulation chez les bivalves sont peu connus et il reste à explorer. En deçà du seuil d'oxyrégulation, des voies métaboliques anaérobies plus ou moins efficaces permettent de maintenir un approvisionnement en énergie. Cependant, la discussion concernant la possible utilisation de ces voies métaboliques pour combler le déficit énergétique des voies aérobies reste ouverte car cela impliquerait un épuisement accéléré des réserves (Sobral et Widdows, 1997). D'autre part, une diminution du taux métabolique («arrêt métabolique») de l'organisme dans des conditions limitantes en oxygène pourrait être plus cohérente sur le plan bioénergétique (Hochachka, 1986). Les résultats présentés dans le chapitre 5 indiquent que le taux de perte de poids observé sur des pétoncles soumis à un jeûne en conditions normoxiques et en conditions d'hypoxie cyclique (100-5% de saturation de O₂) étaient similaires. Ces résultats tendent à indiquer qu'il n'existerait pas chez le pétoncle une consommation massive de réserves lorsque il est soumis à l'hypoxie sévère comme l'affirme (Hochachka, 1986) et tendraient donc à confirmer la seconde hypothèse. D'après les expériences réalisées *ex situ* *A. purpuratus* (Chapitre 4) est un "oxyrégulateur" efficace dans une large plage de température (16 - 22°C). Ces traits résultent sans doute d'adaptations dues à la pression de sélection exercée par la variabilité thermique ainsi que la fréquence des événements hypoxiques qui ont pu être observés au cours des suivis de terrain. Il serait intéressant de tester d'autres populations d'*A. purpuratus* afin de déterminer si les traits observés résultent d'adaptations locales/à l'échelle de l'espèce ou résultent d'un phénomène de plasticité associé à la fréquence et la durée des épisodes hypoxiques/anoxiques. Le pétoncle possède une grande tolérance face à une hypoxie cyclique ; comme l'ont montré nos expériences en laboratoire, cette espèce est capable de maintenir une filtration (alimentation) diminuée seulement de 30% par rapport à la normoxie, ce qui semble limiter les effets de ce stress sur la croissance. Il est probable que le pétoncle péruvien ait développé des adaptations physiologiques et métaboliques particulièrement efficaces pour répondre à des conditions d'hypoxie récurrentes, mais de courte durée. Il est également possible que l'activité métabolique au cours de l'hypoxie génère une dette en oxygène (voir Herreid, 1980) qui provoquerait une augmentation importante de la respiration après l'épisode hypoxique afin d'éliminer des métabolites voire d'effectuer le travail d'assimilation de la nourriture ingérée pendant l'exposition à l'hypoxie. Les effets de l'hypoxie sont toutefois dépendent de la durée, de la fréquence et de l'intensité des événements (Wu, 2002). Bien que nous ayons constaté qu'*A. purpuratus* présente une tolérance à l'hypoxie au travers de l'expérimentation *ex situ* (Chapitre 5) les travaux de terrain ont pu montrer des effets négatifs sur la croissance et la reproduction sont évidents (Chapitre 3), il semble donc que les conséquences énergétiques soient plus importantes que ne le laissent penser les expérimentations en laboratoire. Il faut également prendre en compte que les événements d'hypoxie/anoxie sont *a priori* souvent accompagnés par la présence de H₂S, des changements de pH et une hypercapnie, entre autres. L'interaction entre ces différents facteurs de stress, associés aux importantes variations de température observées consti-

tuent un défi adaptatif pour *A. purpuratus* et les autres espèces qui partagent l'habitat côtier péruvien. Il serait donc intéressant à l'avenir d'explorer ces adaptations au niveau enzymatique, protéomique et génomique pour mieux comprendre les mécanismes impliqués dans la réponse du pétoncle à des conditions hypoxiques/anoxiques.

En milieu naturel, lorsque la limitation en oxygène est forte (anoxie), des effets négatifs sur la croissance et la reproduction sont observés. Lorsque les conditions deviennent anoxiques et sont accompagnées d'épisodes d'eaux blanches, la perte de poids des pétoncles est particulièrement importante (entre 20 et 25%), la reproduction est perturbée (cessation de la gamétogenèse) et la survie même est affectée (mortalités supérieures à 50%). L'anoxie induit donc des défis énergétiques et métaboliques plus complexes que l'hypoxie : il est clair que dans ces conditions particulières, le pétoncle ne peut alors plus faire face à l'interaction de ces facteurs de stress ; les conséquences énergétiques étant sans doutes dramatiques car la maintenance ne peut plus être assurée.

En terme de production, la baisse de la croissance, la perturbation de la reproduction et la diminution de la survie liées aux événements hypoxique/anoxiques compromettent la productivité des cultures de pétoncle. Le seuil critique de régulation de la respiration par le pétoncle peut être utilisé comme un outil pour identifier les zones propices à la culture ou les profondeurs évitant d'exposer les individus cultivés au stress hypoxique.

7.3 La modélisation du bilan énergétique sous hypoxie

Le bilan énergétique d'un organisme peut être modélisé sous l'hypothèse que l'énergie assimilée prélevée dans l'environnement va directement dans un compartiment de réserve. À partir de ce compartiment, l'énergie est mobilisée suivant la règle dite «du κ (kappa)» : une proportion κ du flux sortant des réserves est assignée à l'entretien somatique et la croissance tandis que le restant $1 - \kappa$ est affecté à la maturité et à la reproduction. Ce modèle, basé sur la théorie Dynamic Energy Budget (DEB) de (Kooijman, 2010a), comprend un bilan élémentaire pour l'oxygène. Cependant, les développements actuels de modèles basés sur la théorie DEB ne prennent pas en compte la disponibilité en oxygène en tant que variable forçante. Un des objectifs de ce travail était d'introduire de façon mécaniste et parcimonieuse l'effet de l'hypoxie dans le modèle DEB. Ceci a été réalisé en introduisant une loi qui conditionne l'assimilation et la mobilisation de l'énergie à la disponibilité en oxygène. La limitation de l'ingestion de nourriture en conditions hypoxiques a été observée chez différentes espèces de mollusques (Wu, 2002). Cette stratégie permettrait de réduire les besoins en oxygène élevés liés à la digestion/assimilation. La limitation de la mobilisation résulte quant à elle de la diminution du flux de production d'énergie (ATP) par la voie métabolique aérobie, en conditions d'hypoxie physiologique.

La loi utilisée pour conditionner les flux d'assimilation et de mobilisation de l'énergie correspond à la capacité de *A. purpuratus* à réguler la consommation d'oxygène (voir Chapitre 4). Selon cette loi, la régulation de la consommation d'oxygène permet de maintenir les flux aérobiques sans affecter le bilan énergétique jusqu'à un seuil critique de sous-saturation, où les capacités d'adaptations physiologiques/métaboliques de l'organisme à pourvoir ses besoins en oxygène ne seraient plus suffisantes (Fig. 7.3). En dessous de ce seuil, l'organisme rentre dans une limitation métabolique en oxygène affectant les flux d'assimilation et de mobilisation avec des conséquences sur l'ensemble du bilan énergétique du pétoncle. Bien que l'intégration des effets de l'hypoxie dans le bilan modèle DEB reste préliminaire, les simulations réalisées reproduisent avec succès les tendances observées pour la croissance et la reproduction des pétoncles soumis

à deux conditions contrastées d'exposition à l'hypoxie (culture sur le fond et en suspension) dans la baie de Paracas. Dans l'élevage de fond, où l'exposition à l'hypoxie était élevée (représentant 48% du temps observé), les taux de croissance et les variations de l'indice gonado-somatique reproduits par le modèle étaient moins importants que pour les pétoncles cultivés en suspension. En ce qui concerne la reproduction, *A. purpuratus* est une espèce qui alloue une quantité importante d'énergie à la formation des gamètes (valeur faible pour κ , voir Chapitre 6). Des pontes partielles, synchrones et approximativement cycliques (mensuelles) ont été observées chez les pétoncles cultivés sur le fond et en suspension à Paracas. Cependant, en culture suspendue où l'exposition à l'hypoxie a été plus faible, des poids de gonade plus élevés ont été simulés par le modèle, coïncidant avec les observations. Cet effet négatif de l'hypoxie sur la reproduction pourrait avoir des conséquences sur la dynamique de populations de pétoncle exposées aux conditions limitantes en oxygène.

D'autre part, des effets extrêmes importants sur la croissance somatique (perte de poids de l'ordre 25%) et la reproduction ont été observés en présence d'eaux blanches durant l'été. Pour que le modèle puisse reproduire ces observations, il a été nécessaire d'introduire une forte augmentation des coûts de maintenance (6 fois plus). La présence de H_2S toxique dans l'eau lors des événements d'eaux blanches pourrait être la cause d'une telle augmentation (investissement énergétique dans le métabolisme de l'agent toxique). En effet, H_2S forme une liaison complexe avec le fer dans les cytochromes mitochondriaux, empêchant ainsi la respiration cellulaire. Les coûts de maintenance étant une priorité pour la survie de l'organisme, l'énergie qui reste disponible pour la croissance et la reproduction est ainsi diminuée. D'autre part, dans des conditions de limitation en oxygène, les voies métaboliques anaérobies peuvent, dans une certaine mesure, participer à l'approvisionnement en énergie. Cependant, les métabolites terminaux accumulés lors de l'activation de ces voies sont toxiques et peuvent également contribuer à l'augmentation des coûts de maintenance. En conséquence, lors d'un épisode d'eaux blanches, la présence de H_2S et l'anoxie (voies anaérobies possibles uniquement), font que le flux d'énergie nécessaire pour couvrir les coûts de maintenance augmenterait considérablement. Dans ces conditions extrêmes, la maintenance pourrait augmenter à un point tel que les réserves ne peuvent plus répondre aux besoins. De réserves alloués à la structure et à la reproduction pourraient être réabsorbés pour fournir l'énergie nécessaire à la maintenance de l'organisme. D'après le modèle, la perte de poids, l'arrêt de la reproduction et l'augmentation de la mortalité au cours de l'été (événements d'eaux blanches fréquents) pourraient être expliqués par l'augmentation des coûts de maintenance dus à la toxicité du H_2S , conjointement avec les effets des conditions hypoxiques/anoxiques sur la mobilisation des réserves. En outre, il est probable que la présence d' H_2S ou d'autres facteurs de stress réduisent la capacité de régulation respiratoire, en augmentant l'impact négatif sur le bilan énergétique de *A. purpuratus* et en limitant leur capacité d'adaptation aux conditions critiques et causant des mortalités importantes.

Il est nécessaire de mener des études futures dans le but d'approfondir nos connaissances sur les effets bioénergétiques de l'hypoxie car ses conséquences métaboliques sont susceptibles de varier en fonction de la durée et de l'intensité de la limitation en oxygène en interaction avec d'autres facteurs de stress environnementaux (ex. pH et H_2S). Il est nécessaire de concevoir des études contrôlées pour évaluer les effets de l'hypoxie en combinaison avec d'autres facteurs de stress afin de permettre une modélisation bioénergétique cohérente en tenant également compte de la durée, la fréquence et intensité de l'hypoxie ainsi que des autres facteurs de stress qui l'accompagnent. En

outre, la vulnérabilité des organismes à l'hypoxie pourrait varier en fonction de la taille. En effet, Kooijman (2010a) montre bioénergétique et mathématiquement que le taux de respiration d'un organisme dépend à la fois de sa surface et mais aussi de son volume. En ectothermes comme chez les pétoncles l'incorporation d'oxygène se fait à travers une surface (i.e. les branchies). Cependant, la production d'énergie aérobie permettant de couvrir les coûts de maintenance dépend plutôt du biovolume. Dans des conditions chroniques/sévères d'exposition à des événements hypoxiques il est probable que les plus grands individus de la population/cultures possèdent un point critique plus élevée et soient donc plus vulnérables.

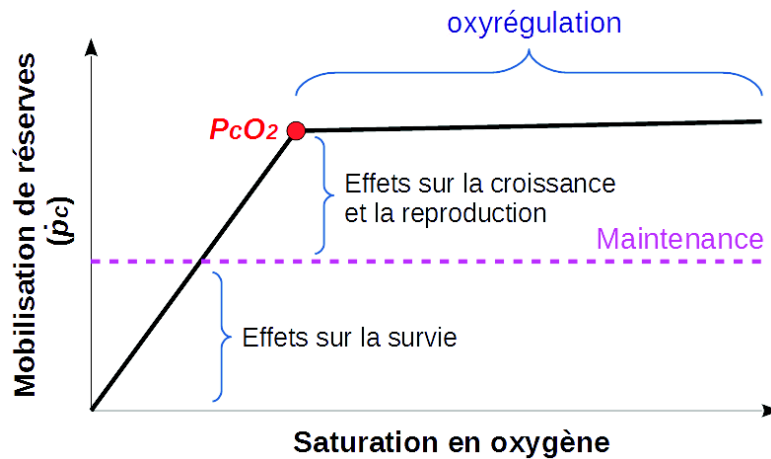


FIG. 7.3: Mobilisation de réserves face à la diminution de la saturation en oxygène de l'eau et ses effets sur le métabolisme en dessous du seuil critique (P_cO_2)

7.4 la durabilité de l'activité aquacole sur la côte péruvienne

La production de pétoncle péruvien a rencontré de sérieuses difficultés au cours des cinq dernières années. Les mortalités massives dans les exploitations aquacoles ont provoqué une forte baisse de la production (PRODUCE, 2015). L'un des événements les plus drastiques a causé la perte presque totale des élevages dans la baie de Sechura à la suite d'une floraison massive de phytoplancton qui a induit une anoxie près du fond (Gonzales *et al.*, 2012a,b). Du fait de cet événement, environ 30000 tonnes de produits se sont perdus (PRODUCE, 2015). Jusqu'à présent des événements de mortalité liés à l'hypoxie/anoxie ont eu lieu à plusieurs reprises le long de la côte péruvienne dans les zones aquacoles. Malheureusement, dans le contexte du changement climatique nous nous attendons à une augmentation de l'hypoxie côtière à cause de l'activité humaine (Levin *et al.*, 2009; Middelburg et Levin, 2009). Pour la région du Pérou-Chili il est également prévu une augmentation du transport vertical lié à l'upwelling qui pourraient transporter plus d'eau pauvre en oxygène vers la surface (Bakun et Weeks, 2008; Bakun *et al.*, 2010) ainsi qu'une augmentation des événements extrêmes tels que El Niño (Timmerman *et al.*, 1999). Dans ce contexte, il est nécessaire d'adapter les pratiques aquacoles pour assurer la durabilité de la culture du pétoncle péruvien. Comme cela a été discuté ci-dessus, la limitation de l'oxygène affecte la croissance, la reproduction et la survie du pétoncle avec des conséquences négatives pour la production commerciale.

Malgré cela, nous ne disposons pas des stations de surveillance permanente à haute fréquence dans les baies de la côte péruvienne. Dans les années à venir il semble donc nécessaire de mener des efforts d'observation dans les baies côtières péruviennes pour en évaluer les conditions environnementales et en particulier la variabilité oxygène. Les données recueillies pourraient servir à identifier des aires critiques où la culture du pétoncle est déconseillée en raison de la disponibilité en oxygène. D'autre part, la majeure partie de la production est aujourd'hui réalisée sur le fond. Selon les données recueillies au cours de l'expérimentation *in et ex situ* il est conseillé de convertir des cultures vers les élevages en suspension, en prenant également soin de placer les structures au-dessus la formation de la thermocline afin de diminuer la probabilité des expositions à l'hypoxie/anoxie.

Dans la baie de Paracas, les événements d'eaux blanches représentent un risque pour la production dans cette zone. Les taux de croissance et les indices gonado-somatiques qui sont généralement réalisés dans cette baie ainsi que l'accès facile aux zones de travail sont intéressants pour les producteurs. Toutefois le risque de mortalité massive est particulièrement important au cours de l'été. Pour une meilleure gestion de la production de Paracas nous avons besoin d'informations océanographiques suffisantes pour mieux comprendre la dynamique des événements d'eaux blanches, les modéliser et les prédire. Quoiqu'il en soit, il semble déconseillé de cultiver au cours des mois d'été pendant lesquels la fréquence de ces événements et d'hypoxie/anoxies est importante. Il semble clair que si dans les années à venir ces conditions tendent à augmenter ou s'étendent à d'autres saisons cela pourrait affecter la durabilité de la production de cette région. En général, des études de capacité de charge devraient être menées dans les zones côtières exploitées pour la culture d'*A. purpuratus* prenant compte la limitation en oxygène et ses effets sur la performance productive.

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La bioénergétique du pétoncle péruvien (*Argopecten purpuratus*) dans un contexte environnemental limitant en oxygène

RÉSUMÉ

Au cours des deux dernières décennies, la culture du pétoncle (*Argopecten purpuratus*) s'est développée dans les baies côtières péruviennes. La disponibilité trophique liée au système d'upwelling est favorable à la production du pétoncle. Cependant, les côtes péruviennes sont également connues pour présenter une forte variabilité environnementale sur tout en domaine océanique. Bien que les élevages du pétoncle soient vulnérables aux aléas de production (mortalité, croissance faible), la variabilité environnementale dans les baies côtières du Pérou et ses effets sur la croissance, la reproduction et survie de cette ressource socialement sensible ont été peu étudiés. La baie de Paracas au Pisco-Pérou est une zone traditionnelle de culture du pétoncle où des hauts et des bas productifs liées aux conditions environnementales ont été enregistrées au long de son histoire. Dans le but d'approfondir nos connaissances sur cette problématique, cette étude se pose sous trois approches : (1) l'observation *in situ*, (2) l'expérimentation en physiologie et (3) la modélisation du bilan énergétique de *A. Purpuratus*. Un suivi environnemental mené dans la baie de Paracas montre que la variabilité océanographique peut être important, en particulier pendant l'été. Des variations de température de 8°C et des conditions oxiques allant de la sursaturation à l'anoxie (absence d'oxygène) dans le cours d'une journée ont été observés. L'enregistrement haute fréquence a permis de révéler une exposition chronique, sévère et prolongée de la baie de Paracas aux conditions hypoxiques. Les pétoncles cultivés sur le fond, où l'exposition à l'hypoxie était importante (47 % du temps observé) ont montré une croissance et les conditions de reproduction plus faibles. Cependant, au cours de l'été, les événements hypoxiques prolongés et sévères ont touché les deux profondeurs de culture – les pétoncles cultivées en suspension comme sur le fond-, causant des pertes de poids de tissu somatique ainsi que l'arrêt de la reproduction. Durant les expériences en laboratoire, les pétoncles ont montré une importante capacité à réguler leur respiration face à la diminution de la saturation en oxygène jusqu'à 24%. De manière surprenante, nous avons trouvé que cette espèce est capable de maintenir une filtration, quoique diminuée, même à des saturations en oxygène basses (5%). Sur la base des réponses physiologiques du pétoncle face à l'hypoxie et le rendement énergétique moindre du métabolisme anaérobie par rapport au métabolisme aérobie nous faisons l'hypothèse d'une diminution de l'ensemble du métabolisme à des saturations en oxygène en dessous de la capacité de régulation de l'espèce. Des simulations d'un modèle incluant cette restriction énergétique (sur les flux d'assimilation et de mobilisation de la réserve) en conditions d'hypoxie parviennent à reproduire avec succès les observations de terrain effectuées dans la baie de Paracas : une plus grande exposition à l'hypoxie a pour conséquence une croissance réduite et un arrêt de la reproduction. Alors que le pétoncle possède des adaptations physiologiques/métaboliques pour faire face à des conditions limitantes en oxygène, la croissance et la reproduction peuvent être compromis, affectant ainsi la productivité des cultures de cette espèce (cela en fonction de la fréquence, durée et intensité de l'hypoxie). Les résultats des observations, des expériences et des simulations réalisées lors de cette étude fournissent des informations utiles pour mieux gérer la culture de pétoncle péruvien. Sur la base de ces travaux, des estimations de capacité de charge des baies, et des évaluations de zones et profondeurs favorables pour la culture de ces pétoncles pourront être réalisées.

Mots clés: *Argopecten purpuratus* ; variabilité environnementale ; bioénergétique ; physiologie ; modélisation ; hypoxie ; aquaculture ; Pérou.

Bioenergetics of the Peruvian scallops (*Argopecten purpuratus*) in an environmental context limiting oxygen

ABSTRACT

During the past two decades, the scallop (*Argopecten purpuratus*) culture developed in the Peruvian coastal bays. The trophic availability linked to the upwelling system supports the production of scallop. However, the Peruvian coast is also known to have a high environmental variability especially in the oceanic domain. Although scallop farms are vulnerable to production hazards (mortality, low growth), environmental variability in coastal bays of Peru and its effects on growth, reproduction and survival of this socially sensitive resource have been poorly studied. Paracas Bay in Pisco, Peru, is a traditional farming area where scallop highs and lows in productivity related to environmental conditions were recorded throughout its history. In order to increase our knowledge on this issue, this study arises from three approaches: (1) observation *in situ*, (2) experimental physiology and (3) modelling of the energy budget of *A. Purpuratus*. An environmental monitoring conducted in the Paracas Bay shows that the oceanographic variability can be important, especially during the summer. Temperature variations of 8°C Celsius and oxic conditions ranging from supersaturation to anoxia (absence of oxygen) in the course of a day were observed. The high frequency monitoring has revealed a chronic, severe and prolonged hypoxic conditions in Paracas Bay. Scallops grown on the bottom, where exposure to hypoxia was important (47% of the observed time) showed lower growth and reproduction conditions. However, during the summer, prolonged and severe hypoxic events affected both deep culture – scallops grown in suspension and on bottom – causing weight somatic tissue losses and cessation of reproduction. During the laboratory experiments, scallops showed significant ability to regulate their oxygen uptake face to decreased oxygen saturation up to 24%. Surprisingly, we found that this species is able to maintain filtration, although diminished, even at low oxygen saturations (5%). Based on the physiological responses of the Peruvian scallops face to hypoxia and the energy performance aerobic and anaerobic metabolism; it is hypothesized that there exist a restriction in the energy flow available for metabolism at oxygen saturations below the regulation capacity of the organism. Model simulations including this energy restriction (on assimilation and reserves mobilization fluxes) against hypoxia can reproduce successfully field observations of Paracas Bay: greater exposure to hypoxia results in a reduced growth and reproductive conditions. Although the scallop has physiological adaptations/metabolism to deal with limited oxygen conditions, growth and reproduction can be compromised, affecting culture productivity of this species (according to the frequency, duration and intensity hypoxia). The results of observations, experiments and simulations obtained during this study provide useful information to better manage of Peruvian scallop cultures (ex. Load capacity estimates in the bays, evaluations of adequate areas/depths for culture, etc.).

Keywords: *Argopecten purpuratus*; environmental variability; bioenergetics; physiology; modelling; hypoxia; aquaculture; Peru.