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Oxygen: A Fundamental Property Regulating Pelagic Ecosystem Structure in the Coastal Southeastern Tropical Pacific

Arnaud Bertrand[1,2]*, Alexis Chaigneau[2,3], Salvador Peraltilla[2], Jesus Ledesma[2], Michelle Graco[2], Florian Monetti[2,4], Francisco P. Chavez[5]

1 Institut de Recherche pour le Développement (IRD), UMR212 EME IFEREMER/IRD/UM2, Sète, France, **2** Instituto del Mar del Perú, Esquina Gamarra y Gral, Valle s/n, Callao, Lima, Peru, **3** IRD, UMR LEGOS, Toulouse, France, **4** IRD, IPSL/LOCEAN, UPMC/CNRS/IRD/MNHN, Paris, France, **5** Monterey Bay Aquarium Research Institute, Moss Landing, California, United States of America

Abstract

Background: In the southeastern tropical Pacific anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) abundance have recently fluctuated on multidecadal scales and food and temperature have been proposed as the key parameters explaining these changes. However, ecological and paleoecological studies, and the fact that anchovies and sardines are favored differently in other regions, raise questions about the role of temperature. Here we investigate the role of oxygen in structuring fish populations in the Peruvian upwelling ecosystem that has evolved over anoxic conditions and is one of the world's most productive ecosystems in terms of forage fish. This study is particularly relevant given that the distribution of oxygen in the ocean is changing with uncertain consequences.

Methodology/Principal Findings: A comprehensive data set is used to show how oxygen concentration and oxycline depth affect the abundance and distribution of pelagic fish. We show that the effects of oxygen on anchovy and sardine are opposite. Anchovy flourishes under relatively low oxygen conditions while sardine avoid periods/areas with low oxygen concentration and restricted habitat. Oxygen consumption, trophic structure and habitat compression play a fundamental role in fish dynamics in this important ecosystem.

Conclusions/Significance: For the ocean off Peru we suggest that a key process, the need to breathe, has been neglected previously. Inclusion of this missing piece allows the development of a comprehensive conceptual model of pelagic fish populations and change in an ocean ecosystem impacted by low oxygen. Should current trends in oxygen in the ocean continue similar effects may be evident in other coastal upwelling ecosystems.

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* E-mail: Arnaud.Bertrand@ird.fr

Introduction

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Th[illegible]
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[illegible] P[illegible] P[illegible] H[illegible]
[illegible] (*Engraulis ringens*) [illegible]
[illegible] 1960s [illegible]
1970s, [illegible] (*Sardinops sagax*) [illegible]
[illegible] 1990s

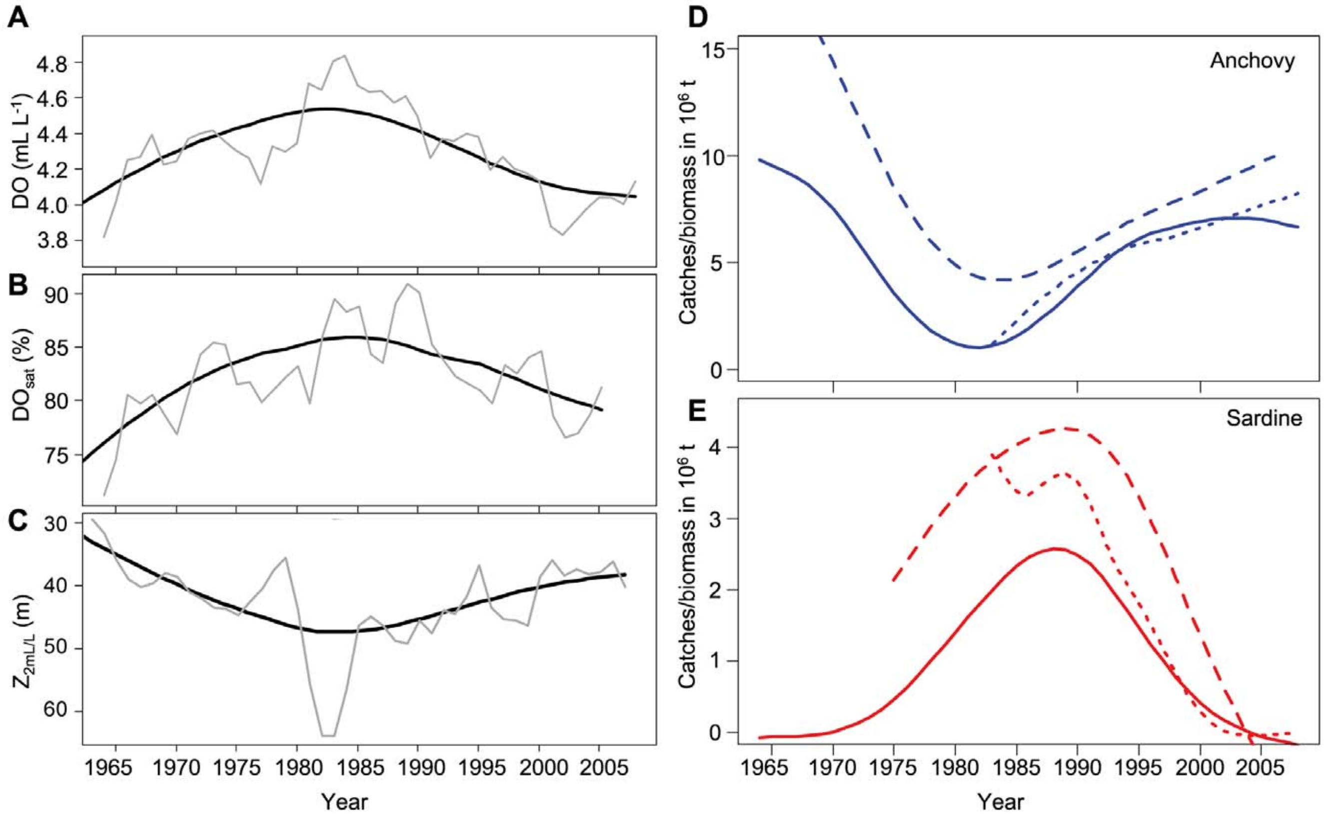

Figure 1. Time series (1964–2009) of oxygen and fish. Temporal variations of DO in mL L^{-1} (black dotted line) (**A**), DO_{sat} in % (black dashed line) (**B**), $Z_{2\ mL/L}$, in m (black solid line). Black solid line show the smoothed time series; gray solid line show the 4-years moving average. **C**. anchovy catches (blue solid line), biomass by VPA (blue dashed line) and acoustic biomass (blue dotted line). **D**. Temporal variations of sardine catches (red solid line), biomass by VPA (red dashed line) and acoustic biomass (red dotted line).

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80% and 40 m, ... in Fig 3B. ... (DO >4.4 mL L^{-1}, DO_{sat} >80%, $Z_{2\ mL/L}$ >40 m) ... 55 ... 1960s ... 1980s. After 1980s ... 1990s ... 1970s ... 2000s ... 1960s ... [illegible]

... During the 1960s ... 1970s and the 1990s–2000s, DO and DO_{sat} ... $Z_{2\ mL/L}$ ... The ... 1970s and 1980s ... DO, DO_{sat} and $Z_{2\ mL/L}$ ... ~4 mL L^{-1}, ~70–80% and ~25–35 m ... [30] ... [illegible]

Local scale

... (GAM) ... DO, DO_{sat} and $Z_{2\ mL/L}$ ... ($p = 0.000$) ... (Fig 4). ... DO, DO_{sat} and $Z_{2\ mL/L}$ ... ~4.5 mL L^{-1}, ~85% and ~40 m ... DO, DO_{sat} and $Z_{2\ mL/L}$, ... ~3.8 mL L^{-1}, ~60–70% and ~25 m ... [illegible]

Discussion

... [illegible]

Larger fish need more oxygen

... Oxygen ... [30]. ... *Engraulis capensis* [39]. ... [35,40] ... <10 ... [illegible]

Oxygen consumption, trophic structure and habitat compression

... [30]. ... [illegible]

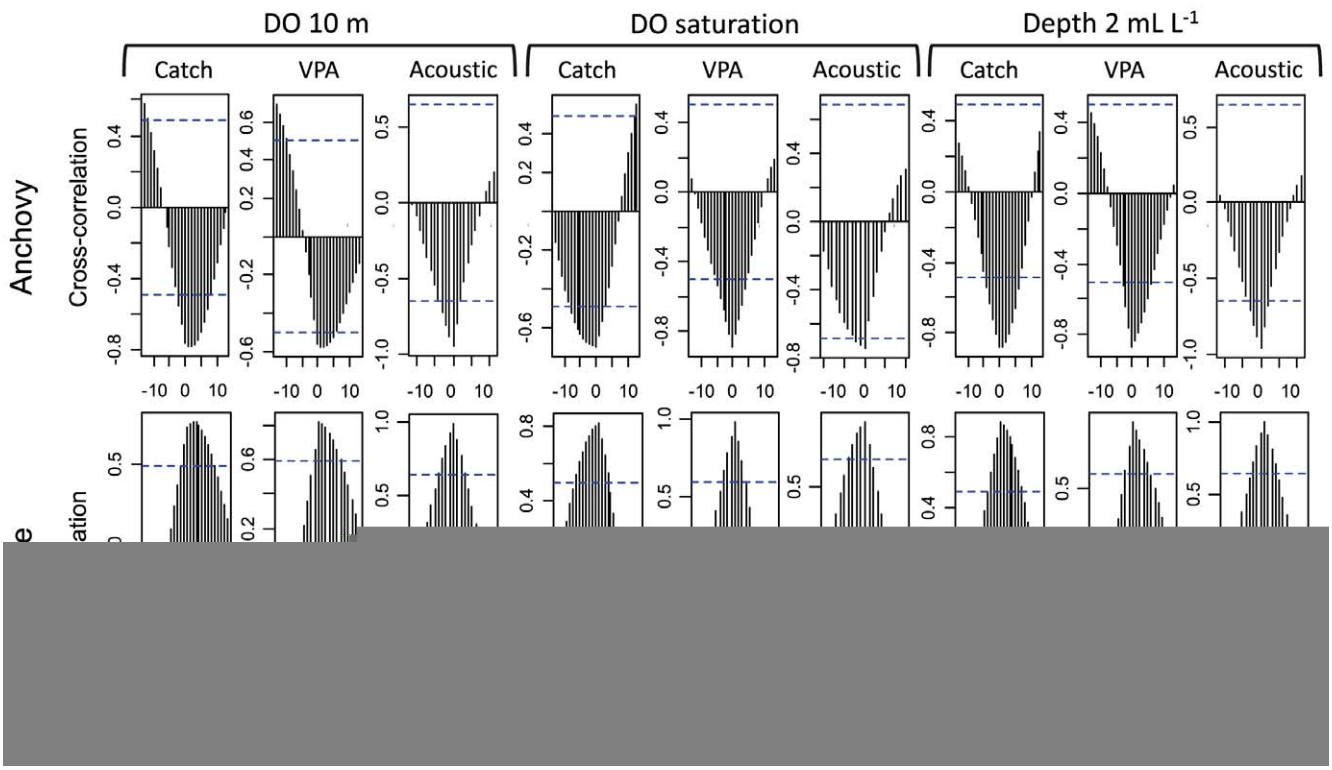

Figure 2. Time-lagged cross correlations of oxygen and fish. Time-lagged cross-correlations in year between smoothed times series of anchovy and sardine catches and biomass by VPA and acoustic biomass and DO, DO_{sat} and $Z_{2\ mL/L}$. Values above (below, respectively) the top (bottom) dotted lines are significant at p = 0.001.
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[illegible] [19]. [illegible]
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[illegible] [9] [illegible]
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[39] [illegible]

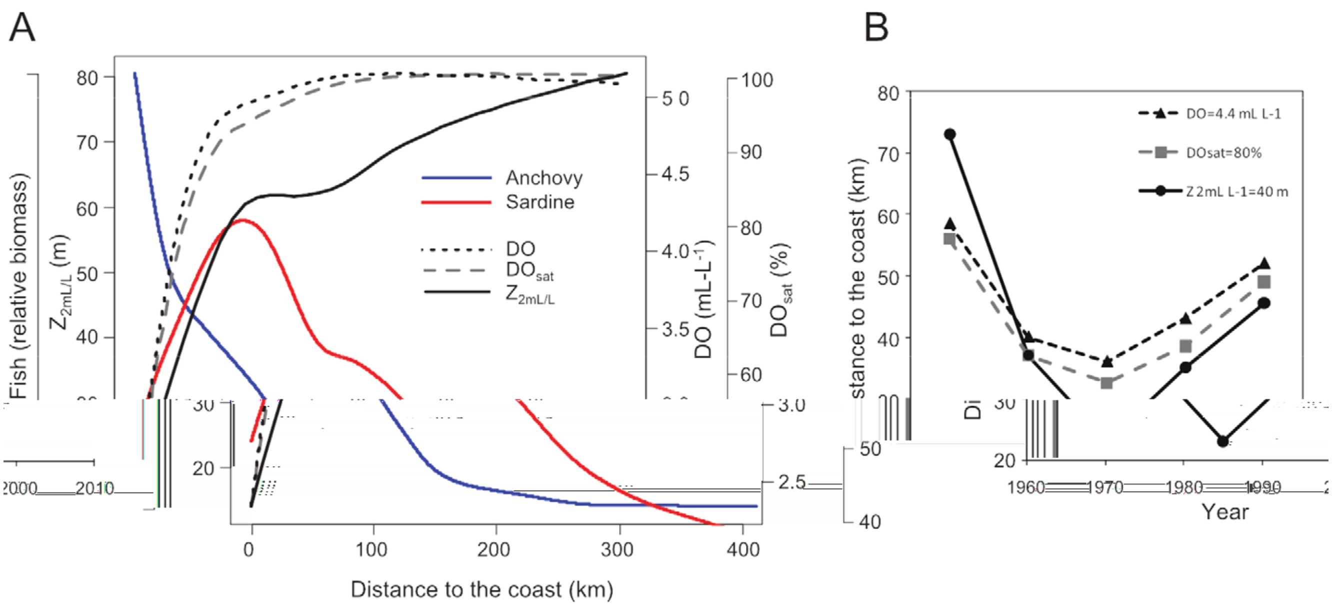

Figure 3. Cross-shore profiles of oxygen and fish biomass. A. Mean cross-shore profiles of DO in mL L^{-1} (black dotted line), DO_{sat} in % (grey dashed line), $Z_{2mL/L}$ in m (black solid line), and the acoustic-estimated biomass of anchovy (blue solid line) and sardine (red solid line). **B**. Decadal evolution, from the 1960s to the 2000s, of the distance from the coast of the DO, DO_{sat} and $Z_{2mL/L}$ isovalues equal to 4.4 mL L^{-1}, 80% and 40 m, respectively.
doi:10.1371/journal.pone.0029558.g003

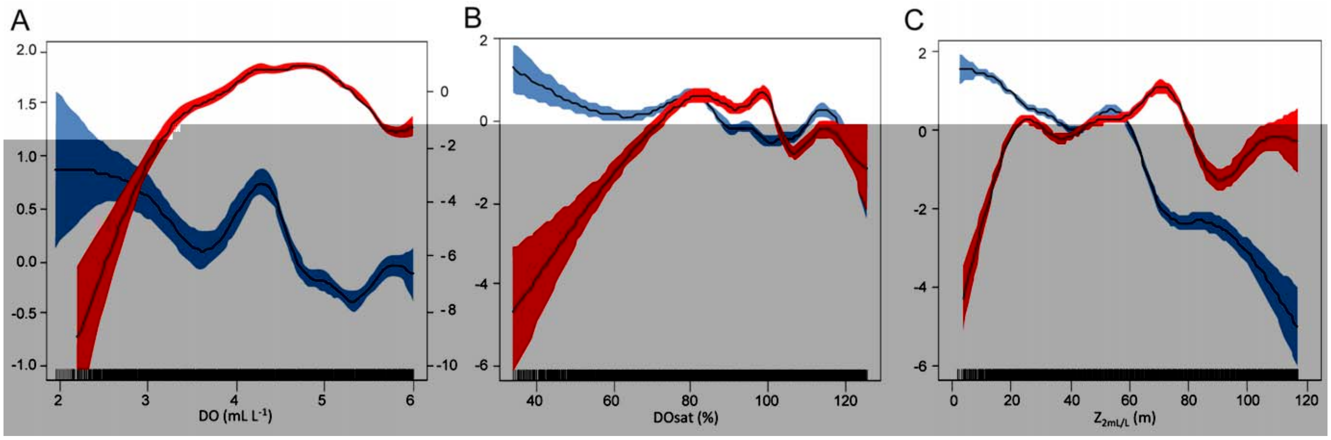

Figure 4. GAM models results. Cubic spline smoother fits (black solid lines) of GAMs (colored areas show 95% confidence limits) of anchovy (blue areas) and sardine (red areas) acoustic local biomass according to **A**. DO in mL L^{-1}, **B**. DO_{sat} in % and **C**. $Z_{2\ mL/L}$ in m. The y-axes are relative and correspond to the spline smoother that was fitted to the data such that a y-value of zero is the mean effect of the variables on the response. Right y-axis corresponds to sardine in **A**.

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Toward a 3D heuristic habitat-based hypothesis

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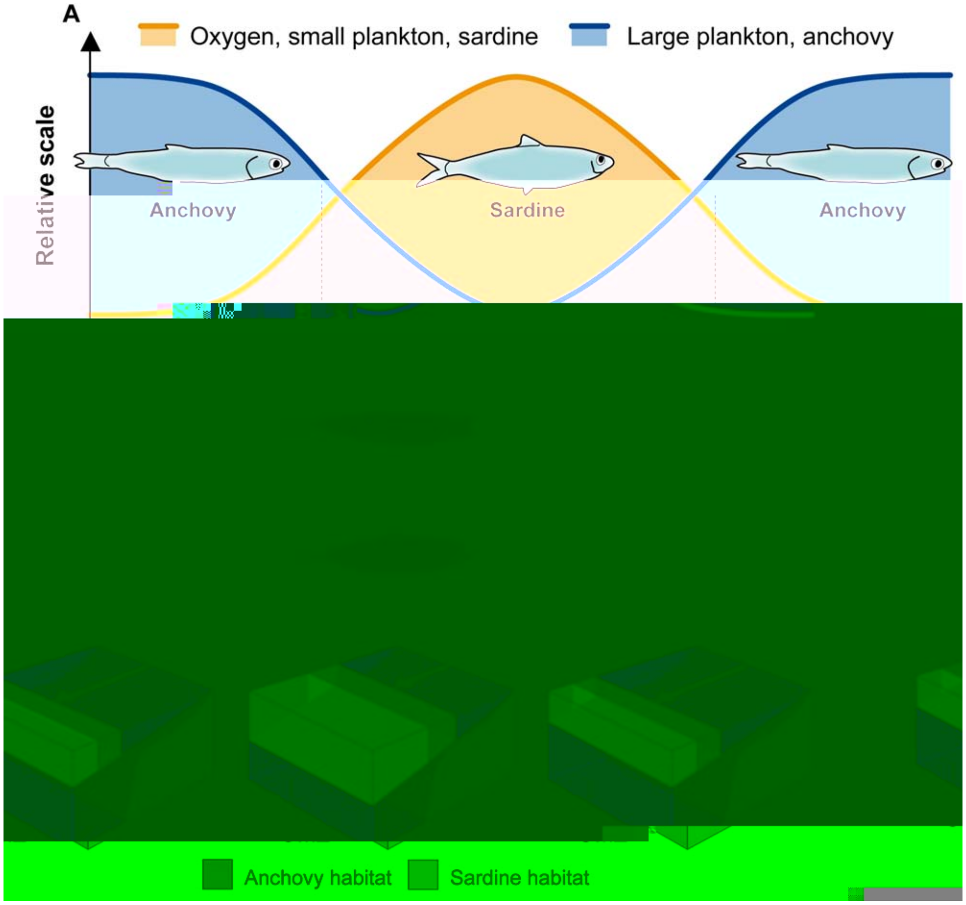

Figure 5. Conceptual model of decadal changes in anchovy and sardine populations in the southeastern tropical Pacific. A. Schematic of the temporal evolution of large plankton and anchovy (blue solid line), and oxygen, small plankton and sardine (red solid line) between 1960 and 2010. **B**. Energetic costs of feeding on dominant plankton size-spectra for anchovy and sardine according to the scenarios from **A**. **C**. Schematic of the available habitat for anchovy (blue shaded area) and sardine (red shaded area).
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Materials and Methods

[illegible]

Environmental data

[illegible]

[illegible] DO [illegible] 1.52 [illegible] L^{-1} (e.g. [32,33]). As [illegible] DO [illegible] 2 [illegible] L^{-1} [illegible] [illegible] [illegible] P [illegible] Z$_{2\ mL/L}$ [illegible] Z$_{0.8\ mL/L}$ [illegible] ($p = 0.000$, $R^2 = 0.91$).

In [illegible] [illegible] 200 [illegible] F [illegible] ~11 000 [illegible] [illegible] 1961 [illegible] 2008. Th[illegible] [illegible] [illegible] [illegible] 4 [illegible] 5 (Fig 1A–C) [illegible] GCV. F[illegible] [illegible] Fig 1 A–C.

C[illegible] 400 km [illegible] 1960s to 2000s. Th[illegible] [illegible] (e.g. Fig 3A). We [illegible] [illegible] 1.4 [illegible] L^{-1}, 80% [illegible] 40 [illegible] [illegible] (Fig 3B).

F[illegible] DO [illegible] Z$_{2\ mL/L}$ [illegible] [illegible] The [illegible] to [illegible] DO [illegible].

Fish data

A[illegible] (1964–2008) [illegible] (VPA) [illegible] (1964–2006) [illegible] IMARPE. A[illegible] 1983 to 2008 by IMARPE [illegible] 49 [illegible] [22]. Th[illegible] ~100 [illegible] ~15 [illegible] Si[illegible] (K[illegible] M[illegible] AS, N[illegible] [illegible] 74. [illegible] 9

4. Gu [illegible] D, En [illegible] E, Pu [illegible] S, Q [illegible] L, M [illegible] R, et al. (2008) O [illegible] P [illegible] O [illegible] 79: 177–189.
5. D [illegible] RJ, R [illegible] R (2008) [illegible] S [illegible] 321: 926–929.
6. S [illegible] L, J [illegible] GC, S [illegible] J, M [illegible] V (2008) E [illegible] S [illegible] 320: 655–658.
7. R [illegible] R, S [illegible] BA (2008) [illegible] P [illegible] N [illegible] A [illegible] S [illegible] USA 105: 20776–20780.
8. Gu [illegible] D, S [illegible] A, F [illegible] DB, O [illegible] L, V [illegible] G, et al. (2009) R [illegible] L [illegible] IcA [illegible] B [illegible] 6: 835–848.
9. C [illegible] F, B [illegible] A, G [illegible] R, S [illegible] P, C [illegible] J (2008) Th [illegible] P [illegible] O [illegible] 79: 95–105.
10. L [illegible] D, S [illegible] RA, S [illegible] R, P [illegible] R, K [illegible] T, et al. (1992) S [illegible] F [illegible] O [illegible] 1: 339–347.
11. C [illegible] J, G [illegible] R, Ca [illegible] G, N [illegible] M, C [illegible] A (1996) S [illegible] *Engraulis ringens* [illegible] *Sardinops sagax* [illegible] 1994 [illegible] C [illegible] N [illegible] B [illegible] M [illegible] P [illegible] 15: 1–23.
12. S [illegible] RA, A [illegible] J, B [illegible] A, B [illegible] TR, C [illegible] R, et al. (1999) W [illegible] S Af J M [illegible] S [illegible] 21: 289–347.
13. C [illegible] FP, R [illegible] J, L [illegible] SE, N [illegible] M (2003) F [illegible] P [illegible] O [illegible] S [illegible] 299: 217–221.
14. A [illegible] J, N [illegible] M (2004) R [illegible] H [illegible] C [illegible] P [illegible] O [illegible] 60: 201–222.
15. [illegible] CD, H [illegible] L, F [illegible] G (2006) C [illegible] *Engraulis encrasicolus* [illegible] *Sardinops sagax* [illegible] B [illegible] Af J M [illegible] S [illegible] 28: 465–477.
16. B [illegible] A, W [illegible] S (2008) T [illegible] P [illegible] W [illegible] P [illegible] O [illegible] 79: 290–299.
17. R [illegible] RR, C [illegible] DM, Jr (2008) I [illegible] Pro Nat Acad Sci USA 105: 19651–1970.
18. J [illegible] AG, P [illegible] T (1989) Th [illegible] *Engraulis capensis* [illegible] G [illegible] J E [illegible] M [illegible] B [illegible] E [illegible] 131: 81–100.
19. E [illegible] P, B [illegible] A (2008) R [illegible] P [illegible] (*Engraulis ringens* [illegible] H [illegible] C [illegible] P [illegible] O [illegible] 79: 215–227.
20. M [illegible] GA, S [illegible] PE, B [illegible] TR, H [illegible] JR (2002) C [illegible] A [illegible] F [illegible] S [illegible] 32: 195–214.
21. B [illegible] A, S [illegible] M, Gu [illegible] M, V [illegible] L (2004) F [illegible] P [illegible] F [illegible] F [illegible] 15: 296–316.
22. G [illegible] M, S [illegible] G, B [illegible] A, B [illegible] S (2007) A [illegible] *Engraulis ringens* [illegible] *Sardinops sagax* [illegible] H [illegible] C [illegible] 1983–2003. F [illegible] O [illegible] 16: 155–168.
23. S [illegible] G, B [illegible] A, Gu [illegible] M, B [illegible] S, V [illegible] L (2008) Th [illegible] H [illegible] C [illegible] 1983 to 2005. P [illegible] O [illegible] 79: 228–237.
24. S [illegible] R, C [illegible] P, R [illegible] C (1998) Th [illegible] C [illegible] S [illegible] (*Sardinops sagax* [illegible] In D [illegible] MH, C [illegible] P, M [illegible] R, R [illegible] C, B [illegible] A, P [illegible] D, [illegible] ORSTOM, P [illegible] 267–274.
25. F [illegible] BP, A [illegible] J, E [illegible] K-C, F [illegible] DB, Gu [illegible] D, et al. (2010) P [illegible] A [illegible] J M [illegible] S [illegible] 79: 316–326.
26. E [illegible] P, B [illegible] A, [illegible] CD, G [illegible] S, DeM [illegible] BJ (2009) D [illegible] *Sardinops sagax* [illegible] H [illegible] C [illegible] P [illegible] O [illegible] 83: 242–250.
27. FAO (2009) Th [illegible] 2008. FAO F [illegible] A [illegible] D [illegible] R [illegible]
28. V [illegible] J, O [illegible] L, M [illegible] L, G [illegible] D, V [illegible] G, et al. (2008) 250 [illegible] M [illegible] B [illegible] C [illegible] P [illegible] O [illegible] 79: 198–207.
29. F [illegible] DB, B [illegible] TR, F [illegible] V, Gu [illegible] D, L [illegible] H, et al. (2009) C [illegible] 4. V [illegible] In C [illegible] DMJ, R [illegible] C, A [illegible] J, O [illegible] Y, [illegible] C [illegible] C [illegible] S [illegible] P [illegible] F [illegible] C [illegible] U [illegible] 45–63.
30. P [illegible] D (2010) G [illegible] (E [illegible] B [illegible] 22. I [illegible] E [illegible] O [illegible] L [illegible]
31. P [illegible] HO, K [illegible] R (2007) C [illegible] S [illegible] 315: 95–97.
32. E [illegible] W, A [illegible] H, Po [illegible] H-O, G [illegible] D (2010) I [illegible] B [illegible] 7: 1669–1699.
33. V [illegible] R, D [illegible] CM (2008) T [illegible] P [illegible] N [illegible] A [illegible] S [illegible] USA 105: 15452–15457.
34. P [illegible] ED, L [illegible] J, G [illegible] CP, H [illegible] P, S [illegible] D, et al. (2010) O [illegible] A [illegible] F [illegible] O [illegible] 19: 448–462.
35. B [illegible] A, B [illegible] M, C [illegible] A (2010) A [illegible] O [illegible] L [illegible] O [illegible] R [illegible] U [illegible] L [illegible] O [illegible] M [illegible] Z [illegible] PLoS ONE 5(4): e10330.
36. S [illegible] BA (2011) C [illegible] J E [illegible] M [illegible] B [illegible] 214: 326–336.
37. P [illegible] A, R [illegible] P [illegible] D, G [illegible] V (2008) Th [illegible] O [illegible] M [illegible] Z [illegible] (OMZ) [illegible] C [illegible] CO2 [illegible] N2O. C [illegible] S [illegible] R [illegible] 28: 2746–2756.
38. F [illegible] R, S [illegible] W, G [illegible] V [illegible] J, B [illegible] L, L [illegible] L (2009) V [illegible] S [illegible] P [illegible] O [illegible] D [illegible] S [illegible] R [illegible] II 56: 1027–1038.
39. [illegible] CD (1995) R [illegible] S [illegible] M [illegible] E [illegible] P [illegible] S [illegible] 129: 41–54.
40. B [illegible] A, G [illegible] F, B [illegible] S, Gu [illegible] M, A [illegible] L, et al. (2008) S [illegible] A [illegible] P [illegible] O [illegible] 79: 264–277.
41. A [illegible] P, S [illegible] G, E [illegible] P, B [illegible] A (2011) L [illegible] P [illegible] H [illegible] C [illegible] S [illegible] C [illegible] M [illegible] E [illegible] P [illegible] S [illegible] 422: 211–222.
42. B [illegible] M, B [illegible] A, L [illegible] D [illegible] A, Gu [illegible] M, A [illegible] P, et al. (2011) I [illegible] P [illegible] A [illegible] P [illegible] O [illegible] 91: 360–381.
43. C [illegible] FP, M [illegible] M, P [illegible] JT (2011) M [illegible] A [illegible] R [illegible] M [illegible] S [illegible] 3: 227–260.
44. E [illegible] W, V [illegible] HM (2005) I [illegible] B [illegible] A [illegible] Af J M [illegible] S [illegible] 27: 629–639.
45. B [illegible] T, L [illegible] C, F [illegible] P (2011) I [illegible] H [illegible] F [illegible] F [illegible] 12: 94–109.
46. C [illegible] F, B [illegible] JA, L [illegible] J, K [illegible] A, W [illegible] H, et al. (2008) E [illegible] C [illegible] C [illegible] S [illegible] 319: 920.
47. F [illegible] P, B [illegible] M, A [illegible] J (2009) E [illegible] B [illegible] U [illegible] E [illegible] P [illegible] O [illegible] 83: 1–14.
48. G [illegible] HE, L [illegible] RA, B [illegible] TP, A [illegible] JI, B [illegible] OK, et al. (2010) W [illegible] O [illegible] A [illegible] 2009, V [illegible] 3: D [illegible] O [illegible] A [illegible] O [illegible] U [illegible] O [illegible] S [illegible] (NOAA A [illegible] NESDIS 70, U.S. G [illegible] P [illegible] O [illegible] W [illegible] D.C.).
49. R [illegible] RF, R [illegible] CF (1968) A [illegible] D [illegible] S [illegible] R [illegible] 9: 185–193.
50. D [illegible] PK, S [illegible] K (2005) S [illegible] T [illegible] S [illegible] C [illegible] 15: 267–280.