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Interannual Variability in Indian Ocean Surface Waters and Tuna-Environment Relationships: Filling the Gaps with a Coupled Bio-Physical Ocean Model

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Dissertation presented for the degree of Master of Science
in the Department of Zoology,
University of Cape Town

February 2011

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Développement - IRD) and Dr Colin Attwood (Zoology Department,
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Live as if you were to die tomorrow.

Learn as if you were to live forever.

-- Mahatma Gandhi

University of Cape Town

Acknowledgements

One of the proudest achievements with this thesis has been that I completed it from start to finish using only open source software. Therefore my gratitude extends to all the open source programmers and developers who have made incredibly useful tools easily and freely available to those of us who are less computer literate. In addition, I relied on continual help from several people when I set on my open-source adventure: Thank you to the students and researchers at CRH (Centre de Recherche Halieutique Méditerranéenne et Tropicale) in Sète, especially Julien Trolet and Norbert Billet, whom remained extremely patient throughout countless queries of linux, R or PostgreSQL. David Kaplan equally fast-tracked me through many frustrating hours of R, emacs and linux problems, as well as providing invaluable guidance into scripts and analyses for chapter two, besides good company and friendship.

Thank you to Emmanuel (Manu) Chassot, Julien Barde, Sylvain Bonhommeau and Nathalie Bodin for their awesome company and friendship and sharing with me their 'house of love' and many good times in 2009. The former two, together with other good friends such as Timothée Brochier deserve much of the credit for keeping my spirits afloat throughout some tough nine months in non-English-speaking Sète, in 2008.

Much appreciation must go to my supervisor, Olivier Maury, who provided support and opened the door to fantastic opportunities and experiences by having faith in me and making my travels to France possible. The ideas driving the investigations in this thesis were largely his and he showed great patience with my independent and at-times stubborn (and as he describes 'perfectionist') nature, besides accepting personal decisions of mine, even when they were detrimental to my thesis work. Much gratitude must also be extended to co-advisors or researchers who took an interest and provided valuable ideas or guidance, namely Matthieu Lengaigne, Ragu Murtugudde, Jérôme Vialard, Alain Fonteneau, Francis Marsac and Frederic Ménard.

Although the overseas experience was incredibly enriching, returning 'home' to Cape Town, UCT and the Zoology department was hugely appreciated. Thank you to the many friends, fellow students, researchers and UCT staff who I have interacted with

and shared laughs with throughout my UCT career. Andrea Plos provided selfless assistance with computer and technical issues that I encountered, as she has always done throughout my UCT career. A special thanks must go to Gilly Smith, who offered to take care of the printing and binding of the finished product (in my absence), typical of her generous, kind and friendly attitude that she serves the Zoology department, and especially the marine community, with.

Thank you also to my UCT supervisor, Colin Attwood, who at first hesitantly agreed to be my vital UCT link (as the subject matter is quite far from his area of interest), but who unerringly provided the support and input when I requested it, especially towards the end.

Funding for my upkeep and research came from a number of sources, to which I am very grateful: The Sam Cohen Scholarship trust provided financial support throughout my earlier university career and did so again for this MSc. Through the UCT Postgraduate Funding Office, I was kindly awarded additional funding from the Harry Crossley Foundation, Janet Goldblat Bursary, and the KW Johnston Bequest. The costly and valuable experience of traveling to and living in France for several months, as well as additional funding to support my extended student life in Cape Town afterwards, was sourced by Olivier Maury from IRD.

Lastly, many thanks to the fantastic people that I've surrounded myself with, most of which I won't mention here. My close friends and family, who have provided endless love and support (much of it over skype!), without which, I would have never managed to finish this challenge. Thank you to Oli for the many good conversations (and fishing stories) over skype, which at times kept me going overseas. Thanks also to Philip and Tessa, for inspiring and sharing the passion for marine life, as well as feeding me during the last few weeks before hand-in. Lastly, thank you to my Mom, who has fuelled the interest and provided the inspiration throughout my marine science career and who has provided unfailing love, support and enthusiasm for all endeavours I have embarked on.

List of Acronyms and Abbreviations Used

APECOSM	Apex Predators ECOSystem Model
CHL	depth-integrated chlorophyll concentration
CPUE	Catch Per Unit of Effort
EEIO	Eastern Equatorial Indian Ocean
ENSO	El Niño-Southern Oscillation
EOF	Empirical Orthogonal Function
FAD	Fish Aggregating Device
FREE	Free-swimming tuna (not associated with a FAD)
GAM	Generalised Additive Model
GLS	Generalised Least Squares
ICCAT	International Commission for the Conservation of Atlantic Tunas
IO	Indian Ocean
IOTC	Indian Ocean Tuna Commission
IOZM	Indian Ocean Zonal Mode
IPCC	Intergovernmental Panel on Climate Change
MSY	Maximum Sustainable Yield
negIOZM	negative IOZM event
NEMO	Nucleus for European Modelling of the Ocean
PISCES	Pelagic Interaction Scheme for Carbon and Ecosystem Studies
posIOZm	positive IOZM event
RFMO	Regional Fishery Management Organisation
SeaWiFS	Sea-viewing Wide Field-of-view Sensor
SEIO	Southeast Indian Ocean
SRES	Special Report on Emission Scenarios
SST	Sea Surface Temperature
STIO	Southern Tropical Indian Ocean
SVD	Singular Value Decomposition
SWIO	Southwest Indian Ocean
Z20	depth of the 20°C isotherm

Dissertation Abstract

Study of the Indian Ocean has lagged behind that of the Atlantic and Pacific, with large knowledge gaps remaining in our understanding of regional or basin-scale controls on productivity and higher trophic levels. A lack of in situ data, especially for mid and upper trophic-level organisms, has commonly limited to small spatio-temporal scales, investigations into environmental control of biological systems. These data gaps are increasingly being filled by coupled bio-physical ocean models. Throughout this thesis, outputs from such a coupled ocean model (NEMO-PISCES) were employed to provide hindcast (1961-2001) records of three-dimensional environmental fields in the Indian Ocean.

In the first of two research chapters, the Indian Ocean basin-wide patterns caused by dominant interannual climatic modes, the El Nino Southern Oscillation (ENSO) and the Indian Ocean Zonal or Dipole Mode (IOZM), were investigated for sea surface temperature (SST), depth of the 20°C isotherm (Z20; as a proxy of thermocline depth) and depth-integrated chlorophyll (CHL). As was shown before, the dominant interannual mode of variability in SST was an ENSO-related basin-wide signal, while Z20 and CHL revealed a similar dipolar zonal pattern across equatorial regions. The thermocline depth (as estimated by Z20) strongly regulates chlorophyll concentrations across most of the Indian Ocean, by limiting the amount of nutrients reaching sun-bathed surface waters and thereby causing almost mirror-image anomalies of these two variables.

Composite averages were employed to describe the distinct anomaly patterns among different combinations of positive and negative ENSO and IOZM events, as well as those that occur on their own ('pure' ENSO and 'pure' IOZM events). Results presented here are perhaps most interesting and novel in their description of large-scale phytoplankton responses to interannual climatic extremes. In some regions, such as the southern tropical Indian Ocean, the integrated chlorophyll fields reveal Rossby Wave-induced interannual anomalies that are seemingly not well detected by SeaWiFS sensors. The diagnostic anomalies shown in composite averages, have important implications for predicting physical or ecosystem responses to ENSO/IOZM events and should be considered during any investigations of Indian Ocean variability.

In the second research chapter, historical (1981-2001) purse-seine catches of skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*), from French and Spanish fleets operating in the Indian Ocean, were compared to gridded environmental variables using Generalised Additive Models (GAMs). A delta approach was employed as the data had a large proportion of zero catches: Presence-absence models were evaluated, whereafter catch-per-unit-effort (CPUE) was modelled on condition that catches were positive (present). Important differences were revealed between relationships obtained from catches associated with fish aggregating devices (FADs) and those of free-swimming schools. FADs apparently act to reduce catchability effects, allowing relationships that are interpreted in terms of tuna abundances or habitat, to come to the fore. This allowed interesting interpretations of tuna ecology, including that deeper thermocline depths translate to greater skipjack and yellowfin tuna abundances, and that tuna densities seem to react to a proxy of prey concentrations, by a Holling type II functional response, which has been assumed in modelling attempts, but not shown empirically before. The non-linear tuna-environment relationships described here, are valuable in their potential application to data and/or simulations, in order to map tuna habitats: Applied to quasi real-time data or simulated fields, they could provide habitat maps to inform the spatial adjustments of mobile no-take zones. In addition, if applied to forecast models, forced for example by predictions emanating from IPCC SRES scenarios, they could provide best estimates of how tuna habitat might respond to global climate change during the coming century.

In the concluding chapter, the interpretations from research chapters are summarised and put into context of their value to aiding fisheries management and in predictions of ecosystem responses to climate variability. It is argued that understanding environmental controls on biological systems and resources is of critical importance for their sustainable management in a changing world.

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Chapter 1

General Introduction

Bottom-up Control and Climate Impacts on Ocean Ecosystems and Tuna

The importance of climatic effects on marine ecosystems is well established (e.g. Chavez et al., 1999; Parsons and Lear, 2001; Stenseth et al., 2002; Lehodey et al., 2006), although perhaps not always well understood. Interactions between the atmosphere and ocean impact heavily on the upper layers of the ocean, changing for example, heat content, current flows, mixing dynamics and stratification (e.g. Chavez et al., 1999; Murtugudde et al., 2000). While these processes impact many populations directly, perhaps more importantly, they commonly control the trophic base of the ecosystem, by affecting nutrient transfers from deeper fertile waters to photosynthetically-active surface layers, and also by governing the retention or loss of autotrophs from those sunlit layers (e.g. Polovina et al., 1995). Well-stratified tropical waters are commonly nutrient-starved and especially sensitive to climatic disturbances that affect mixed-layer depths and nutrient entrainment into surface layers (e.g. Murtugudde et al., 1999). In addition, these food-starved environments are likely to be strongly controlled by bottom-up forcing (White, 2008), forming a strong link between climatic perturbations and population dynamics (e.g. Lehodey et al., 2003, 2006). The difficulty in describing and understanding these linkages is due to a number of reasons, including a) our inability to accurately measure mid- or upper-trophic level populations or ecosystem indices in such wide-ranging environments; b) the complexity caused by different levels of biological organisation being impacted by climate in different ways (Lehodey et al., 2006); and c) the fact that the biotic responses are commonly non-linear (Ottersen et al., 2010).

In a variable and rapidly changing climate, understanding the impacts of climatic changes on species and ecosystems, and gaining predictability of them, is of central importance to the conservation of biodiversity and sustainable management of resources. However feedbacks between many different physical, chemical and biological parts of the entire ocean-atmosphere system, make this a challenging task. Attempts at a simplified, yet holistic view of this complexity, and assessment of interactions between different parts, have become increasingly possible in recent

decades through the use of coupled bio-physical numerical models. Great strides have been made in this domain, allowing the development of realistic models that are resolving increasingly accurate and higher-resolution simulations of physical, biogeochemical and ecosystem processes, including mid and upper trophic levels in recent years (e.g. Maury, 2010). Such models are able to provide hindcast records of environmental variables at spatio-temporal scales often not attainable in the observational records. Throughout this dissertation, outputs from such a coupled bio-physical ocean model (NEMO-PISCES; Aumont and Bopp, 2006) are employed to provide long-term, three-dimensional hindcasts of environmental measures in the Indian Ocean (IO). NEMO-PISCES consists of an ocean general circulation model based on OPA version 8.2 (Madec et al., 1998), coupled to the biogeochemistry/foodweb model 'Pelagic Interaction Scheme for Carbon and Ecosystem Studies' (PISCES; Aumont and Bopp, 2006; Aumont et al., 2008).

Tuna are apex predators that occupy large ranges in tropical and subtropical waters around the globe and are strongly impacted by climate variability (e.g. Lehodey et al., 1998, 2003; Marsac and Le Blanc, 1998). Their catches are characterised by high variability over space and time (e.g. Fonteneau et al., 2008), most probably resulting from a combination of climate-driven fluctuations in ecosystem productivity, as well as changes in distribution and catchability of the tuna populations (Miller, 2007). Being fast-swimming predators, whose high metabolic rates require consistent and large food intake (Stéquert and Marsac, 1989; Dickson, 1995), even though they live in relatively food-sparse environments, means that tuna are likely constantly on the search for prey. Therefore regional and temporal changes in food resources, as well as vital physiological parameters such as temperature and oxygen concentration, affect the behaviour and distribution of these highly mobile predators (Stéquert and Marsac, 1989; Sharp, 2001).

Although we know that climate perturbations and oceanographic features affect tuna behaviour and thereby their distribution and/or catchability (e.g. Lehodey et al., 1997; Bertrand et al., 2002), our understanding of the relationships between tuna and their environment remains fairly rudimentary. Moreover, the erratic nature of tuna catches (e.g. Fonteneau et al., 2008), together with the challenges posed by the fact that the ranges of these highly mobile predators commonly cover international waters as well as several countries' exclusive economic zones, has made effective management of

stocks extremely challenging (Miller, 2007). In order to coordinate the data collection and cooperation necessary among many stakeholders, regional fisheries management organisations (RFMOs) were created throughout the global oceans, in an attempt to overcome a 'tragedy of the commons' and take up the difficult task of sustainably managing high seas fisheries. Yet despite the formation of RFMOs, evidence suggests that the application of traditional fisheries management approaches to tuna stocks have been falling short (e.g. Safina, 1993; Polacheck, 2002; Fromentin and Ravier, 2005). As a result of this failure, alternative approaches need to be considered and the implementation of pelagic marine protected areas (MPAs) has been called for (e.g. Mills and Carlton, 1998; Sumaila et al., 2007; Game et al., 2009). Game et al. (2009) suggest that moving (as opposed to traditionally static) MPAs are likely more effective in the dynamic pelagic environment, where intraseasonal, seasonal and interannual changes in oceanography alter the spatio-temporal ecosystem structure. The authors point out that necessary tools to implement and manage such closed areas have recently become a reality. The management of a mobile protected area in the pelagic environment is already in practice off the East coast of Australia, effectively decreasing the bycatch of southern bluefin tuna in the local longline fishery (Hobday and Hartmann, 2006).

Conservation of sustainable stocks could therefore potentially be achieved by protecting a proportion of suitable habitat in a network of protected areas, and/or in certain cases, smaller isolated time-space closures that protect specific regions or oceanographic features where the stock becomes especially sensitive to overexploitation (localised spawning aggregations for example; Game et al., 2009). However to most effectively apply such spatial protection, there is an urgency to improve our understanding of the environmental relationships which affect the distributions or catchability of target species. Disentangling the relationships between the target species and environmental parameters, is vital for designing MPAs in the variable pelagic realm. Furthermore, application of such relationships to quasi real-time environmental data, or forecast simulations, could allow rapid responses in the positioning (or shape) of closed areas, allowing effective real-time management of a mobile no-take zone, that constantly protects a proportion of favourable habitat in the dynamic open ocean.

Indian Ocean Tuna Fisheries

Tropical tuna species are targeted by a collection of commercial and artisanal fisheries throughout their ranges. The largest proportion of commercial catches are made up of those from long-lining and purse-seine fleets, while relatively smaller contributions are made from gill-net, pole-and-line (baitboat) and other minor fishing operations (Anon, 2009). While global longline activity expanded rapidly from the fifties onwards, tuna targeting purse-seine fleets were slower to develop and expand, becoming established in the eastern Pacific and Atlantic Oceans in the sixties, while notable catches in the Indian Ocean were only recorded from the early eighties onwards. Longliners target mostly mature fish and deeper-swimming species such as albacore, bigeye, bluefin and mature yellowfin tuna (as well as swordfish), while purse-seiners are limited to surface catches (down to about 250-300 m), as is reflected by their larger proportion of young/smaller individuals (of yellowfin and bigeye tuna) and skipjack catches (Fonteneau, 1997). Significant catches of adult yellowfin are made by purse-seiners in certain regions however, a large proportion of which are likely surface aggregations of spawning adults, as spawning activity makes them far more vulnerable to surface fishing gears (Itano, 2000). A development which greatly increased the efficiency of purse-seiners was the rapid adoption and wide-spread use of artificial fish aggregating devices (FAD) during the eighties (Fonteneau et al., 2000; Moreno et al., 2007). These raft-like structures act to concentrate parts of the ecosystem, including skipjack and mostly immature individuals of some larger tuna species, greatly reducing the time spent by vessels searching for surface schools and increasing the success rate of seine sets (Bromhead et al., 2000). The intensity and wide-spread implementation of FADs has likely contributed towards recruitment overfishing, over-exploitation (Bromhead et al., 2000), as well as raising concerns over the potential detrimental effects of altered fish behaviour on the ecosystem (e.g. Marsac et al., 2000; Hallier and Gaertner, 2008).

Exploitation of Indian Ocean tuna stocks by commercial fleets lagged behind that of the other oceans (Stéquert and Marsac, 1989), likely due to their remoteness from traditionally tuna-fishing countries and major tuna markets. As a result, the tropical tuna stocks are generally considered to be less-exploited and in a more robust state than their counterparts in other oceans (A. Fonteneau, personal comment). The dominant tropical tunas in the Indian Ocean, namely bigeye, yellowfin and skipjack tuna, have all shown a levelling-off trend of total IO catches in the recent decade,

although with considerable variability between years (Anon, 2009). Total catches and catch rates peaked in 2004-2005 for yellowfin; in the early 2000s for skipjack; and in the late nineties for bigeye tuna (Anon, 2009). Tag and recapture results have supported the notion of a single stock throughout the Indian Ocean for all three species (Anon, 2009). While longlining fleets fish most of the Indian Ocean, down to about 40°S, purse-seine effort occurs mainly in warmer surface waters north of 20°S and is concentrated in the western regions of the IO, as the deep thermocline of the eastern basin allows tuna to escape the vertical reach of the nets, effecting relatively poor surface catches in this area (A. Fonteneau, personal comment). Oceanographic variability plays a large role in tuna catchability, and likely regional distribution, so that climatic perturbations such as ENSO events, cause notable variability in the success and geographic distribution of catches (e.g. Lehodey et al., 1997; Marsac and Le Blanc, 1999). The main species making up purse-seine targets in the IO are skipjack and yellowfin tuna, although (mostly juvenile) bigeye are also caught on FAD-associated sets (Fonteneau, 1997). Bigeye, yellowfin, albacore and southern bluefin tuna, together with swordfish, make up the majority of IO longline catches.

Indian Ocean Oceanography

Knowledge of Indian Ocean variability and its interaction with atmospheric dynamics has historically lagged behind those of the other major oceans. However in recent decades, the IO has increasingly been recognised as playing a strong role in far-reaching tropical atmosphere-ocean interactions and concerted research effort has greatly progressed such knowledge (Schott et al., 2009). As a coupled system, it is unique in many ways, largely due to the Asian landmass-affected seasonally-reversing monsoon circulation, which dominates atmospheric surface flows northwards of about 10°S (Schott and McCreary, 2001). Northeast surface winds blow during the boreal winter, while southwest winds (or mostly southeast winds in the southern hemisphere) blow during the summer months, changing over the spring and fall Intermonsoon seasons. The lack of sustained easterlies along the equator means there is no consistent climatological upwelling in eastern equatorial areas and the thermocline slants downwards from west to east, unlike other tropical oceans.

The changing winds translate to seasonally-varying surface ocean circulations, fuel regions of seasonal upwelling, change Ekman convergence and divergence patterns and control thermocline depths, thereby impacting heavily on productivity and

ecosystems at a variety of scales. Cool, productive waters upwell in the western Arabian Sea and either side of the southern tip of India during the southwest monsoon (Schott et al., 2009). A permanent doming of the thermocline in the southwest Indian Ocean between 5° and 10°S (Seychelles-Chagos thermocline ridge; Hermes and Reason, 2008), identifies another region of open-ocean upwelling and enhanced productivity, which is influenced by wind-driven Ekman pumping, wind-stress curl caused by the interaction of southern hemisphere trade winds and the equatorial westerlies, and remotely triggered Rossby waves (Jury and Huang, 2004; Hermes and Reason, 2008; Schott et al., 2009). The equatorial westerly winds that peak during either Intermonsoon, also fuel the semi-annual Wyrтки Jets (Wyrтки, 1973), which transport warm western surface waters into the eastern Indian ocean, deepening the thermocline and thereby dampening the effect of upwelling-favourable winds in this region. Besides impacting equatorial thermocline depths, productivity and ecosystems, these jets also impact off-equatorial regions by north and southward propagating coastal Kelvin Waves, as well as westward-propagating off-equatorial Rossby Waves, after colliding with the Sumatran landmass (Schott et al., 2009).

South of about 10°S, southeast trade winds govern surface circulation and fuel a south Indian gyre, similar to those of other ocean basins. The southern Indian Ocean flow is dominated by the westward South Equatorial Current, which is partly fed by waters from the Indonesian Throughflow and splits north- and south-wards when it hits Madagascar (Schott et al., 2009). A return flow is found south of this in the form of a diffuse northeastward surface flow, but also in the form of a narrow South Indian Countercurrent between 22° and 26°S (Siedler et al., 2006). Flows around the equator are mostly eastwards, with the main zonal flow shifting from south of the equator in boreal winter to north of the equator in summer, either side (in space and time) of the the strong equatorial Wyrтки Jet of the Intermonsoon seasons. Counter-clockwise circulation patterns are evident in the Bay of Bengal and Arabian Sea during northeast monsoons, while those of the southwest monsoon are largely clockwise.

Environmental Controls in the Indian Ocean: Goals of the Dissertation

Via its role in tropical atmosphere-ocean interactions, the Indian Ocean affects local, regional and remote weather patterns (e.g. Saji et al., 1999; Saji and Yamagata, 2003; Meyers et al., 2007). At the same time, these interactions modify the structure of surface waters and thereby must transfer a signal through to productivity and

ecosystems. This dissertation consists of two chapters that address separate disciplines, but which are inextricably linked, firstly by the same geographic region of the Indian Ocean, and secondly by the strong interaction between climate, ocean and biosphere, and the environmental control of biology by bottom-up impacts. The first of two research chapters will address and compare the basin-scale signature of the two dominant climatic modes in the IO, namely ENSO and the Indian Ocean Dipole or Zonal Mode, on surface ocean variables and with an emphasis on phytoplankton productivity. The second research chapter then shifts to top predators, in the form of tuna, using historical purse-seine fishery catches and attempting to best describe the environmental relationships that have impacted on these.

Although different tools are used to address different questions in the Indian Ocean system, both investigations similarly endeavour to build upon our knowledge of how a specific variable, or resource, will react to perturbations of its surrounding environment (environment in the broad sense of the word). Such knowledge is urgently needed in the rapidly-changing anthropocene world (Crutzen, 2002), where predictability of how systems or resources will respond to perturbations or inputs, becomes increasingly more important in our efforts to sustainably manage resources, biodiversity and functionality of ecosystems.

References

- Anon, 2009. IOTC Report of the Eleventh Session of the IOTC Working Party on Tropical Tunas. IOTC, Mombasa, Kenya.
- Aumont, O., Bopp, L., 2006. Globalizing results from ocean in situ iron fertilization studies. *Global Biogeochemical Cycles* 20, GB2017.
- Aumont, O., Bopp, L., Schulz, M., 2008. What does temporal variability in aeolian dust deposition contribute to sea-surface iron and chlorophyll distributions? *Geophysical Research Letters* 35, L07607.
- Bertrand, A., Josse, E., Bach, P., Gros, P., Dagorn, L., 2002. Hydrological and trophic characteristics of tuna habitat: Consequences on tuna distribution and longline catchability. *Canadian Journal of Fisheries and Aquatic Sciences* 59, 1002-1013.
- Bromhead, D., Foster, J., Attard, R., Findlay, J., Kalish, J., 2000. A review of the impact of fish aggregating devices (FADs) on tuna fisheries. Bureau of Rural Sciences, Australia.
- Chavez, F.P., Strutton, P.G., Friederich, G.E., Feely, R.A., Feldman, G.C., Foley, D.G., McPhaden, M.J., 1999. Biological and Chemical Response of the Equatorial Pacific Ocean to the 1997-98 El Niño. *Science* 286, 2126-2131.
- Crutzen, P.J., 2002. Geology of mankind. *Nature* 415, 23.
- Dickson, K.A., 1995. Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Environmental Biology of Fishes* 42, 65-97.
- Fonteneau, A., 1997. Atlas of tropical tuna fisheries. ORSTOM Editions, Paris.
- Fonteneau, A., Pallares, P., Pianet, R., 2000. A worldwide review of purse seine fisheries on FADs, in: Le Gall, J.Y., Cayre, P., Taquet, M. (Eds.), *Pêche thonière et dispositifs de concentration de poissons*. Ifremer, Martinique, pp. 15-35.
- Fonteneau, A., Lucas, V., Tewkai, E., Delgado, A., Demarcq, H., 2008. Mesoscale exploitation of a major tuna concentration in the Indian Ocean. *Aquatic Living Resources* 21, 109.
- Fromentin, J.M., Ravier, C., 2005. The East Atlantic and Mediterranean bluefin tuna stock: looking for sustainability in a context of large uncertainties and strong political pressures. *Bulletin of Marine Science* 76, 353-362.
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P., Richardson, A.J., 2009. Pelagic protected areas: the missing dimension in ocean conservation. *Trends in*

Ecology and Evolution 24, 360-369.

- Hallier, J.P., Gaertner, D., 2008. Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series* 353, 255-264.
- Hermes, J.C., Reason, C.J.C., 2008. Annual cycle of the South Indian Ocean (Seychelles-Chagos) thermocline ridge in a regional ocean model. *Journal of Geophysical Research* 113, 04035.
- Hobday, A.J., Hartmann, K., 2006. Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fisheries Management and Ecology* 13, 365-380.
- Itano, D.G., 2000. The Reproductive Biology of Yellowfin Tuna (*Thunnus albacares*) in Hawaiian Waters and the Western Tropical Pacific Ocean: Project Summary. University of Hawaii, Joint Institute for Marine and Atmospheric Research.
- Jury, M.R., Huang, B., 2004. The Rossby wave as a key mechanism of Indian Ocean climate variability. *Deep Sea Research Part I: Oceanographic Research Papers* 51, 2123-2136.
- Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J., Hare, S.R., Ottersen, G., Perry, R.I., Roy, C., van der Lingen, C.D., Werner, F., 2006. Climate variability, fish, and fisheries. *Journal of Climate* 19, 5009.
- Lehodey, P., André, J., Bertignac, M., Hampton, J., Stoens, A., Menkes, C., Memery, L., Grima, N., 1998. Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical biogeochemical model. *Fisheries Oceanography* 7, 317-325.
- Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., Picaut, J., 1997. El Niño Southern Oscillation and tuna in the western Pacific. *Nature* 389, 715-718.
- Lehodey, P., Chai, F., Hampton, J., 2003. Modelling climate-related variability of tuna populations from a coupled ocean-biogeochemical-populations dynamics model. *Fisheries Oceanography* 12, 483-494.
- Madec, G., Delecluse, P., Imbard, M., Levy, C., 1998. OPA 8.1 general circulation model reference manual, in: Notes du Pole de Modelisation de l'Institut Pierre-Simon Laplace. France, p. 91.
- Marsac, F., Fonteneau, A., Ménard, F., 2000. Drifting FADs used in tuna fisheries: an ecological trap? *Peche thoniere et dispositifs de concentration de poissons*. Edition Ifremer. Actes Colloq 28, 36-54.

- Marsac, F., Le Blanc, J.L., 1998. Interannual and ENSO-associated variability of the coupled ocean-atmosphere system with possible impacts on the yellowfin tuna fisheries of the Indian and Atlantic oceans. *Collective Volume Science Papers, ICCAT 50*, 345-377.
- Marsac, F., Le Blanc, J.L., 1999. Oceanographic changes during the 1997-1998 El Niño in the Indian Ocean and their impact on the purse seine fishery. *IOTC Proceedings 2*, 147-157.
- Maury, O., 2010. An overview of APECOSM, a spatialized mass balanced "Apex Predators ECOSystem Model" to study physiologically structured tuna population dynamics in their ecosystem. *Progress In Oceanography 84*, 113-117.
- Meyers, G., McIntosh, P., Pigot, L., Pook, M., 2007. The Years of El Niño, La Niña, and interactions with the tropical Indian Ocean. *Journal of Climate 20*, 2872-2880.
- Miller, K.A., 2007. Climate variability and tropical tuna: Management challenges for highly migratory fish stocks. *Marine Policy 31*, 56-70.
- Mills, C.E., Carlton, J.T., 1998. Rationale for a system of international reserves for the open ocean. *Conservation Biology 12*, 244-247.
- Moreno, G., Dagorn, L., Sancho, G., Itano, D., 2007. Fish behaviour from fishers knowledge: the case study of tropical tuna around drifting fish aggregating devices (DFADs). *Canadian Journal of Fisheries and Aquatic Sciences 64*, 1517-1528.
- Murtugudde, R.G., Signorini, S.R., Christian, J.R., Busalacchi, A.J., McClain, C.R., Picaut, J., 1999. Ocean color variability of the tropical Indo-Pacific basin observed by SeaWiFS during 1997-1998. *Journal of Geophysical Research 104*, 18351-18366.
- Murtugudde, R., McCreary, J.P., Busalacchi, A.J., 2000. Oceanic processes associated with anomalous events in the Indian Ocean with relevance to 1997-1998. *Journal of Geophysical Research 105*, 3295-3306.
- Ottersen, G., Kim, S., Huse, G., Polovina, J.J., Stenseth, N.C., 2010. Major pathways by which climate may force marine fish populations. *Journal of Marine Systems 79*, 343-360.
- Parsons, L.S., Lear, W.H., 2001. Climate variability and marine ecosystem impacts: a North Atlantic perspective. *Progress in Oceanography 49*, 167-188.
- Polacheck, T., 2002. Experimental catches and the precautionary approach: the Southern Bluefin Tuna dispute. *Marine Policy 26*, 283-294.

- Polovina, J.J., Mitchum, G.T., Evans, G.T., 1995. Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960-88. *Deep Sea Research Part I: Oceanographic Research Papers* 42, 1701-1716.
- Safina, C., 1993. Bluefin tuna in the west Atlantic: negligent management and the making of an endangered species. *Conservation Biology* 7, 229-234.
- Saji, N.H., Goswami, B.N., Vinayachandran, P.N., Yamagata, T., 1999. A dipole mode in the tropical Indian Ocean. *Nature* 401, 360-363.
- Saji, N.H., Yamagata, T., 2003. Possible impacts of Indian Ocean Dipole mode events on global climate. *Climate Research* 25, 151-169.
- Schott, F.A., McCreary, J.P., 2001. The monsoon circulation of the Indian Ocean. *Progress in Oceanography* 51, 1-123.
- Schott, F.A., Xie, S., Jr, J.P.M., 2009. Indian Ocean circulation and climate variability. *Reviews of Geophysics* 47, RG1002.
- Sharp, G.D., 2001. Tuna oceanography - an applied science, in: Block, B.A., Stevens, E. (Eds.), *Tuna: Physiology, Ecology, and Evolution*. Academic Press, pp. 345-389.
- Siedler, G., Rouault, M., Lutjeharms, J.R.E., 2006. Structure and origin of the subtropical South Indian Ocean Countercurrent. *Geophysical Research Letters* 33, L24609.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K., Lima, M., 2002. Ecological Effects of Climate Fluctuations. *Science* 297, 1292-1296.
- Stéquert, B., Marsac, F., 1989. Tropical tuna - surface fisheries in the Indian Ocean, *FAO Technical Fisheries Paper*, No 282. Rome.
- Sumaila, U.R., Zeller, D., Watson, R., Alder, J., Pauly, D., 2007. Potential costs and benefits of marine reserves in the high seas. *Marine Ecology Progress Series* 345, 305-310.
- White, T.C.R., 2008. The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews* 83, 227-248.
- Wyrtki, K., 1973. An equatorial jet in the Indian Ocean. *Science* 181, 262-264.

Chapter 2

ENSO and Zonal Mode Signals in the Upper Indian Ocean: Insights from a Coupled Bio-Physical Ocean Model

Abstract

Indian Ocean effects of ENSO and the Indian Ocean Dipole or Zonal Mode (IOZM) were investigated in 1961-2001 hindcasts from a coupled bio-physical ocean model, NEMO-PISCES. The basin-wide patterns were investigated for gridded fields of sea surface temperature (SST), depth of the 20°C isotherm (Z20; as a proxy of thermocline depth) and integrated chlorophyll (CHL). Empirical orthogonal functions analyses (EOFs) confirmed that the dominant interannual mode of variability in surface temperature is an ENSO-related basin-scale warming signal, while those in Z20 and CHL are a dipolar zonal pattern across equatorial regions. The thermocline depth (as estimated by Z20) is inversely related to chlorophyll productivity across most of the Indian Ocean, due to its important role in controlling the amount of nutrients reaching sun-bathed surface waters. As a result, the strong IOZM effects on thermocline depths via Rossby Waves, Kelvin Waves and changes in Wyrtki Jet flow, translate to mirror-image patterns in chlorophyll anomalies across much of the basin. Composite averages were used to describe these patterns, differentiating among distinct combinations of positive and negative ENSO and IOZM events, as well as those that occur on their own ('pure' ENSO and IOZM events). ENSO and IOZM do have distinct anomaly expressions in the Indian Ocean, with SST being under predominantly ENSO control, but Z20 and CHL anomalies being affected mainly by IOZM dynamics when the two climate modes co-occur, as in 1997. Results presented here compare well to previous studies based on a range of data sources, and are perhaps most valuable and novel in their description of large-scale phytoplankton responses to interannual climatic extremes. In addition, the integrated chlorophyll fields reveal Rossby Wave-induced interannual anomalies in the southern tropical Indian Ocean, that are not well detected by SeaWiFS sensors. Such diagnostic anomalies have important implications for predicting physical or ecosystem responses

to interannual climate modes and need to be considered during descriptions or interpretations of interannual variability in the Indian Ocean.

Introduction

Climatic modes such as the El Niño Southern Oscillation (ENSO) interact with Ocean surface waters on a range of scales, resulting in two-way ocean-atmosphere feedbacks, impacting surface water thermodynamics and modifying horizontal and vertical flows in the upper oceans (e.g. Bjerknes, 1969; Alexander et al., 2002; Wang and Fiedler, 2006). Such perturbations affect water-column structure and control the distribution of nutrients in surface waters, thereby driving phytoplankton community dynamics (e.g. Cermeño et al., 2008) and fuelling spatio-temporal changes in productivity (Murtugudde et al., 1999). Thus climatic variability steers the flow of carbon through the ecosystem, affecting the biological carbon pump (De La Rocha and Passow, 2007) as well as upper trophic levels via bottom-up control of marine food webs (White, 2008). A better understanding of the impacts of climatic modes on the dynamics and primary productivity of surface oceans is much needed for developing predictive capabilities on future impacts of global warming, and to aid effective management of ecosystems and marine resources in light of climate variability and long-term change.

ENSO Signals in the Indian Ocean

ENSO is well-known as the dominant interannual climatic mode affecting tropical atmosphere-ocean variability globally (McPhaden et al., 2006). Besides its prominent expression in the Pacific (e.g. Wang and Fiedler, 2006), significant atmospheric and surface-ocean impacts of ENSO have been documented within the Indian basin (e.g. Reason et al., 2000; Su et al., 2001). Surface temperatures in the Indian basin are for example largely driven by ENSO variability via atmospheric teleconnections, due to changing cloud cover and wind patterns that relate to changes in ascending and descending branches of the Walker circulation (Venzke et al., 1997, 2000, Reason et al., 2000). Heat content in the south Indian Ocean (IO) is also affected by westward-propagating Rossby Waves, which are seemingly related to ENSO variability (Jury and Huang, 2004). Such physical perturbations in turn affect the biology: Murtugudde et al. (1999) investigated SeaWiFS chlorophyll concentrations from the Indo-Pacific region and noted a strong chlorophyll bloom associated with the anomalous cool

upwelled water in the eastern Indian Ocean in late 1997 and early 1998, coinciding with a strong El Niño and subsequent switch to La Niña. Applying empirical orthogonal functions (EOF) analyses to four years of global SeaWiFS data, Yoder and Kennelly (2003) identified two interannual modes of variability, both of which they ascribed to ENSO control. Both of these spatial modes displayed opposing signals in the eastern versus central and western Indian Ocean, with enhanced productivity in the eastern area during the strong 1997-1998 event.

Indian Ocean Dipole or Zonal Mode

Much interest on ocean-atmosphere dynamics in the Indian Ocean was sparked after the recognition of an additional climatic mode in the Indian Ocean (Saji et al., 1999, Webster et al., 1999). It appears to be a natural mode of coupled variability within the Indian Ocean (Yamagata et al., 2004), which intensifies in some years due to external forcing (Annamalai et al., 2003; Li et al., 2003). Often referred to as the Indian Ocean Dipole (e.g. Saji et al., 1999, Abram et al., 2008), this name is avoided by some authors, as it is argued that 'dipole' is an inaccurate description due to the absence of a consistent zonal SST 'see-saw' (Hastenrath, 2002). In the rest of this thesis, it will be referred to as the Indian Ocean Zonal Mode (IOZM), as in Annamalai et al. (2003).

A positive IOZM event is characterised by cold sea surface temperature (SST) anomalies in the eastern equatorial Indian Ocean (EEIO), warm SST anomalies in the western IO and easterly zonal wind anomalies along the equator (Saji et al., 1999; Webster et al., 1999). A negative event features opposite anomalies in the same regions (e.g. Vinayachandran et al., 2002). Similar patterns of zonal anomalies are concurrently seen in sea surface height and subsurface temperature structures (e.g. Rao et al., 2002; Feng and Meyers, 2003). Such an event typically starts along the south coast of Java in boreal spring, grows during the summer to peak in fall, before disintegrating rapidly in winter (Annamalai et al., 2003), although SST anomalies in the western basin may be seen as late as boreal summer in the following year (e.g. Wiggert et al., 2009). Some recent research has pointed towards the fact that eastern SST anomalies might be a better measure of IOZM events, as western anomalies seen in composite averages may be largely a signal of (co-occurring) ENSO teleconnections rather than a purely IOZM diagnostic (Chowdary and Gnanaseelan, 2007; Drbohlav et al., 2007).

Ocean-atmosphere feedbacks in the area surrounding the west and south coasts of Sumatra and Java are critical to the initiation and growth of IOZM events and it is here where anomalous SSTs first appear (Annamalai et al., 2003). Although not always sufficient or necessary, the main external force identified as a trigger to IOZM events is an El Niño event in the Pacific (e.g. Cai et al., 2005, Zhong et al., 2005). Annamalai et al. (2003) identify boreal spring/early summer as the critical period when eastern equatorial Indian Ocean dynamics are sensitive to such triggers and concluded that El Niño-like conditions in the west Pacific Ocean and the resultant changes in Walker Circulation initiate positive IOZM events.

Separating ENSO and IOZM Effects

The fact that ENSO dynamics are able to initiate IOZM events and thereby commonly co-occur with them, has led to debate over the independence of the IOZM from ENSO (e.g. Allan et al., 2001; Hastenrath, 2002; Yamagata et al., 2003). Although significant correlations are found between their indices (e.g. Allan et al., 2001; Yamagata et al., 2004), there are several examples of IOZM events that take place without a corresponding ENSO event in the Pacific and vice versa (e.g. Meyers et al., 2007; Song et al., 2007). These circumstances have led some authors to examine the differences between 'pure' IOZM events and those co-occurring with El Niño or La Niña. Yamagata et al. (2004) compare IO SST and global rainfall anomalies between 'pure' and 'all' IOZM and ENSO events ('all' including pure and co-occurring events). Their composite results show a zonal dipole SST pattern for pure and all IOZM events, which is however not as pronounced for all ENSO composites and virtually absent for those of pure ENSO events. The same authors also use longer time-series of SST, wind stress and sea surface height from a coupled general circulation model to show the absence of IOZM characteristics in pure ENSO anomalies, supporting their conclusion that the IOZM is independent of ENSO. Meyers et al. (2007) examine June–November average Indo-Pacific SST anomalies as well as Australian rainfall anomalies for pure and co-occurring events. They note that unexpectedly, both negative and positive 'pure' IOZM composites display cool anomalies in the Pacific cold tongue, suggestive that the latter develop in the absence of El Niño conditions. Song et al. (2007) similarly investigate composites of ENSO and IOZM events from a 250-year simulation of a coupled global general circulation model. They conclude that ENSO and IOZM are independent large-scale ocean-atmosphere phenomena, which can occur on their own, but are both triggered by similar anomalies in the West Pacific warm pool

and thus frequently co-occur.

Both climate modes are seasonally phase-locked. ENSO events typically start in boreal spring or summer (March-September), peak in winter and then dissipate the following spring to summer (Trenberth, 1997). IOZM events are perhaps even more strongly locked to seasons due to the strong monsoon influence, with anomalous easterly winds and associated SSTs first seen off Indonesia in boreal spring, peaking in September or October and then quickly dissipating at the end of the calendar year with the start of the northeast monsoon. SST and biological anomalies are however slower to erode than wind, and so can persist into the first half of the following calendar year (e.g. Wiggert et al., 2009).

Climate Impacts on Phytoplankton Productivity

The great majority of research into past Indian Ocean variability has focused on physical fields such as SST, sea height anomalies, ocean-atmosphere dynamics and surface flow fields, undoubtedly due to the availability of physical datasets for analyses and the development of realistic numerical models. In comparison, fewer studies have focused on biological or biogeochemical variability, which are critical to ecosystems and natural resources. With the launch of SeaWiFS at the end of 1997 and the concurrent progression of realistic coupled bio-physical models, biogeochemical and biological fields at resolutions necessary to investigate basin-wide seasonal and interannual variability have recently become available (e.g. Yoder and Kennely, 2003; Wiggert et al., 2006; Rodgers et al., 2008). Within the Indian Ocean, most of these efforts have been focused on biogeochemical effects of the reversing monsoon winds in the Arabian Sea (Murtugudde et al., 1999, see Wiggert et al., 2005 and references therein), while few studies have focused on basin-wide responses to physical controls.

Murtugudde et al. (1999) made use of the initial SeaWiFS period to investigate Indo-Pacific chlorophyll dynamics during late-1997 and 1998. Although without an extended SeaWiFS record for comparison, they point out some obvious chlorophyll features and relate them to the physical anomalies forcing them. A strong phytoplankton bloom off the west coast of Sumatra in October-December 1997 coincided with the anomalously strong upwelling signal of the 1997 positive IOZM event. The authors also note an area north-east of Madagascar (10°S, 60°E) characterised by high variability of wind-stress curl and associated Ekman pumping, as well as a zonal band along 5°-10°S

with shallow mixed layer depths and enhanced mixed layer entrainment, which displayed higher biological productivity than surrounding waters during the austral winter of 1998. The latter regions in the southern tropical Indian Ocean (STIO) coincide with the Seychelles-Chagos thermocline ridge (Hermes and Reason, 2008); a region that plays an important role in ocean-atmosphere dynamics due to Rossby Wave variability linked to ENSO and IOZM perturbations (Xie et al., 2002; Jury and Huang, 2004).

Wiggert et al. (2006) used a coupled bio-physical ocean general circulation model to investigate biogeochemical variability across the Indian Ocean. They reason that the semi-annual Wyrтки Jet (Wyrтки, 1973) largely controls equatorial biogeochemical variability by affecting thermocline (and nutricline) depths along the equator, causing a downward slant from west to east, which allows for prominent phytoplankton blooms in western areas but low productivity in the eastern basin. Chlorophyll concentrations in the STIO are noted to show variability due to the influence of westward-propagating Rossby Waves and local Ekman pumping, with greater productivity seen during austral winter and spring (Wiggert et al., 2006).

Wiggert et al. (2009) used SeaWiFS data to investigate basin-wide chlorophyll and productivity changes in response to the two most recent positive IOZM events (1997 and 2006). They show a substantial increase in eastern tropical IO chlorophyll, especially in the area south and west of Sumatra, while most western areas exhibited below normal productivity during the events. The 1997 anomalies were stronger in most regards, with below-average chlorophyll concentrations in the Arabian Sea and prominent positive anomalies in the east spreading further west than in 2006, due to a reversal (as opposed to a weakening) of the Wyrтки Jet in the boreal fall Intermonsoon (Murtugudde et al., 1999, Wiggert et al., 2009). Employing a primary production algorithm, Wiggert et al. (2009) point out that there seems to be minimal net primary productivity impact at the basin-wide IO scale for the two events investigated, even though the spatial distribution of productivity is substantially affected.

Although the SeaWiFS period now provides a decade of data at high spatial and temporal resolution, this period is still restrictive in addressing interannual cycles and long-term changes with confidence. Moreover, there are problems associated with

remotely sensed chlorophyll in some oligotrophic regions (e.g. Claustre et al., 2002; Dandonneau et al., 2003) and sensors miss a large proportion of depth-integrated chlorophyll when chlorophyll maxima are deeper than the first attenuation depth or 'penetration depth' (on the order of 20m; Gordon and McCluney, 1975). Wiggert et al. (2009) recently made use of the coverage of two positive IOZM events by SeaWiFS (1997 and 2006), to address basin-wide biological implications of these events. A sample size of two is however limiting and furthermore these two (positive IOZM - El Niño) events represent only one of a number of potential IOZM-ENSO configurations. Fortunately longer-term biogeochemical and biological hindcasts are becoming available from state-of-the-art coupled bio-physical models, which are resolving seasonal and interannual variability to a very good (and ever-improving) degree (e.g. Wiggert et al., 2006; Rodgers et al., 2008; Koné et al., 2009; Maury et al., 2010). Given that they resolve the variability of interest sufficiently accurately, model outputs can provide long time-series of three-dimensional high-resolution hindcasts, often including variables for which in situ datasets may be inadequate (or completely lacking) to answer questions of interest.

Knowledge Gaps and Objectives

Although the work of Murtugudde et al. (1999) and Wiggert et al. (2009) provide some useful descriptions of basin-scale biological signals that follow a positive IOZM - El Niño event, and explain their physical control, only a narrow understanding of the overall consequences of these climatic modes on Indian Ocean phytoplankton productivity exists. Even physical properties which have been more extensively covered in the literature, are not completely understood and differences amongst results and interpretations are evident. It is well-known that both pure IOZM and pure ENSO events occur, however the majority of evidence and interpretations emanate from the last two positive events (1997, 2006), which were both co-occurring positive IOZM - El Niño events. Few studies have separated pure events from co-occurring ones (e.g. Yamagata et al., 2004, Saji and Yamagata, 2003a) and similarly few authors have included or addressed negative IOZM or La Niña effects in the Indian Ocean (e.g. Vinayachandran et al., 2002; Meyers et al., 2007). We are therefore still lacking a good understanding of the basin-wide signals for the various configurations of ENSO and IOZM events. How do such events affect the primary trophic level across the Indian Ocean and are there predictable basin-wide or regional responses to such events?

This chapter attempts to address such questions, aiming to identify the role that ENSO and IOZM play in interannual fluctuations of surface temperatures, thermocline depths and depth-integrated chlorophyll concentrations. Using 41 years of Indian Ocean outputs from a coupled bio-physical ocean model, NEMO-PISCES (Aumont and Bopp, 2006), and employing a combination of correlations, EOFs, composite averages and linear models, an attempt will be made to characterise the main regional and basin-scale responses of the above variables, to different combinations of ENSO and IOZM. The novel part of this work will be to include long-term chlorophyll hindcasts to better resolve the effects of these climate modes on spatio-temporal patterns in biological productivity. An improved understanding of such dynamics should contribute towards making constructive hypotheses about, and interpretations of, ecosystem links to climate variability and thereby contribute towards attaining predictability of impacts from similar events in future. Such predictability is vital to effective resource management and is what climate-change scientists strive to achieve in an ever-changing world.

Methods

Areas of relevance to this study are shown in Figure 1. Indian Ocean longitudinal limits were defined as 25°E and 120°E. As tropical dynamics and their control on permanently-stratified waters are the focus of this study, latitudinal limits were restricted to surface waters >15°C (as in Behrenfeld et al., 2006). However empirical orthogonal function and composite analyses require a fixed geographic area and were thus restricted to the area north of 30°S. The depth of the 20°C isotherm (hereafter Z20) had to be treated differently, as it seasonally outcrops to the surface in the southern IO. Therefore the average Z20 time-series was calculated from those cells where Z20 remained below the uppermost depth level (5m), whereas EOF and composite analyses were restricted northwards of 22°S. In addition to the EEIO box (commonly used in calculating the dipole mode index; 0-10°S, 90-110°E; Saji et al., 1999), two tropical regions of interest were identified and were investigated in more detail. They are the southwestern IO (SWIO; 50-70°E, 0-15°S) and southeastern IO (SEIO; 85-105°E, 0-15°S; Figure 1).

Model Outputs and Data

Outputs from the coupled physical-biogeochemical ocean model, NEMO-PISCES, were used as hindcast datasets for the period of 1961-2001. The oceanic global circulation model (NEMO-OPA8.2) simulates ocean physics and dynamics on a global numerical grid (ORCA2) based on OPA version 8.2 (Madec et al., 1998). The model has 31 depth levels, separated by 10-m layers in the upper ocean (below 150 m depth) and with thicker layers (up to 500 m thick) deeper down. The zonal resolution is about 2° , with the meridional resolution 0.5° at the equator and larger at higher latitudes. The simulation used here was forced using daily ERA40 surface wind data (Uppala et al., 2005), while surface heat fluxes were calculated by bulk formulae. For further details of the physical model, see Lengaigne et al. (2004), Rodgers et al. (2008) and references therein.

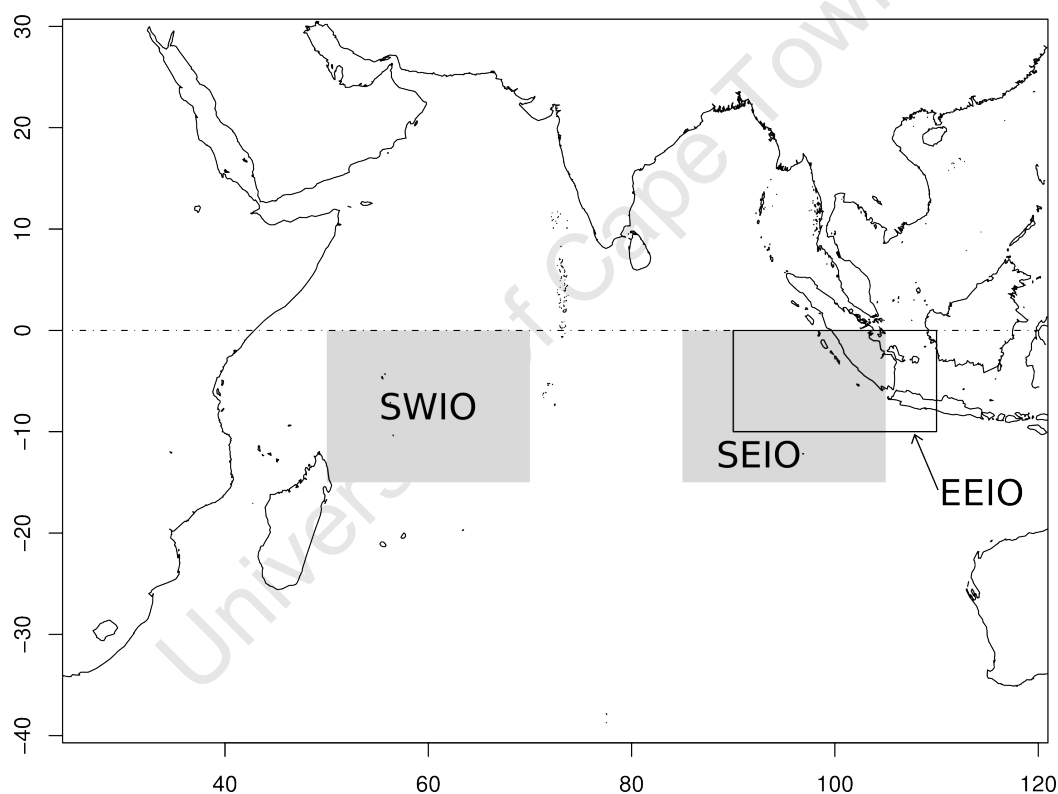


Figure 1. Map of Indian Ocean, indicating the regions of interest referred to in the study. EEIO: East equatorial Indian Ocean; SEIO: Southeast Indian Ocean; SWIO: Southwest Indian Ocean;

The biogeochemical model (PISCES; Aumont and Bopp, 2006; Aumont et al., 2008) simulates chemical fluxes through 24 compartments including Fe, Si, PO_4 , NO_3 , NH_4 , two phytoplankton and two zooplankton groups. The outputs used here are exactly

the same as those of the "PISCERA" simulation used by Rodgers et al. (2008). Details on the Red-Green-Blue model by which light penetration profiles (and thus photosynthetically available radiation levels) are calculated, are given in Lengaigne et al. (2007). Phytoplankton chlorophyll and carbon are modelled by a method based on Geider et al. (1998). Further details of PISCES can be found in Aumont and Bopp (2006) and Aumont et al. (2008), while manuals for NEMO and PISCES are available online (<http://www.nemo-ocean.eu/About-NEMO/Reference-manuals>). Outputs were available on an interpolated 1° by 1° grid and were arranged in global fields of 15 time-steps per year. The first three years (1958-1960) were not included in analyses, so as to avoid potential bias due to drift after model spin-up (Aumont, personal comment).

Analyses

All analyses in this study were performed using R programming language (R Development Core Team, 2009). The three oceanographic variables included in analyses were sea surface temperature (SST), depth of the 20°C isotherm as a proxy of thermocline depth (hereafter Z20; Masumoto and Meyers, 1998; Vinayachandran et al., 2002; Annamalai et al., 2003), and total chlorophyll concentration integrated over the euphotic zone (hereafter CHL). The former two variables were extracted from the temperature field: Surface temperature was taken as the uppermost (5 m) level, while Z20 was estimated by linear interpolation of the fixed depth levels. The euphotic zone was estimated from the photosynthetically available radiation (PAR) outputs: Surface PAR was estimated by linear extrapolation of the gradient between the two uppermost depth levels (5 m and 15 m), after which the depth of 1% of the surface value was estimated by linear interpolation of the fixed levels below. Total chlorophyll-a concentrations were calculated by adding diatom and nano-phytoplankton chlorophyll fields, which were separate outputs. The derived chlorophyll field was then integrated over the euphotic zone depth to attain the mg/m² concentrations used in analyses.

To verify that interannual signals were well represented in the simulations, monthly time-series from HadISST1 (Hadley Centre's sea ice and sea surface temperature data set, version 1.1; Rayner et al., 2003) were compared to the model outputs. To do so, the land-mask used for model outputs was applied to the HadISST1 data, to ensure corresponding ocean/land boundaries. The higher temporal resolution model outputs (15 time-steps per year) were interpolated onto 12 regular calendar 'months' using a cubic spline, to allow computation of correlation coefficients.

Correlation Analyses

Most environmental time-series contain serial autocorrelation (Bakun, 1996), which violates the assumption of statistically independent replicates that most classical inference tests subscribe to (Hurlbert, 1984). As a consequence, a sample correlation will produce a Type I error rate higher than the prescribed level, due to fewer degrees of freedom (or a larger variance) than is assumed (Pyper and Peterman, 1998). Pearson's product-moment correlations have been employed here, with adjusted degrees of freedom as described in Bonhommeau et al. (2008), who use modifications suggested by Pyper and Peterman (1998) on the method of Chelton (1984). Cross-correlations were performed to attain appropriate lags between time-series.

Empirical Orthogonal Functions (EOFs)

Dominant spatio-temporal modes of variability in the Indian Ocean were explored by EOF analyses. These were performed by singular-value decomposition of the space-time matrix (e.g. Lawson and Hanson, 1974). Before application of the SVD, the fields were prepared in the following way: For each grid point, a six-year running mean was subtracted, as well as the average seasonal cycle for the entire time-series (1961-2001), to produce interannual anomalies without a trend component. A linear trend, as opposed to the high-pass filter applied here, is often removed in EOF analyses (e.g. Rao et al., 2002). However decadal oscillations and sudden shifts in mean state, such as are documented in climate records (e.g. Fiedler, 2002), would not be as well accounted for by removal of a linear trend line, which resulted in the choice of a multi-year running mean instead. As interannual signals are of interest and to avoid noise EOFs, anomalies were then smoothed using a five-month (six-timestep) running mean, before a latitudinal weight (square root of the cosine of latitude) was applied to account for the converging longitudes and greater density of cells polewards (Hannachi et al., 2007).

Composite Analyses

To characterise effects of the dominant climate modes in the tropical IO, composite maps and spatially-averaged temporal plots of SST, Z20 and CHL were prepared for different events (and combinations thereof). To isolate positive and negative ENSO and IOZM events, SST indices were employed from ocean regions that represent upwelling dynamics related to those events, as upwelling is an essential controlling process in the growth and development of both tropical climate modes (Meyers et al.,

2007). The dipole mode index (DMI; Saji et al., 1999) has commonly been used in identifying IOZM years and is calculated as the SST difference between a western equatorial box and the EEIO. While eastern upwelling-related SST changes are a robust feature of IOZM events, western SST anomalies are variable amongst events (e.g. Huang and Kinter, 2002) and may in fact be controlled by ENSO dynamics (Chowdary and Gnanaseelan, 2007, Drbohlav et al., 2007). Several authors have preferred to emphasize SST dynamics in the eastern IO as a measure of IOZM activity (e.g. Xie et al., 2002; Annamalai et al., 2003, Rao and Behera, 2005; Meyers et al., 2007) and such a strategy is followed here.

The Niño-3 index was used as a measure of ENSO activity. The index is calculated as the average SST within a box located in the eastern equatorial upwelling region of the Pacific Ocean (5°S-5°N, 90°W-150°W) and is commonly employed as a proxy of ENSO variability (e.g. Jury and Huang, 2004; Meyers et al., 2007). Similarly, average SST in the eastern equatorial Indian Ocean box (EEIO; 0-10°S, 90-110°E; Figure 1) was used as the IOZM index. SST dynamics in this region are largely driven by upwelling activity off Sumatra and Java, which is central to the development of IOZM events (Annamalai et al., 2003).

Before identifying event years, a six-year running mean as well as the average seasonal signal were removed from indices, in order to focus on interannual anomalies, without the effects of low-frequency trends or seasonal fluctuations. ENSO events were identified as periods when five-month running means were outside of $\pm 0.5^{\circ}\text{C}$ for six consecutive months, similar to the method of the Japan Meteorological Agency (JPA; Trenberth, 1997). IOZM events were identified as years when five-month running means were beyond $\pm 0.5 \times \text{standard deviation}$ for six consecutive months, after the IOZM index had been normalised to a variance of one. Note that the IOZM SST index has been inverted in plots and correlations, so that an anomaly peak corresponds to a positive IOZM event and a trough to a negative event.

As the thresholds used here are sensitive to identifying weaker events relative to those used in several other reported cases (e.g. Saji et al., 1999; Annamalai et al., 2003; Meyers et al., 2007; Saji and Yamagata, 2003a, b), each identified year was carefully inspected, including June-November and December-May averaged spatial anomalies, to check whether a coherent and representative spatial SST signature was

evident in the prescribed region. The spatio-temporal anomalies, together with their classification in the literature, were used to remove any falsely identified years.

In this way, composite groups of 'pure' and co-occurring climatic events were distinguished. 'Pure' negative or positive IOZM (ENSO) groups were made up of years in which there is no concurrent ENSO (IOZM) event in the Pacific (Indian) Ocean, while co-occurring composites were made up of distinct combinations of coinciding IOZM/ENSO events. Within these categories, spatial anomalies were averaged over two seasons, namely ~June-November of the years identified (JJASON; eight timesteps) and the following ~December-May (DJFMAM; seven timesteps). This choice of seasons was due to the strong seasonal phase-locking of IOZM dynamics (Annamalai et al., 2003), as well as an attempt to capture effects of ENSO events, which typically peak in between November and January in the Pacific Ocean (Trenberth, 1997), but whose IO signal lags about four months behind that in the Pacific (e.g. Yamagata et al., 2004). Along with the maps, area-averaged anomaly plots (+/- standard deviation) for the IO, SWIO and SEIO areas were drawn for ~June (identified year) to May (following year).

As opposing events (e.g. pure El Niño versus pure La Niña) provided strikingly symmetrical spatial anomalies in most cases, 'positive' and 'negative' events were combined ((positive-negative)/2) in the interest of space, as has been done elsewhere (e.g. Yamagata et al., 2004). A one sample Student's t-test (Sokal and Rohlf, 1995) was applied to each grid cell containing the spatial composites, to provide an indication of anomalies that were significantly different from zero ($p < 0.05$). For the temporal line plots, the positive and inverted negative anomalies were combined into an 'average' anomaly in black, although both the former are also represented separately in red and blue respectively.

Linear Regressions

To add statistical weighting and explore predictability behind some of the effects interpreted from composite analyses, the significance of ENSO and IOZM indices in predicting variability in the IO basin were investigated by the use of linear regression models. The models investigated were of the form:

$$RegionVar_t = \beta_1 * IOZM_{t-i} + \beta_2 * ENSO_{t-n} + \beta_3 * (IOZM_{t-i} * ENSO_{t-n}) + \epsilon_t$$

with $RegionVar_t$ representing the variable of interest (SST, Z20 or CHL) in the specific region under consideration (SEIO, SWIO or IO) at time t , while $IOZM_{t-i}$ and $ENSO_{t-n}$ represent the indices of these climate modes, appropriately lagged as identified by cross-correlation. The same area-averaged SST indices of ENSO/IOZM were used as in composite analyses, with their average seasonal signal removed and having been normalised to a variance of one. The $RegionVar$ time-series had only their average seasonal signal removed. If model coefficients were non-significant ($p > 0.05$), they were removed in search of the simplest model that related ENSO/IOZM indices to Indian Ocean environmental variables. As the IOZM index was derived from SST within the IO, it is not independent of IO SSTs and so only the ENSO (Niño-3) index was included in regressions of SST.

The inherent serial autocorrelation within the environmental time-series and indices similarly complicates this procedure (as with correlation analyses). Linear regressions, like most classical inference tests, assume that all samples are independent of one another (Hurlbert, 1984). To account for the potential lack of independence caused by autocorrelation in the dependent variable, autoregressive-correlated residuals were modelled during generalised least squares (GLS) fitting of the regressions, using the Linear and Nonlinear Mixed Effects Models (nlme) library in R (Pinheiro et al., 2010). Results were investigated using residual correlation structures of autoregressive order one, two and three (AR1, AR2, AR3) models. The Akaike Information Criterion (AIC; Akaike, 1974) was used to choose the most suitable model. To demonstrate the difference in results obtained if autocorrelation considerations were not taken into account, unadjusted linear models were additionally fitted. Normality and homoscedastic variance structures were visually checked, both before fitting and in the residuals resulting from fitted models.

Results

At both ocean-basin and regional scales, SST time-series correspond well to those of the HadISST1 dataset (Figure 2), with the mean state, seasonality and interannual variability well captured by the model outputs. At global and basin scales, model SSTs are on average slightly higher (~ 0.1 - 0.3°C) and the 1976 shift is slightly exaggerated relative to HadISST1 (Figure 2c, d). Additionally, there is an upward trend in the latter half of the HadISST1 time-series, which is not as evident in the model outputs. The

lacking trend, superimposed on the exaggerated 1976 shift, account for an apparent decadal-scale variability in the goodness-of-fit between the two time-series.

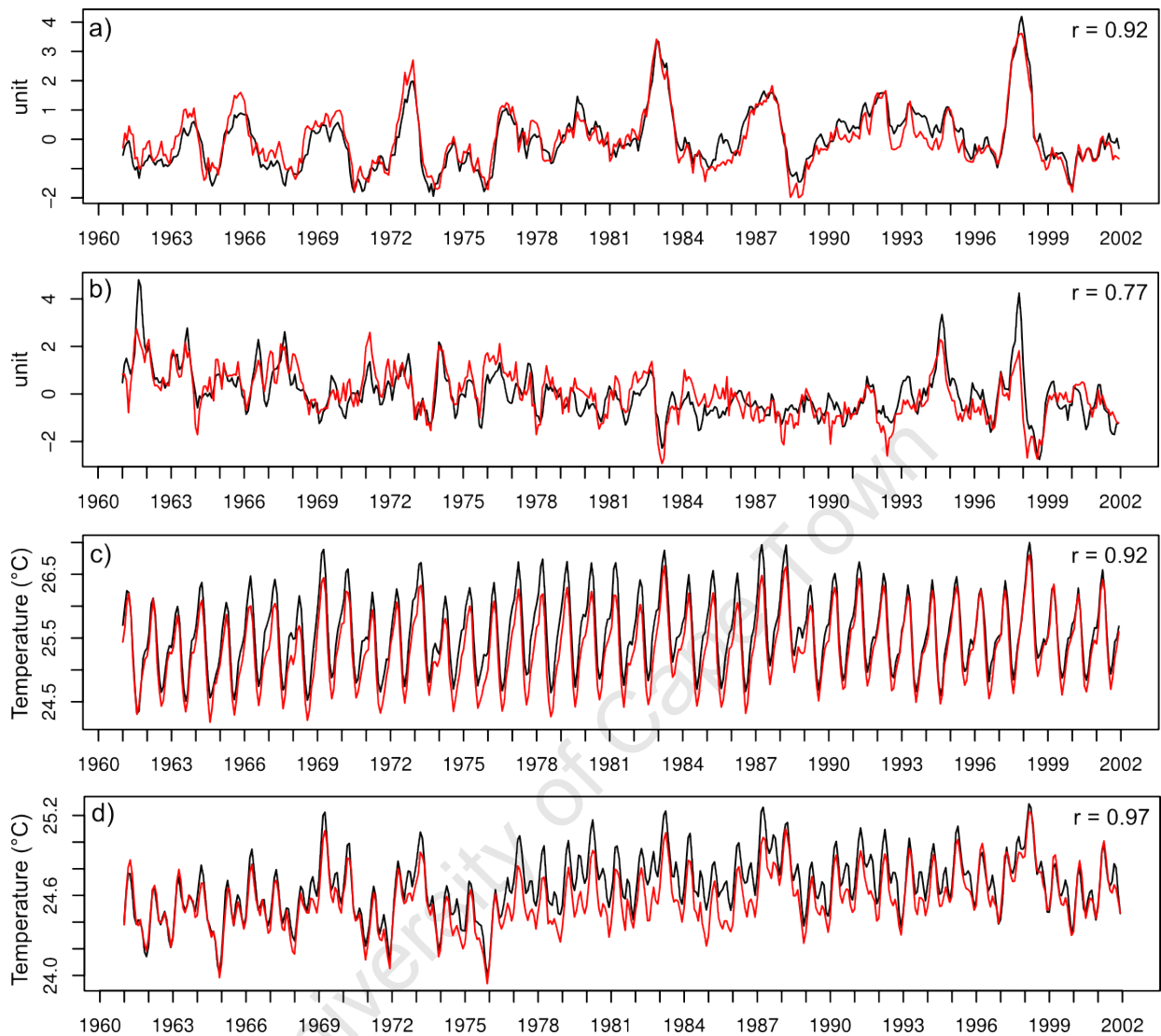


Figure 2. Comparison of model output (black) and HadISST (red) SST indices for a) ENSO (Niño-3), b) IOZM (EEIO), as well as average SST for c) the Global Ocean and d) the Indian Ocean (bounded latitudinally by waters $>15^{\circ}\text{C}$ and 25° to 120°E for the latter). The indices have had their average seasonal signal removed and are normalised to unit variance. The EEIO index has been inverted to have positive peaks corresponding to positive IOZM events. All Pearson correlation coefficients are highly significant ($p < 0.01$; with adjusted degrees of freedom for serial autocorrelation).

As ENSO and IOZM indices used here are representative of SST in a confined region, they are not strictly independent of basin or global-scale SST variability and therefore results of correlations with SST need to be treated with caution. Bearing this in mind,

results suggest that globally averaged SST as well as chlorophyll concentrations of permanently stratified waters are tightly coupled to ENSO variability (Figure 3). El Niño peaks in the Niño-3 index generally correspond to warmer average surface waters and lower average chlorophyll concentrations, while La Niña troughs correspond to cooler surface waters and higher chlorophyll concentrations, as indicated by the positive and negative correlation coefficients with SST ($r=0.80$; $p<0.01$) and chlorophyll ($r=-0.67$; $p<0.01$) respectively (Figure 3).

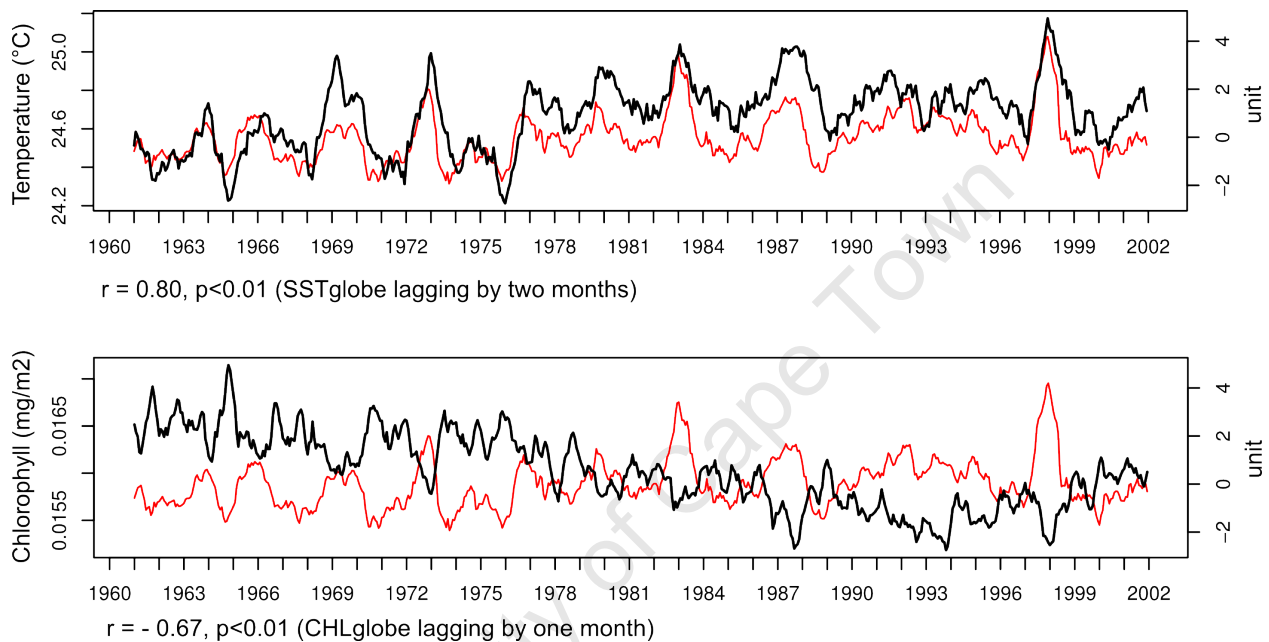


Figure 3. Globally averaged SST (top) and CHL concentrations (bottom) are strongly correlated to ENSO variability (Niño-3 index in red). The time-series have had their average seasonal cycle removed, while the Niño-3 index was additionally normalised to unit variance.

Indian Ocean variables are also correlated with major climate indices (Table 1), although to a lesser degree than ENSO control on globally averaged SST and chlorophyll (Figure 3). While IO SST is more highly-correlated with the Niño-3 than IOZM index, average chlorophyll and Z20 are more highly-correlated with the IOZM at regional and basin scales. According to the correlations (Table 1), positive IOZM events are associated with higher chlorophyll concentrations and a shallower thermocline in the IO basin and especially the SEIO, while in the SWIO region they are associated with lower chlorophyll and a deeper thermocline. El Niño events are associated with lower CHL in the Indian Ocean and SWIO, as well as deeper

thermocline depths in the SWIO area. At the IO basin scale, average CHL is inversely correlated to thermocline depth ($r=-0.51$, $p<0.001$), with this correlation substantially stronger in the SWIO and SEIO subregions ($r=-0.87$ and $r=-0.77$ respectively; $p<0.001$).

Table 1. Correlations between climate indices (Niño-3 and IOZM) and 1961-2001 time-series of average SST, CHL and Z20 from the Indian Ocean areas of interest. The time-series have had their average seasonal signal removed, while indices were additionally normalised to unit variance. * $p<0.05$; ** $p<0.01$; NS=not significant

Area	Variable	Nino3	lag	IOZM	lag
Indian Ocean	SST	0.63**	SST lagging ~4 months	-0.50**	none
	Chl	-0.3**	Chl lagging ~5 months	0.4**	IOZM lagging ~1 month
	Z20	NS	--	-0.35**	IOZM lagging ~2 months
SWIO	SST	0.61**	SST lagging ~2 months	NS	--
	Chl	-0.39**	Chl lagging ~2 months	-0.42**	Chl lagging ~5 months
	Z20	0.34**	T20 lagging ~4 months	0.39**	T20 lagging ~7 months
SEIO	SST	0.28**	SST lagging ~6 months	-	not independent
	Chl	NS	--	0.70**	Chl lagging ~1 month
	Z20	-0.2*	Nino3 lagging ~1 month	-0.46**	T20 lagging ~1 month

In terms of EOF analyses, the dominant mode explaining 34% of interannual SST variability in the IO, is an almost basin-wide monopole highly correlated with ENSO variability (Figure 4a). For CHL and Z20 (Figure 4b, c), a zonal dipolar mode explains the highest amount of interannual variability (32% and 36% respectively). The latter modes are significantly correlated to both Niño-3 and IOZM indices, implying that the two climatic modes are not orthogonal. A significant correlation of -0.3 ($p<0.01$; Niño-3 leading by ~7 months) between Niño-3 and IOZM indices supports this conclusion.

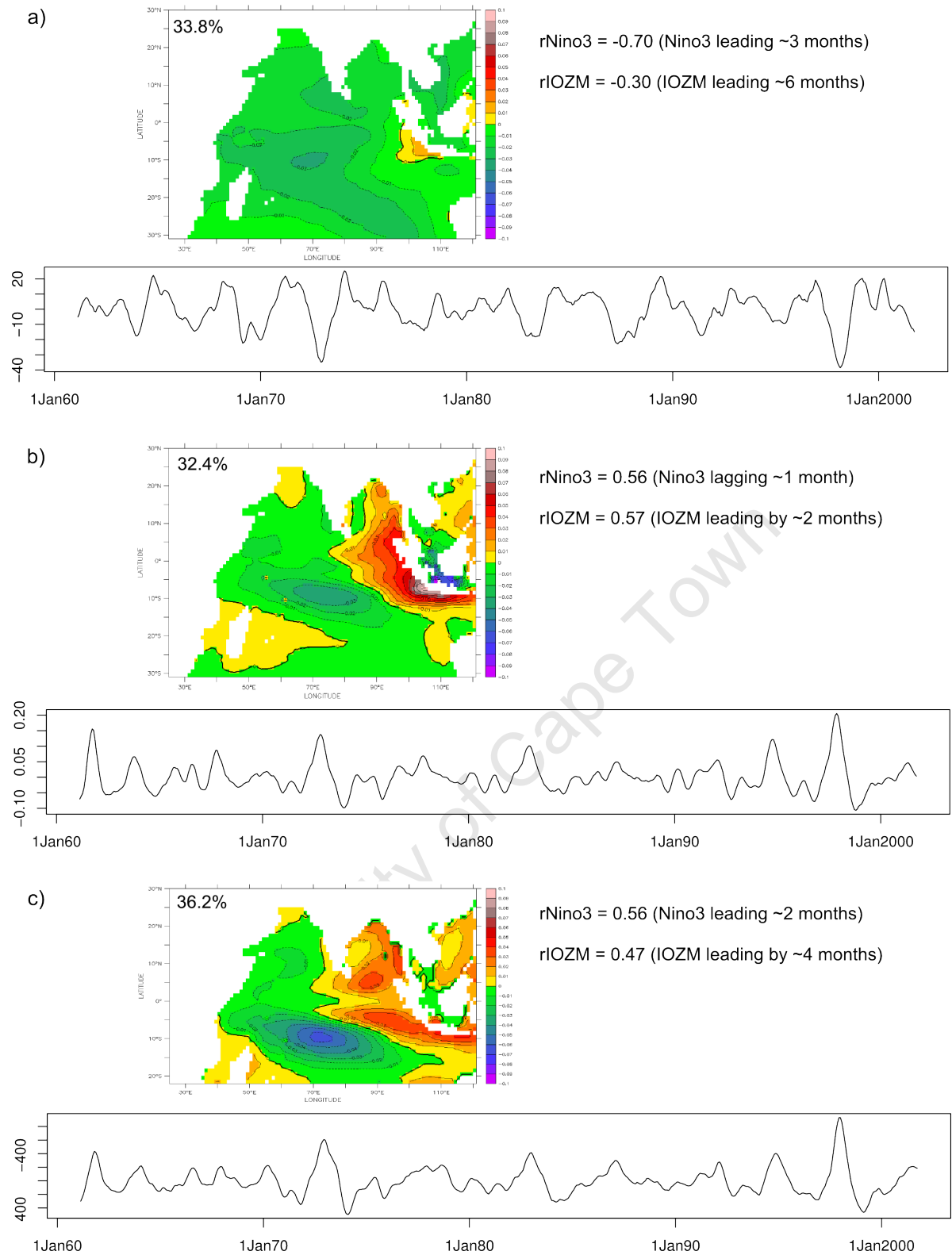


Figure 4. Dominant EOFs and their respective principal component (PC) time-series for a) SST, b) CHL and c) Z20. The Z20 EOF was restricted to northwards of 22°S to exclude latitudes at which the 20°C isotherm surfaces seasonally. The percentage of interannual variance explained by each EOF is included in the figures and significant correlations ($p < 0.01$) of PC time-series with Niño-3 and IOZM indices are reported. The values of c) have been inverted in order to facilitate visual comparison with b).

Composite Analyses

By inspecting spatio-temporal anomalies of each identified (event) year, two categories of 'falsely identified' years were dealt with: Firstly, in some years a rapid change from El Niño to La Niña conditions (or vice versa) takes place within the same calendar year. Secondly, some particularly strong events cause prevailing SST anomalies to persist into the following year, even though there is no development of a new event. The latter case is easily recognised and such years were removed. The former, however, is more troublesome, as a changeover from one extreme to the other potentially complicates both local and remote impacts within that year. With such cases, their classification in the literature as well as relative strength and duration of anomalies were examined, in order to assign them as one event or the other. Using this rationale, years removed from La Niña events were 1968, 1983 and 1989, while 1998 was removed from El Niño years.

Table 2. Years of ENSO and IOZM events used in the composite analyses. Those marked with an asterisk and in bold are 'pure' events.

	El Niño	La Niña	Positive IOZM	Negative IOZM
1	1963	1964	1961*	1964
2	1965*	1966	1963	1968
3	1968	1967	1966	1973
4	1969*	1970*	1967	1974*
5	1972	1971*	1972	1975
6	1976	1973	1976	1980
7	1979*	1975	1977*	1984
8	1982	1978*	1982	1990*
9	1983*	1980	1991	1992
10	1986*	1981*	1994*	1995
11	1987*	1984	1997	1996
12	1991	1985*	-	1998
13	1992	1988*	-	-
14	1997	1995	-	-
15	-	1996	-	-
16	-	1998	-	-
17	-	1999*	-	-

Table 2 lists the years defined as IOZM and ENSO events. Composite anomalies plotted in Figure 5 include both 'positive' and inverted 'negative' events ((positive-negative)/2). Although they are described and discussed mostly in the 'positive' sense as seen in Figure 5, the opposite or inverted colour scale would equally represent the 'negative' event states.

IOZM Events

During the peak season of June-November, positive (negative) IOZM events are characterised by an anomalous cool (warm) SST plume off the west coasts of Java and Sumatra, which coincides with a strong positive (negative) chlorophyll anomaly along these coasts, stretching northwards into the Bay of Bengal (Figure 5a-b; note that 'posIOZM' and 'negIOZM' refers to positive and negative IOZM events respectively). Relative to average conditions, cool (warm) surface temperatures, a shallow (deep) thermocline and positive (negative) CHL anomalies are seen in much of the eastern Indian Ocean. Over the same season of JJASON, warmer (cooler) surface temperature, positive (negative) thermocline depths and low (high) CHL anomalies are present over much of the western and southern Indian Ocean, although most of these anomalies are not statistically significant in pure IOZM composite group (Figure 5b). The western and southern anomalies generally spread eastwards, especially near the equator, and tend to intensify in the subsequent season of DJFMAM, while those on the eastern side become less intense, less extensive and more fragmented to varying degrees (Figure 5a-b). The development of a warm (cool) patch of water with a relatively intense negative (positive) CHL anomaly and deeper (shallower) than normal thermocline depths, is notable during this second season in the south-western Indian Ocean (around 10°S, 65°E). Most features are more clearly defined and more significant (lower p-value) in all IOZM event composites (Figure 5a) than in those of pure events (Figure 5b). CHL and Z20 spatial anomalies coincide notably well during both seasons, but with opposite sign.

ENSO Events

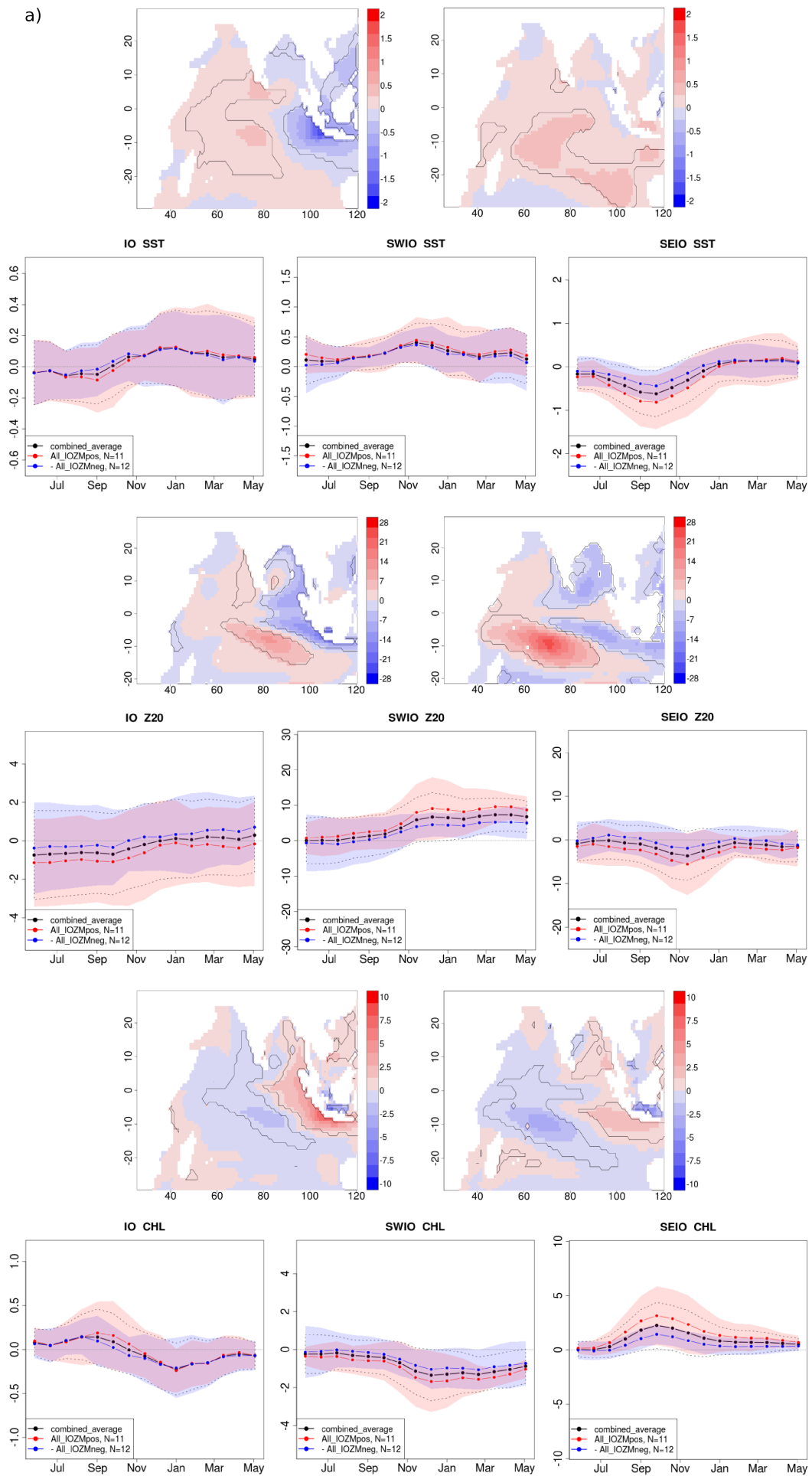
ENSO events display some similar anomaly patterns to IOZM events, although eastern anomalies are smaller in spatial extent and less intense (or even absent), whereas western anomalies seem more dominant (Figure 5c-d). El Niño (La Niña) surface temperature anomalies are mostly positive (negative) throughout the basin and stronger during the subsequent season, while the distinct cool (warm) SST anomalies off western Indonesia are not well developed in all event composites (Figure 5c) and are weak in pure ENSO events (Figure 5d). Anomalies of CHL and Z20 are significant in only a few limited regions for pure El Niño (pure La Niña) events and the area-averaged line plots show a lack of consistency between positive and (inverted) negative ENSO events in some regions. The distinct patch of anomalies in the south-western Indian Ocean characteristic of IOZM events (mentioned above) is present in

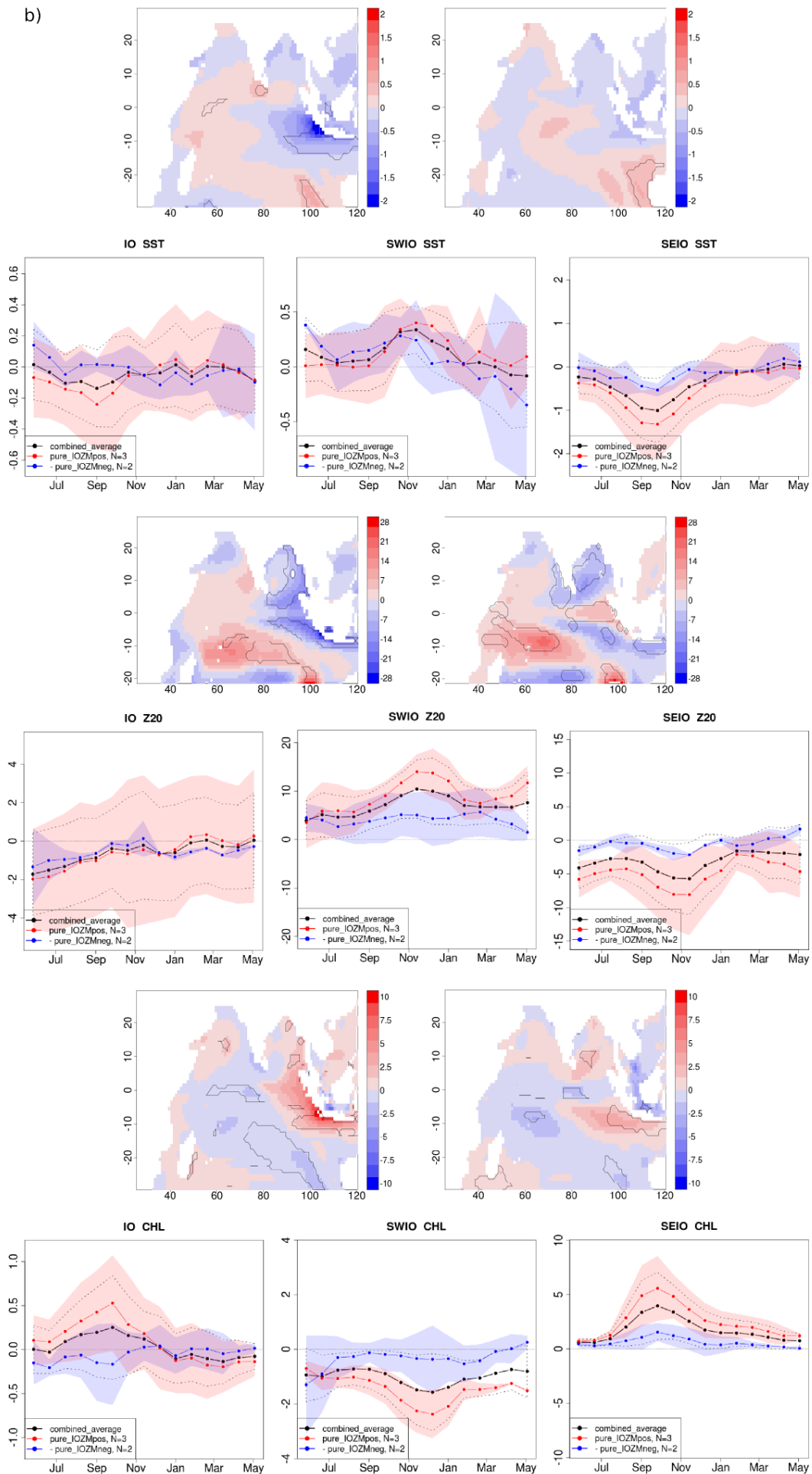
all ENSO composites (Figure 5c), but relatively poorly developed in pure ENSO plots (Figure 5d).

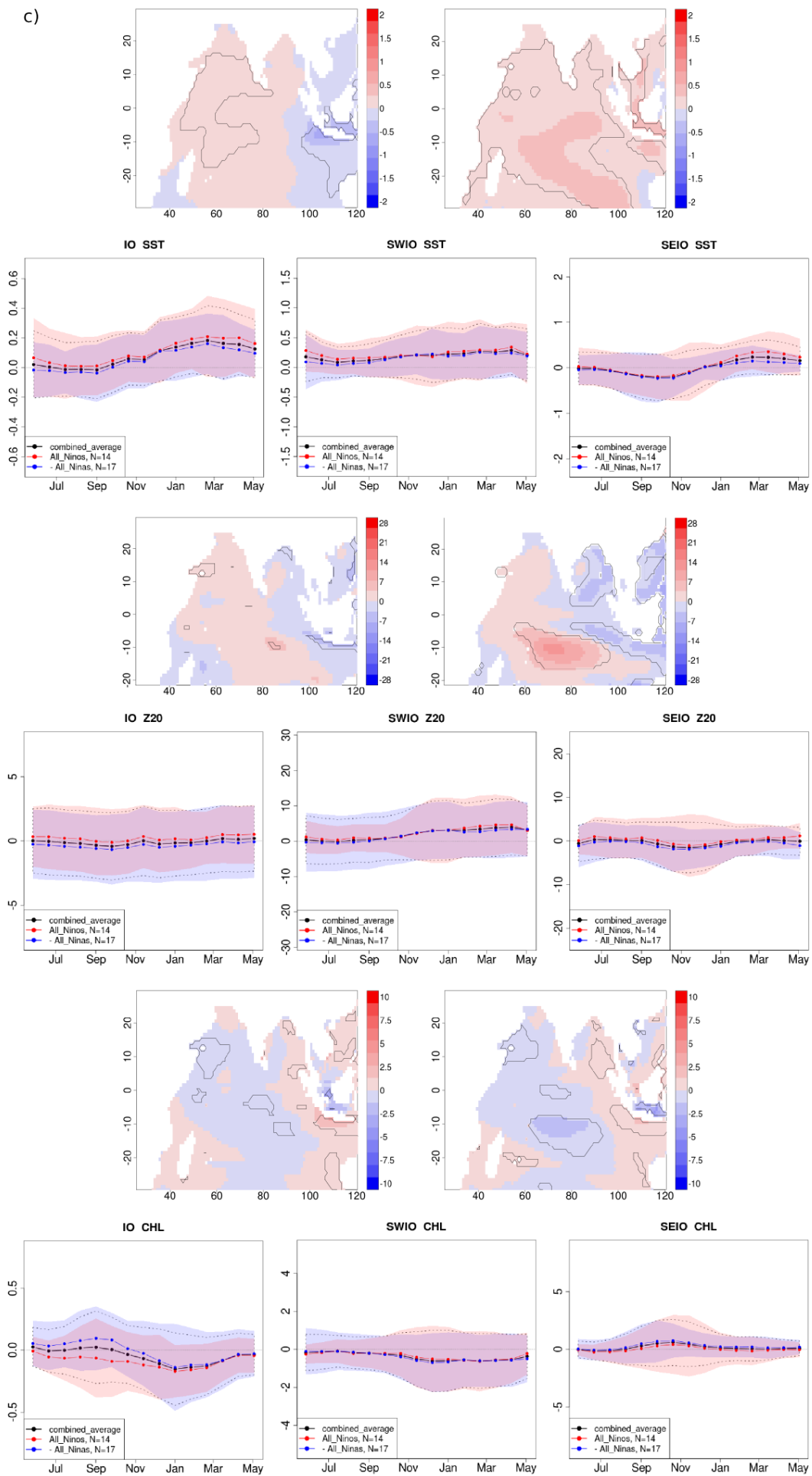
Co-occurring Events

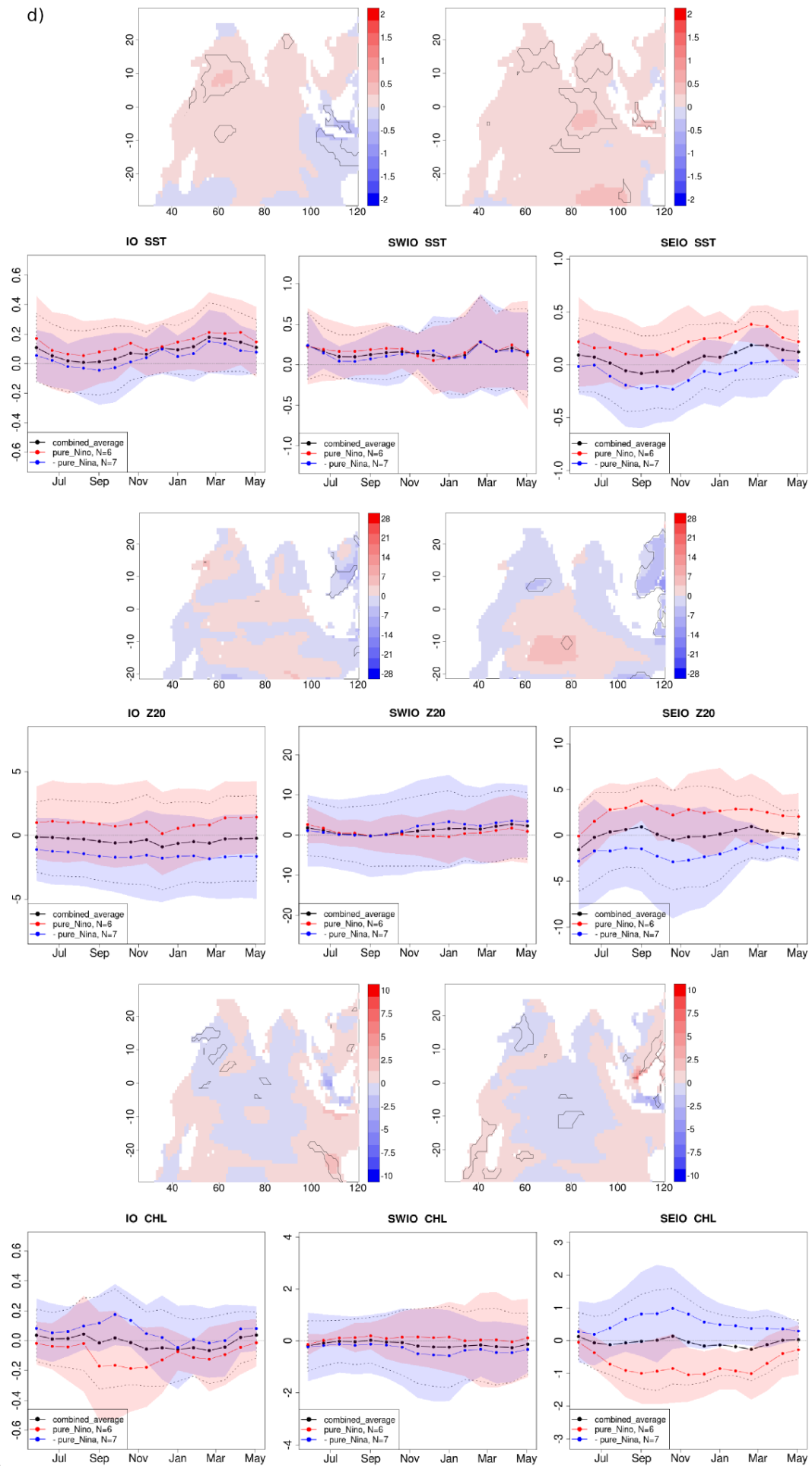
Co-occurring posIOZM - El Niño (negIOZM - La Niña) composites (Figure 5e) share more similarities with pure IOZM events (Figure 5b) than with pure ENSO events (Figure 5d), except for surface temperatures, which display more widespread and intense positive (negative) anomalies that grow in the DJFMAM season. Similar to IOZM events, a distinctive patch of water with anomalous thermocline depths and chlorophyll concentrations is evident in the STIO. It intensifies and moves westward in the subsequent DJFMAM season, where it is associated with a warm (cool) sea surface signal (Figure 5e).

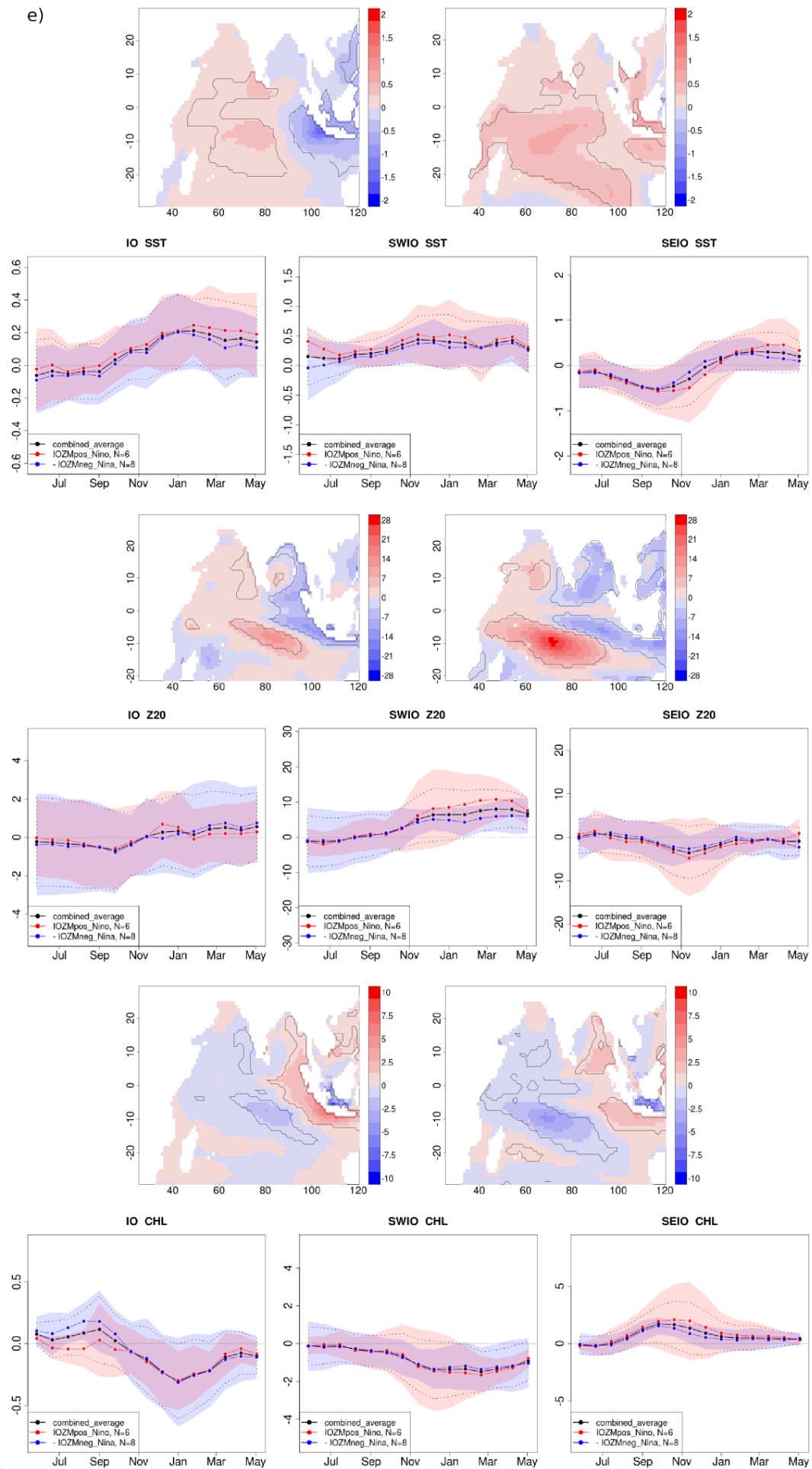
Although only represented by two events each, co-occurring posIOZM - La Niña (negIOZM - El Niño) conditions were identified. Anomalies amongst these events are not very consistent, however a brief description of some of the features is provided. From comparisons with previous composites, it seems that the IOZM-related patterns are most prevalent in the composites, but with significant anomalies mainly restricted to the STIO area, which propagate westward in the subsequent (DJFMAM) season. Some cool SST and below-average Z20 anomalies also appear along the east African coastline and eastern Arabian Sea.











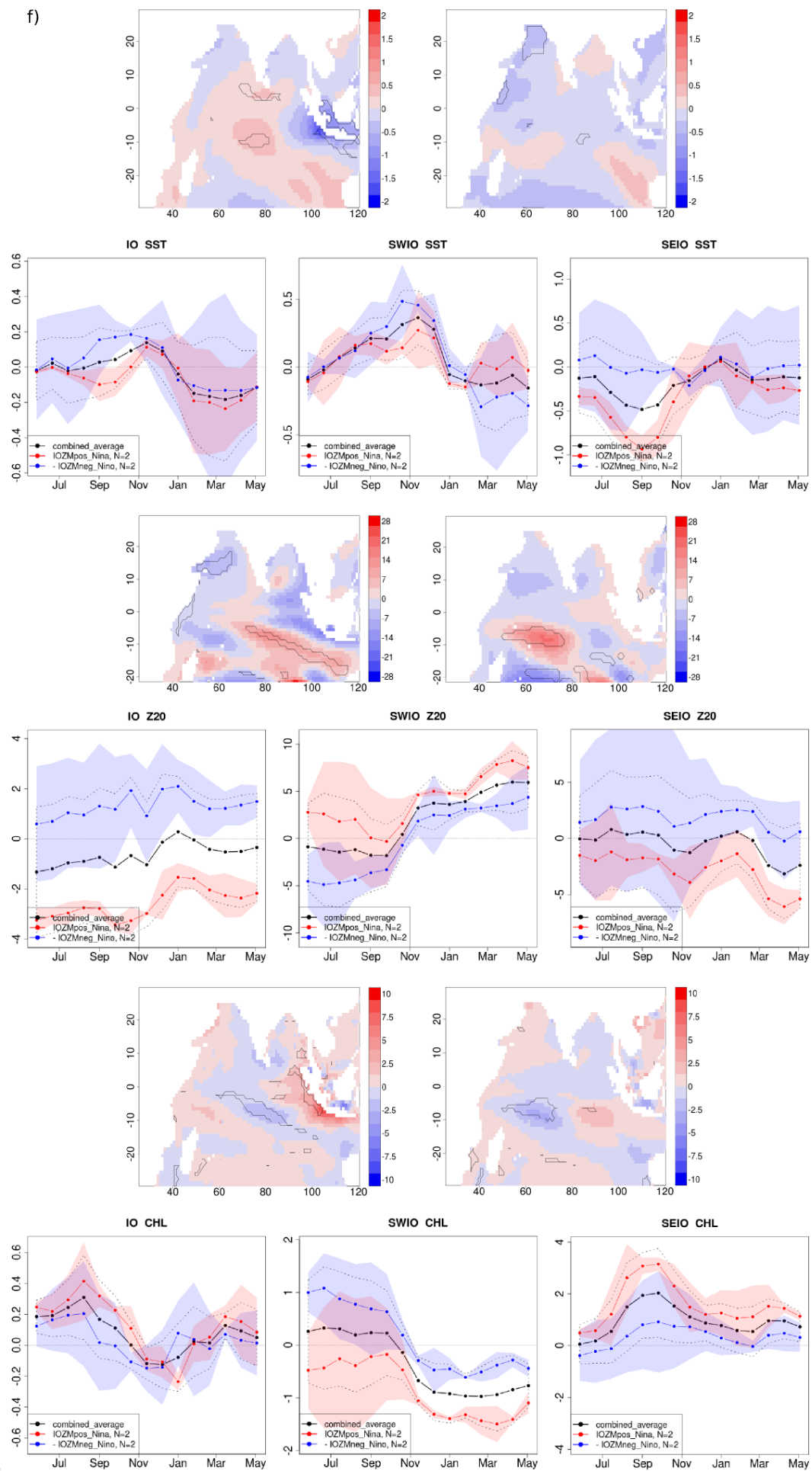


Figure 5. Composite plots of a) all IOZM, b) pure IOZM, c) all ENSO, d) pure ENSO, e) posIOZM - El Niño (negIOZM - La Niña), f) posIOZM - La Niña (negIOZM - El Niño) events: Maps of temporally-averaged anomalies (June-November left, December-May right) and underneath are spatially-averaged plots (June-May) for the three areas of interest (IO, SWIO, SEIO) for SST (top; °C), Z20 (centre; m) and CHL (bottom; mg/m²). Black contours on maps indicate areas where spatial anomalies are significantly different from zero (Student's t-test; $p < 0.05$). Black line and thin dashed envelope on line plots represent average anomalies $\pm$ standard deviation of all events $((\text{positive} - \text{negative})/2)$; red solid line and envelope are 'positive' event average anomalies $\pm$ standard deviation; same for blue, except they represent 'negative' event anomalies.

Linear Regressions

Results of the GLS regressions are summarized in Table 3. As the IOZM index is derived from SST in a defined Indian Ocean area (albeit a relatively small area), it is not independent of Indian Ocean SSTs and therefore not included in regressions of these. Thermocline depths from the entire IO basin display a bimodal distribution and have not been included in regression results, as they would violate the assumption of normality. Histograms, normal probability plots and residual plots used to judge normality and homoscedasticity are provided in Appendix A (Figure A1).

Using a significance level of $\alpha = 0.05$ (t-test; Pinheiro and Bates, 2000), the linear regressions using GLS (Table 3) showed that monthly SST anomalies are significantly related to ENSO in the SWIO, SEIO and entire IO areas. Z20 anomalies are significantly related to IOZM and an ENSO-IOZM interaction factor in the SEIO region. Neither climate index provides a significant relationship with Z20 in the SWIO, although the IOZM index was marginally non-significant ($p = 0.079$). IO basin CHL is positively related to IOZM, but negatively related to ENSO. SEIO CHL is related only to IOZM (positively), while in the SWIO region there is no significant relationship with either of the two indices (Table 3).

Table 3. Results of linear regressions fitted by GLS, allowing for autocorrelated errors using autoregressive (AR) models. Models fitted for variables SST, CHL and Z20 in regions Indian Ocean (IO), southwest and southeast Indian Ocean (SWIO, SEIO respectively). Bold values are estimated coefficients, while below them in normal font are associated p-values (calculated from t-statistic). If Phi2 has a value, an AR2 model was used as opposed to an AR1 when only Phi1 has an estimated coefficient. Coefficient estimates are in °C, mg/m² and m respectively. See Methods for details.

Model Formula	Coefficients and p-values				Estimated AR Coefficients	
	Intercept	IOZM	ENSO	IOZM* NINO	Phi1	Phi2
$SST.IO_t = \beta_1 * ENSO_{t-6} + \epsilon_t$	25.599 <0.0001	-	0.077 <0.0001	-	0.884	-
$SST.SWIO_t = \beta_1 * ENSO_{t-2} + \epsilon_t$	27.724 <0.0001	-	0.158 <0.0001	-	0.820	-
$SST.SEIO_t = \beta_1 * ENSO_{t-8} + \epsilon_t$	28.567 <0.0001	-	0.082 0.007	-	1.219	-0.356
$Z20.SWIO_t = \beta_1 * IOZM_{t-9} + \beta_2 * ENSO_{t-5} + \epsilon_t$	116.769 <0.0001	0.346 0.079	0.233 0.452	-	1.438	-0.490
$Z20.SEIO_t = \beta_1 * IOZM_{t-1} + \beta_2 * ENSO_{t+1} + \beta_3 * (IOZM_{t-1} * ENSO_{t+1}) + \epsilon_t$	124.601 <0.0001	-0.944 <0.0001	-0.287 0.320	-0.265 0.040	1.048	-0.220
$Chl.IO_t = \beta_1 * IOZM_{t+1} + \beta_2 * ENSO_{t-6} + \epsilon_t$	17.387 <0.0001	0.050 <0.0001	-0.055 0.002	-	0.852	-
$Chl.SWIO_t = \beta_1 * IOZM_{t-6} + \beta_2 * ENSO_{t-2} + \epsilon_t$	17.422 <0.0001	-0.027 0.453	-0.076 0.173	-	1.420	-0.490
$Chl.SEIO_t = \beta_1 * IOZM_{t-1} + \epsilon_t$	18.727 <0.0001	0.384 <0.0001	-	-	1.339	-0.441

As mentioned in the Methods section, additional 'regular' linear regressions were performed on the same model formulae. These regressions assume no correlation structure among residuals when estimating coefficients and calculating their p-values. Their results are summarised in Table A1 of Appendix A, but in summary, all coefficients listed in Table 3 were of the same sign, but greater (further from 0) and highly significant ($p < 0.01$). In addition, the regular regression for SEIO CHL suggested a significant positive ENSO term unlike its GLS counterpart.

Discussion

Use of Hindcast Simulations

Investigation of long-term marine hydrographic and biological variability is largely hampered by a lack of historical sample coverage in space and time, especially in oceanic environments far removed from human populations and popular shipping routes. Although impressive progress has been made to interpolate the gaps and maximise the value of existing in situ data, the coverage needed to meaningfully

address basin-scale dynamics was often lacking up until the advent of high-quality remotely-sensed measurements (e.g. 1981 for SST; McClain et al., 1985; arguably September 1997 for chlorophyll; Behrenfeld et al., 2006). Although largely overcoming the problem of spatial and temporal resolution, remote sensors can not penetrate the depths of the oceans and thus lack a three-dimensional perspective of the variables they measure. For example satellites sensing chlorophyll-a only estimate photosynthetic pigment concentrations for the first attenuation length (or penetration depth; Gordon and McCluney, 1975) thereby missing a significant proportion of chlorophyll biomass, especially in regions with deep chlorophyll maxima (DCM; Kirk, 1994). In recent years, limiting in situ data coverage (up to the present for many biogeochemical, biological and below-surface hydrographic variables) are increasingly being filled with hindcasts from rapidly-improving modelling efforts (e.g. Aumont et al., 2008; Rodgers et al., 2008; Maury, 2010). Assuming that the models are simulating dynamics of interest with sufficient accuracy, the advantage of working with their outputs is a complete (often 3-dimensional) and measurement-error-free variable field with spatial and temporal resolutions that are growing with the exponential rise in computing capabilities.

Interpretations of results here do need to be made with consideration of uncertainties in the accuracy of the model outputs. Considerable effort has been spent on the validation of variables from NEMO-PISCES outputs, including temperature and chlorophyll fields used here: Compared to in situ datasets, the model accurately reproduces oceanic spatio-temporal dynamics in tropical regions, including those of sea level height, surface currents, surface temperatures and vertical thermal structures (e.g. Vialard et al., 2001; Lengaigne et al., 2003; Faure, 2007). Although the limited overlap between model outputs (1958-2001) and SeaWiFS data (September 1997 onwards) makes a comprehensive comparison difficult, investigations have suggested good agreement between the two: Focusing on the Seychelles-Chagos thermocline ridge region, Resplandy et al. (2009) shows that a chlorophyll time-series from the model (integrated over the optical depth) resolves intra-seasonal, seasonal and interannual changes well, as compared to SeaWiFS. Comparing surface chlorophyll dynamics throughout the Indian Ocean, Koné et al. (2009) show how the isolation of regions according to their bloom characteristics (taking into account both timing and accumulated chlorophyll during the blooms), corresponds well with the results from SeaWiFS, despite different climatological

periods used. The areas where differences are most notable, are the north-western parts of the Arabian Sea and a region either side of the southern half of Madagascar. The authors also point out that the model under-estimates extreme chlorophyll values close to the coastline, most notably in the Arabian Sea.

The OPA circulation model has been used in many applications, including the investigation of ENSO dynamics in the Pacific Ocean (e.g. Lengaigne et al., 2004; Cravatte et al., 2007) and tidal mixing effects on surface waters in the Indonesian archipelago (Koch-Larrouy et al., 2009). The coupled bio-physical version used here has been used to study phytoplankton-induced warming of surface waters and its interplay with ENSO (Lengaigne et al., 2007), as well as long-term biogeochemical changes in the eastern Pacific (Rodgers et al., 2008).

In this study, comparison of global, basin-scale and regional SST time-series with HadISST1 data, provided remarkably good correlations (Figure 1). Although absolute values (mean states) do not correspond perfectly, the seasonal variability and relative interannual changes are captured well by the model, allowing confidence in its use for investigating these dynamics. The lowest correlation of 0.77 for the surface temperature index of EEIO is likely due to the fact that the EEIO box straddles the land masses of Sumatra and Java, while the spatial resolution of the model is unable to accurately reproduce finer scale coastal dynamics. Therefore it likely misses some variability in the coastal waters adjacent to these islands. Certain short-duration events that the model seems to lack (compared to the HadISST1 time-series) might be a result of this restriction. Despite the lower correlation, most of the prominent interannual changes and also the decadal changes are captured by the model.

ENSO Control on Global Temperature and Chlorophyll

Globally averaged surface temperature and chlorophyll fields suggest a strong influence of ENSO dynamics on permanently stratified waters (Figure 2). ENSO is acknowledged to be the dominant mode affecting global interannual sea surface temperatures (Schott et al., 2009) and is especially linked to temperature perturbations in tropical latitudes (e.g. Tourre and White, 1995). Global chlorophyll concentrations have also previously been linked to ENSO variability: Using EOF analyses on SeaWiFS data, Yoder and Kennelly (2003) suggest ENSO as the main source of interannual variability in global chlorophyll concentrations. Similar to results

obtained here, but with data from a shorter (almost 10 year) SeaWiFS period, Behrenfeld et al. (2006) show that primary productivity in permanently stratified waters is correlated to a multivariate ENSO index with a coefficient of 0.77. The highly significant correlations between Niño-3 and globally averaged surface temperature and chlorophyll concentrations in permanently stratified waters (Figure 2), are therefore not so surprising. The strength of these impacts is undoubtedly partially due to the dominant size of the tropical Pacific area (as opposed to that of the Atlantic or Indian ocean) and the fact that ENSO has such a strong basin-wide expression over this large tropical ocean. ENSO signals are additionally well known in the Indian Ocean (e.g. Tourre and White, 1995; Reason et al., 2000) however, and teleconnections with the Atlantic have also been demonstrated (Enfield and Mayer, 1997).

Behrenfeld et al. (2006) furthermore point out that permanently stratified waters largely drive interannual changes in total global marine primary productivity. Thus despite inter-regional differences in response to ENSO, and variability amongst events, results here and those of Behrenfeld et al. (2006), suggest that ENSO variability explains a large part of fluctuations in global marine productivity. Understanding global ENSO effects and gaining predictability of the response of ENSO (and other dominant climate modes) to global warming, is therefore critical to considerations of future regional ecosystem (and fishery) productivity, as well as the long-term response of the biological carbon pump (e.g. De La Rocha and Passow, 2007).

ENSO versus IOZM Influence on Indian Ocean SST, Thermocline Depth and Chlorophyll

From the above, it is evident that studies of interannual environmental variability in tropical oceans require careful consideration of potential ENSO impacts. However an additional tropical coupled mode impacts interannual surface dynamics in the Indian Ocean (e.g. Saji et al., 1999, Webster et al., 1999, Murtugudde et al., 1999) and beyond (e.g. Saji and Yamagata, 2003b; Yamagata et al., 2004; Meyers et al., 2007) and is referred to here as the Indian Ocean Zonal Mode (IOZM). Basin-wide as well as SWIO average surface temperatures are positively related to ENSO variability (Table 1). This ENSO-related control of interannual surface temperatures is confirmed in the dominant EOF mode (Figure 3a), which is commonly described as a basin-wide warming of Indian Ocean surface temperatures following El Niño events (e.g. Klein et

al., 1999, Murtugudde and Busalacchi, 1999). The IOZM index has a significant negative correlation with Indian Ocean SST (Table 1), which means that the two tropical climate modes have opposing effects on average IO surface temperature when they co-occur with the same sign (as evident in the well-documented case of 1997). Peak IOZM cooling (warming) precedes ENSO warming (cooling) by about four months however. When comparing Indian Ocean temperatures to the IOZM index, one must acknowledge that the two variables are not completely independent of one another, as the IOZM index consists of EEIO surface temperatures. This problem will remain as long as IOZM indices are derived from surface temperatures. The EEIO represents only a small fraction of Indian Ocean waters and furthermore SSTs in this area are driven largely by local upwelling dynamics (Annamalai et al., 2003), hence one can argue that SSTs are relatively independent of adjacent IO basin SSTs. Nonetheless, results of IOZM-IO SST comparisons need to be treated with caution.

Unlike surface temperature, interannual IO chlorophyll concentrations and Z20 are more highly correlated to IOZM variability than to ENSO (Table 1). Similar to SST, the two climatic modes have opposing effects on average IO chlorophyll, though with a temporal separation of about six months. The highest IOZM-IO chlorophyll correlation was found with the climate index lagging ~one month behind CHL, which raises a question over the processes underlying this relationship. Tropical waters are characterised by deep chlorophyll maxima, made up of low-light adapted communities closely associated with nutrients diffusing across the pycnocline (Pollehne et al., 1993), whose growth is therefore likely dependent on thermocline dynamics that typically precede expressions of surface temperature in the tropics (e.g. Annamalai et al., 2003; Zelle et al., 2004; Rao and Behera, 2005). Such reasoning is supported by the fact that the highest correlation between the IOZM index and Z20 was obtained by lagging the surface index behind Z20 by approximately two months.

As expected from previous results (e.g. Murtugudde et al., 1999, Rao and Behera, 2005; Wiggert et al., 2009), anomalous upwelling in the EEIO is associated with a shallower thermocline and higher chlorophyll concentrations in the SEIO region, but a deeper thermocline and lower CHL in the SWIO region. Thus there is clearly a zonal pattern across the equatorial regions for these variables, although the temporal peaks of the respective poles are separated by a 3-5 month lag. Evidence of a similar zonal effect of ENSO on Indian Ocean thermocline dynamics has been shown (e.g. Xie et al., 2002), which help explain why the principle component time-series of the dipolar EOF

modes of Z20 and integrated chlorophyll significantly correlate with both IOZM and ENSO (Figure 3). These dipole-like EOF modes account for roughly a third of interannual Indian Ocean variability for both variables. The regions around their east and west poles revealed high interannual variance across multiple environmental variables (not shown), which prompted the initial selection of the SWIO and SEIO boxes for closer investigation.

In stratified tropical waters, thermocline (or pycnocline) depth is commonly linked to phytoplankton productivity (e.g. Murtugudde et al., 1999; Wilson and Adamec, 2002), which explains the similarities between thermocline and chlorophyll EOFs (Figure 3). A shoaling thermocline indicates upwelling activity, which directly infuses nutrient-rich waters into surface layers. Even in the absence of upwelling, a shallower-than-normal pycnocline would bring greater amounts of nutrient-rich subsurface waters into the euphotic zone and within reach of deep phytoplankton communities. Thermocline depth is therefore often strongly (negatively) correlated to phytoplankton biomass and Indian Ocean waters north of about 20°S are dominated by such a negative correlation (Wilson and Adamec, 2002). The SWIO displays an especially strong CHL-Z20 correlation ($r=-0.87$), confirming that thermocline dynamics largely drive productivity changes in this region. Regions do exist where this chlorophyll-thermocline relationship breaks down however, such as the southeastern IO between 10-30°S (Wilson and Adamec, 2002) and oligotrophic gyres (see e.g. McClain et al., 2004), which are presumably responsible for the substantially lower basin-wide CHL-Z20 correlation ($r=-0.51$).

Interannual subsurface IO variability has been related to both ENSO (e.g. Chambers et al., 1999, Xie et al., 2002) and IOZM (Rao et al., 2002, Vinayachandran et al., 2002, Rao and Behera, 2005) and is largely driven by off-equatorial Rossby Waves (Masumoto and Meyers, 1998) and Intermonsoon Wyrтки Jet variability (Schott et al., 2009). Much conjecture exists over the dependence or independence of IOZM and ENSO events (e.g. Allan et al., 2001, Dommenges and Latif, 2002; Hastenrath, 2002; Murtugudde et al., 2003; Yamagata et al., 2003). While the aim of this investigation was not to address this point, previous evidence (e.g. Allan et al., 2001; Yamagata et al., 2003) and results obtained here point to the fact that IOZM and ENSO dynamics are to some degree correlated. As a result, EOF analyses do not successfully separate the two climatic modes (Figure 3). However they do summarize the most important

spatio-temporal patterns of interannual variability, and here demonstrate the importance of the zonal dipole pattern in thermocline and chlorophyll dynamics. This is the first time (as far as the author is aware) that this dominant dipole mode in interannual CHL anomalies is documented. In their global EOF analysis of the first four years of SeaWiFS data, Yoder and Kennelly (2003) do obtain similar zonal patterns in two dominant interannual EOFs, however they attribute these patterns to ENSO variability.

Composite Analyses and Linear Regressions

As referred to in the Methods, thresholds used to identify ENSO and IOZM event years are fairly sensitive and more/weaker events are distinguished (Table 2) relative to similar time-periods in some studies (e.g. Trenberth, 1997; Saji et al., 1999; Saji and Yamagata, 2003a, b; Meyers et al., 2007). However, when making comparisons between 'pure' and co-occurring events, such heightened sensitivity is an advantage: A 'weak event', which nonetheless produces regional or basin-wide SST anomalies and thus potentially influences near and distant coupled ocean-atmosphere dynamics, is more likely to be identified and one can thus have greater confidence in the designation of 'pure events'. In addition, composite samples are made up of greater rather than smaller sample sizes in this way, and are therefore more robust to peculiarities of certain years. To guard against the false inclusion of a year (with SST structures unrelated to ENSO/IOZM), averaged June-November and December-May spatial SST anomalies were visually checked for regionally coherent and representative signals in every identified year. A similarly stringent method to isolate pure events was recently used by Song et al. (2007), and not surprisingly, results agree well between the two studies.

Average June-November IOZM event anomalies (Figure 5a, b) display the typical zonal surface temperature gradients that characterise such events (e.g. Saji et al., 1999). Northeast monsoon winds in boreal winter, overcome the anomalous southeasterly winds of positive events and cold eastern SST anomalies rapidly dissipate as a result (e.g. Meyers et al., 2007), congruent with the disappearance of strong anomalies close to the Indonesian coast in DJFMAM composites. Although present in pure IOZM events (Figure 5b), western anomalies are not as prominent and do not spread and intensify during the subsequent season, as they do during co-occurring ENSO events (Figure 5e). Further comparison with pure ENSO events (Figure 5d) suggests that

widespread warm (cool) surface temperature anomalies and their growth to a basin-wide expression, are largely a signal of ENSO. These observations agree with recent results that attribute the western (and subsequent basin-wide) IO warming mainly to ENSO control, while the upwelling and associated anomalies in the eastern IO are seen as a characteristic feature of IOZM events (e.g. Chowdary and Gnanaseelan, 2007; Drbohlav et al., 2007). Although the non-independent nature of the IOZM index precluded it from regressions of SST, the highly significant positive effect of ENSO on average Indian Ocean and also SWIO SSTs was demonstrated, with a lesser though still significant positive effect on SEIO surface temperatures (Table 3). Composite analyses here (Figure 5c, d) and previously (e.g. Song et al., 2007) show the almost basin-wide warming (cooling) that develops during El Niño (La Niña) events, which drives these positive correlations.

Meyers et al. (2007) prepared similar June-November spatial SST anomaly composites for different events and comparisons can be made with their (Figure 3) results, which stem from the 1876-1999 HadISST1 dataset (Rayner et al., 2003). Such a visual comparison reveals good agreement between the two studies, even though 'positive' and 'negative' anomalies have been combined here and the classification of events compares less well. As their anomalies are often not of the same intensity (and/or duration), negative ENSO/IOZM events are not as straightforward to identify as are positive events (Wiggert et al., 2009). This point is demonstrated by the fact that about 70% of positive events identified here coincide with those of Meyers et al. (2007), while less than half of negative events are in agreement (during the overlapping time-period). The relative difficulty of confidently identifying negative events, together with the fact that they are regarded as less extreme in nature, has presumably led to some authors excluding negative events in their analyses (e.g. Annamalai et al., 2003, Chowdary and Gnanaseelan, 2007; Song et al., 2007).

Using a 250-yr simulation of the GFDL coupled climate model, Song et al. (2007) compare SST, precipitation, surface wind, upper ocean heat content and sea level pressure anomalies amongst pure posIOZM, pure El Niño and co-occurring posIOZM - El Niño events. Good agreement between their SST results and those shown here are likely due to the relatively stringent criteria used to define pure events in both studies. Song et al. (2007) suggest that posIOZM and El Niño interact linearly in their effect on IO SST, with co-occurring events producing anomaly patterns similar to what one

would expect by superimposing pure posIOZM and pure El Niño events. Such an hypothesis agrees quite well with composites presented here, except that western SST anomalies seem enhanced in co-occurring events, as has been noted previously (e.g. Meyers et al., 2007). These amplified western SST anomalies, especially noticeable in the Seychelles-Chagos thermocline ridge area, are due to Rossby Wave activity (and thus ocean dynamics) driven by zonal wind anomalies in the south Indian Ocean, as opposed to mainly latent heat fluxes and short-wave radiation during pure ENSO warming/cooling (Chowdary and Gnanaseelan, 2007).

Besides the characteristic SST pattern during IOZM events, thermocline depth and chlorophyll concentrations also show a zonal anomaly pattern. A positive event results in shallow thermocline and high chlorophyll anomalies in the east (Figure 5a, b), while most western tropical areas display a deeper thermocline and lower chlorophyll concentrations. Although the eastern anomalies do not disintegrate as rapidly as those of surface temperatures, an obvious feature is the erosion of their signal along equatorial regions during the subsequent DJFMAM season. This signal is largely due to positive events and is caused by the return of the Intermonsoon Wyrтки Jet in boreal spring, following its suppression during the previous (fall) Intermonsoon by the anomalous equatorial easterly winds (Murtugudde et al., 1999). Under 'normal' conditions, the semi-annual Wyrтки Jet maintains a relatively unproductive warm pool in the eastern IO via semi-annual advection of warm central IO surface waters towards Sumatra, which deepen the thermocline and suppress phytoplankton productivity there (Wiggert et al., 2006). Thus the normal dynamics of the Wyrтки Jet, and perturbations thereof, play a crucial role in equatorial biogeochemistry (Wiggert et al., 2006), as well as in the development of IOZM anomalies (e.g. Chowdary and Gnanaseelan, 2007).

Although not investigated previously (as far as the author is aware), the relatively unusual co-occurrence of posIOZM - La Niña and negIOZM - El Niño have been noted (e.g. Saji et al., 1999; Saji and Yamagata, 2003a, b). Unfortunately the low sample size does not allow for a consistent picture from these four years (Figure 5e). The lack of consistency between the two groups of events in fact suggests that perhaps these events do not mirror each other well and should be dealt with in separate composites in future. What one can tell from these composites is that anomalies seem to resemble pure IOZM events more than they do pure ENSO events, and additionally,

that there is a lack of the basin-wide SST warming (cooling) signal that is seen in DJFMAM in co-occurring posIOZM - El Niño (negIOZM - La Niña) events.

Not surprisingly, the IOZM index is highly significant in predicting eastern chlorophyll and thermocline anomalies (Table 3), which result from the anomalous upwelling dynamics associated to IOZM events. The large CHL increases (decreases) during positive (negative) IOZM events, mainly seen in eastern parts of the basin, also translate to a significant positive effect on average Indian Ocean chlorophyll (Table3), despite the negative (positive) anomalies seen in central and western regions (Figure 5a, b, e, f). As alluded to earlier, ENSO seems to have a negative effect on average Indian Ocean chlorophyll, which is confirmed by its significant negative coefficient. These results suggest that ENSO and IOZM effects on CHL counteract one another at the average basin scale, which is interesting as their events commonly co-occur as in 1997 or 2006. Using these latter two events, Wiggert et al. (2009) estimated changes in primary productivity and suggested that basin-scale Indian Ocean productivity may change little during positive IOZM years, as eastern positive and western negative anomalies largely counterbalance one another.

An obvious feature in many of the composite plots is a patch of enhanced anomalies in the central STIO, which intensifies and moves further west by the subsequent DJFMAM season (Figure 5). Noticeable mainly in the subsurface variables of thermocline depth and vertically-integrated chlorophyll concentrations, these anomalies are driven by interannual variability in westward-propagating Rossby Wave activity (Masumoto and Meyers, 1998). Fuelled by wind stress curl, the waves propagate from the southeastern IO westwards, affecting SST expressions in their path as they reach the Seychelles-Chagos thermocline ridge (Xie et al., 2002; Rao and Behera 2005). Rao and Behera (2005) provide evidence that north of 10°S, these waves are dominantly forced by IOZM dynamics, while in the non-IOZM season (January-June) and south of this, ENSO teleconnections dominantly drive these waves. Recently however, Chowdary and Gnanaseelan (2007) suggested that weaker wind anomalies associated with pure El Niños do not excite downwelling Rossby Waves, as compared to positive IOZM events, which is congruent with composite results shown here: Pure ENSO composites lack the pronounced STIO anomaly expression (Figure 5d), relative to composites including IOZM events (Figure 5a, b, e, f). Anomalies of certain pure ENSO years do show similar characteristic Rossby Wave activity (not shown), however these

are not consistent amongst different events and are averaged out in composite plots. Therefore the prominent Rossby Wave signals seen in the Seychelles-Chagos ridge area in thermocline depth, CHL and to a lesser degree SST, which propagate westwards and intensify in the second season (DJFMAM), seem to be a consistent expression of IOZM, but not of ENSO. These predictable interannual anomalies have their most intense expression in the central and western STIO during austral summer to fall (Figure 5; Rao and Behera, 2005) and likely impact the ecosystem and forage-availability of important fishery species in the surrounding waters (e.g. yellowfin and skipjack tuna; Fonteneau, 1997).

Unexpectedly, linear regressions did not indicate significant effects for ENSO or IOZM indices on SWIO chlorophyll and thermocline depths (Table 3), despite the Rossby Wave-associated anomalies seen in IOZM composites suggesting otherwise (Figure 5a, b, e, f). The IOZM coefficient was marginally non-significant for Z20, which could be caused by various factors: As noted above, the Rossby Waves responsible for SWIO anomalies in the composite plots are seasonally phase-locked. Outside of the season of their peak expression, factors unrelated to the climate modes may control these variables, necessitating a seasonal stratification to bring the IOZM (or ENSO) variability to the fore. In addition, seasonal and intra-seasonal perturbations to the thermocline structure play a significant role in the biogeochemical variability of this region (e.g. Resplandy et al., 2009), which would create added noise in the signal and thereby diminish significance of interannual effects being investigated.

Rao and Behera (2005) compared IO sea surface height anomalies (as a proxy for thermocline depth) for pure posIOZM and pure El Niño composites, using the Simple Ocean Data Assimilation product (SODA; Carton et al., 2000). Although their monthly anomalies are difficult to compare to semi-annual anomalies here, the pure IOZM anomalies qualitatively agree well in most regards. A stronger, more coherent expression of STIO anomalies seems evident in their July, September, November plots than seen in June-November composites here (Figure 5b), while the model outputs perhaps have an exaggerated positive anomaly off the west coast of Australia in December-May, relative to their plots of January, March and May. Their pure El Niño July, September and November composites display more negative anomalies, especially in the northern hemisphere, relative to corresponding June-November composites shown here, although similar features are recognisable (Figure 5d).

January, March, May pure El Niño plots of theirs show the development of a prominent positive anomaly centered at about 15°S in the STIO and propagating westwards. Pure ENSO December-May average anomalies presented here lack such a prominent Rossby Wave signal. This discrepancy may be partly due to the fact that Rao and Behera (2005) include two years (1976, 1991) in their pure El Niño group, which were found to be weak posIOZM events in this study. Chowdary and Gnanaseelan (2007) use the HadISST1 and SODA product to construct SST and isopycnal depth anomaly composites respectively, for both pure and co-occurring El Niño and IOZM events. Those results agree well with corresponding composites presented here, undoubtedly due to the similar classification of event years. As mentioned above however, the conclusion here is not that pure ENSO events do not excite Rossby Wave activity (as in Chowdary and Gnanaseelan, 2007), but rather that they are not consistent amongst ENSO-only events, unlike in those of IOZM.

Wiggert et al. (2009) investigated SeaWiFS data together with physical fields, to characterise chlorophyll signatures from the last two positive IOZM events (1997 and 2006) and interpret them in view of underlying mechanisms. Both events coincided with an El Niño event in the Pacific, thus representing one of the possible ENSO/IOZM combinations explored and presented in this study. Congruent with composites presented here, they document positive anomalous chlorophyll concentrations in the eastern IO and negative anomalies in western parts of the basin. The consistencies noted between their two events are visible in JJASON posIOZM - El Niño (negIOZM - La Niña) composites, including negative anomalies off Somalia, the west coast and around the base of the Indian subcontinent, as well as positive anomalies in the south-eastern Bay of Bengal (Figure 5e; Wiggert et al., 2009). The 1997 event was the strongest IOZM event since at least 1961 and Wiggert et al. (2009) show the chlorophyll anomalies to be notably stronger, more extensive and more persistent than in 2006. In 1997, the boreal fall Wyrтки Jet collapsed completely and even reversed, allowing the development of a cold tongue along the equator. This equatorial surface anomaly was fed by advection of upwelled water from the east, as well as anomalous equatorial upwelling (Murtugudde et al., 1999), and fuelled positive chlorophyll anomalies that extended as far west as 65°E (Figure 10 in Wiggert et al., 2009). Additionally, the 1997 event displayed negative chlorophyll anomalies throughout the Arabian Sea, whereas in 2006 anomalies in this area were more heterogeneous (Wiggert et al., 2009). In agreement with their results, CHL anomalies

clearly reveal a westward-extending tongue of cool, chlorophyll-rich water along the equator in 1997 (Figure A2, Appendix A). Also, negative anomalies are evident throughout the Arabian Sea in 1997, whereas in some El Niño-posIOZM years such as 1963, patches of positive CHL anomalies are additionally present (not shown).

Although Wiggert et al. (2009) show much of the western and southern Indian Ocean to exhibit below-normal primary productivity, the notable Rossby Wave-associated low-chlorophyll anomalies of the STIO do not seem to be evident in their results. This discrepancy is likely due to a combination of factors: Firstly, the model output nutricline depth is slightly underestimated, and seasonal primary production variability is exaggerated in the Seychelles-Chagos thermocline ridge area, relative to in situ and satellite data (O. Aumont, personal comment). Therefore the interannual chlorophyll response may be exaggerated in this region. Secondly however, a collection of evidence suggests that SeaWiFS is not sensing these types of integrated chlorophyll dynamics proficiently. Remotely sensed sea-level anomalies (e.g. Rao and Behera, 2005; Wiggert et al., 2009) and model outputs (e.g. Hermes and Reaon, 2008; Figure 5a, b, e, f), suggest that deeper-than-normal thermocline depths in the western STIO are associated with positive IOZM events. Coincident shipboard data from this area during January-February 2007, confirmed that there was indeed an unusually deep thermocline, accompanied by a suppressed nutricline and a deeper-than-normal (by ~60 m) DCM at ~90 m (Wiggert et al., 2009). The depth of this DCM is well below the penetration depth of remote sensors in open ocean waters (20-30 m; Gordon and McCluney 1975) and thus would be overlooked in SeaWiFS estimates of chlorophyll concentration. If the climatological DCM (~30 m according to Wiggert et al., 2009) is normally adequately measured by SeaWiFS, this line of reasoning seems to counter the argument however, as the anomalously deep DCM associated with a posIOZM event would then be expected to result in a (considerably) depressed chlorophyll anomaly, with the remote sensors measuring only the chlorophyll-deplete surface waters above the DCM. Perhaps the climatological state, when the DCM is at or just below the limit of the SeaWiFS penetration depth, may not be adequately sensed to be able to pick up the chlorophyll anomalies that must accompany a DCM that is ~60 m deeper than normal. Whatever the reason, these heightened anomaly structures driven by Rossby wave activity, are seemingly not sensed by SeaWiFS, even though they are supported by model and in situ evidence.

Chlorophyll responses to propagating Rossby Waves have been demonstrated in satellite fields (Cipollini et al., 2001), although Dandonneau et al. (2003) suggest that such chlorophyll anomalies in subtropical gyres are likely surface accumulations of non-chlorophyllous organic particulates and not enhanced phytoplankton productivity, as these positive 'chlorophyll tracks' are associated with warm convergent (downwelling) fields, rather than the expected cooler divergent (upwelling) areas. This evidence, together with the apparent failure of SeaWiFS to sense the western STIO anomalies, highlights the usefulness of using three-dimensional model outputs. Additionally, it questions whether regular SeaWiFS products are appropriate to study phytoplankton responses to dynamical forcing within oligotrophic regions (e.g. McClain et al., 2004; White et al., 2004), where the majority of water-column chlorophyll can be substantially deeper than the sensor penetration depth. There are methods available for estimating the vertical chlorophyll profile, and thereby integrated water-column concentrations from surface values (Morel and Berthon 1989; Uitz et al., 2006), which together with accurate bio-physical models, might provide better tools to use in such regions.

Composite analyses are unfortunately absolutely dependent on the component years included in their design and discrepancies amongst studies are likely due to the groups of years chosen, rather than substantial differences amongst datasets. These discrepancies need to be addressed and a standardisation of event classification would be highly desirable. However ocean-atmosphere interactions and resultant climatic modes operate on a continual range rather than a binary on/off basis, and thus a clear undisputed list of events/non-events is highly unlikely. In this study, sensitive thresholds were chosen, but they were combined with a holistic inspection of SST anomalies to ensure representative regional or basin-wide structures were present. It is, after all, such large-scale SST anomalies that drive ocean-atmosphere feedbacks and their presence, even if weaker than the most extreme events, likely cause perturbations to physical and biological systems, both locally and distant.

Conclusion

Over recent decades, numerical models have played a great part in the elucidation of atmosphere-ocean interactions and their impact within the Indian Ocean. Here hindcasts from the coupled bio-physical ocean model, NEMO-PISCES, have allowed investigation of simple, large-scale patterns that characterise ENSO and IOZM control

on surface temperature, thermocline depth and integrated chlorophyll in the Indian Ocean. In acknowledgement that the complexity of phytoplankton dynamics will not be perfectly resolved in these numerical models, interpretations of chlorophyll anomalies have been limited to broad regional patterns and are supported by explanations of the mechanisms driving them.

ENSO is shown to largely drive average surface temperatures and integrated chlorophyll concentrations in globally stratified waters (Figure 2). Although difficult to tease apart, within the Indian Ocean, the often-co-occurring IOZM seems to have greater effects on interannual thermocline depth and chlorophyll concentrations (Table 1, 3). In stratified waters, as dominate much of the Indian Ocean, the pycnocline (as estimated by the thermocline) is elemental in limiting nutrients from reaching sun-bathed surface waters. As a result, the strong IOZM effects on thermocline depths via Rossby Waves, Kelvin Waves and changes in Wyrtki Jet flow, translate to similar patterns in chlorophyll anomalies, with a shallower thermocline depth resulting in greater chlorophyll concentrations in most regions. It follows that the dominant interannual mode of variability in thermocline depths, a zonal dipole across equatorial latitudes, is almost mirrored by the dominant mode in depth-integrated chlorophyll anomalies. This spatial dipole mode in interannual chlorophyll anomalies is significantly related to both IOZM and ENSO indices and has not (to the author's knowledge) been shown before.

Composite results confirm distinct anomaly patterns for pure IOZM, pure ENSO and co-occurring events, which has important implications for predicting localised physical or ecosystem responses to these events. Such differences need to be recognised and taken into account during interpretation or description of interannual variability within the Indian Ocean. As with EOFs, CHL and Z20 anomaly composites mirror each other remarkably well in most regions. Two main features of opposite anomalies consistently characterise positive (and negative) IOZM events in thermocline depth and chlorophyll: High (low) chlorophyll and shallow (deep) thermocline anomalies hug the western coast of Indonesia, while low (high) chlorophyll and deep (shallow) anomalies are seen over the Seychelles-Chagos thermocline ridge region, peaking there 4-6 months later. Pure ENSO events do not produce the same prominent anomalies in these two areas. Such anomalies (or the lack thereof) likely have important implications for regional ocean-atmosphere dynamics, marine productivity, and

thereby ecosystem effects, in their respective areas. The SWIO is an important fishing region in the Indian Ocean and quantification of water-column productivity, and how this changes during an IOZM event would be very useful in inferring ecosystem and fisheries impacts. Such studies would also be useful to compare to concomitant SeaWiFS data, allowing evaluation of the effectiveness of SeaWiFS in sensing such changes in productivity.

Results presented here compare well to previous studies based on a range of data sources, and are perhaps most valuable (and novel) in their description of large-scale spatio-temporal phytoplankton responses to interannual climatic extremes. Perturbations at this basal trophic level directly affect the productivity of the entire ecosystem. Understanding climate controls on such perturbations is thus vital to understanding, predicting and managing their impact at higher trophic levels, many of which are valuable natural resources.

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References

- Abram, N.J., Gagan, M.K., Cole, J.E., Hantoro, W.S., Mudelsee, M., 2008. Recent intensification of tropical climate variability in the Indian Ocean. *Nature Geoscience* 1, 849-853.
- Aikake, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19, 716–723.
- Alexander, M.A., Bladé, I., Newman, M., Lanzante, J.R., Lau, N.C., Scott, J.D., 2002. The atmospheric bridge: The influence of ENSO teleconnections on air-sea interaction over the global oceans. *Journal of Climate* 15, 2205–2231.
- Allan, R.J., Chambers, D., Drosowsky, W., Hendon, H., Latif, M., Nicholls, N., Smith, I., Stone, R.C., Tourre, Y., 2001. Is there an Indian Ocean dipole and is it independent of the El Niño-Southern Oscillation? *CLIVAR Exchanges* 6, 18-22.
- Annamalai, H., Murtugudde, R., Potemra, J., Xie, S.P., Liu, P., Wang, B., 2003. Coupled dynamics over the Indian Ocean: spring initiation of the Zonal Mode. *Deep Sea Research Part II: Topical Studies in Oceanography* 50, 2305-2330.
- Aumont, O., Bopp, L., 2006. Globalizing results from ocean in situ iron fertilization studies. *Global Biogeochemical Cycles* 20, GB2017.
- Aumont, O., Bopp, L., Schulz, M., 2008. What does temporal variability in aeolian dust deposition contribute to sea-surface iron and chlorophyll distributions? *Geophysical Research Letters* 35, L07607.
- Bakun, A., 1996. Patterns in the ocean: Ocean processes and marine population dynamics. California Sea Grant College System, National Oceanic and Atmospheric Administration in cooperation with Centro de Investigaciones Biologicas del Noroeste, La Paz, Mexico.
- Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M., Boss, E.S., 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444, 752–755.
- Bjerknes, J., 1969. Atmospheric teleconnections from the equatorial Pacific. *Monthly Weather Review* 97, 163-172.
- Bonhommeau, S., Chassot, E., Rivot, E., 2008. Fluctuations in European eel (*Anguilla anguilla*) recruitment resulting from environmental changes in the Sargasso

Sea. Fisheries Oceanography 17, 32-44.

- Cai, W., Hendon, H.H., Meyers, G., 2005. Indian Ocean dipole-like variability in the CSIRO Mark 3 coupled climate model. *Journal of Climate* 18, 1449-1468.
- Carton, J.A., Chepurin, G., Cao, X., Giese, B., 2000. A simple ocean data assimilation analysis of the global upper ocean 1950-95. Part I: Methodology. *Journal of Physical Oceanography* 30, 294-309.
- Cermeño, P., Dutkiewicz, S., Harris, R.P., Follows, M., Schofield, O., Falkowski, P.G., 2008. The role of nutricline depth in regulating the ocean carbon cycle. *Proceedings of the National Academy of Sciences* 105, 20344-20349.
- Chambers, D.P., Tapley, B.D., Stewart, R.H., 1999. Anomalous warming in the Indian Ocean coincident with El Niño. *Journal of Geophysical Research* 104, 3035-3047.
- Chelton, D.B., 1984. Commentary: short-term climatic variability in the northeast Pacific Ocean, in: Pearcy, W. (Ed.), *The influence of ocean conditions on the production of salmonids in the North Pacific*. Oregon State University Press, Corvallis, Oregon, pp. 87-99.
- Chowdary, J.S., Gnanaseelan, C., 2007. Basin-wide warming of the Indian Ocean during El Niño and Indian Ocean dipole years. *International Journal of Climatology* 27, 1421-1438.
- Cipollini, P., Cromwell, D., Challenor, P.G., Raffaglio, S., 2001. Rossby waves detected in global ocean color data. *Geophysical Research Letters* 28, 323-326.
- Claustre, H., Morel, A., Hooker, S.B., Babin, M., Antoine, D., Oubelkheir, K., Bricaud, A., Leblanc, K., Quéguiner, B., Maritorena, S., 2002. Is desert dust making oligotrophic waters greener? *Geophysical Research Letters* 29, 107-1.
- Cravatte, S., Madec, G., Izumo, T., Menkes, C., Bozec, A., 2007. Progress in the 3-D circulation of the eastern equatorial Pacific in a climate ocean model. *Ocean Modelling* 17, 28-48.
- Dandonneau, Y., Vega, A., Loisel, H., du Penhoat, Y., Menkes, C., 2003. Oceanic Rossby Waves acting as a "hay rake" for ecosystem floating by-products. *Science* 302, 1548-1551.
- De La Rocha, C.L., Passow, U., 2007. Factors influencing the sinking of POC and the efficiency of the biological carbon pump. *Deep Sea Research Part II: Topical*

Studies in Oceanography 54, 639-658.

Dommenget, D., Latif, M., 2002. A Cautionary Note on the Interpretation of EOFs. *Journal of Climate* 15, 216-225.

Drbohlav, H.L., Gualdi, S., Navarra, A., 2007. A diagnostic study of the Indian Ocean dipole mode in El Niño and non El Niño years. *Journal of Climate* 20, 2961-2977.

Enfield, D.B., Mayer, D.A., 1997. Tropical Atlantic sea surface temperature variability and its relation to El Niño-Southern Oscillation. *Journal of Geophysical Research* 102, 929-945.

Faure, V., 2007. Validation of physical simulations: Outputs interpolations (No. 2), GLOBEC: Climate and Fishing Impacts on the Spatial Population Dynamics of Tunas. OCEANOMOD, GLOBEC.

Feng, M., Meyers, G., 2003. Interannual variability in the tropical Indian Ocean: a two-year time-scale of Indian Ocean Dipole. *Deep Sea Research Part II: Topical Studies in Oceanography* 50, 2263-2284.

Fiedler, P.C., 2002. Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. *Marine Ecology Progress Series* 244, 265-283.

Fonteneau, A., 1997. Atlas of tropical tuna fisheries. ORSTOM Editions, Paris.

Geider, R.J., MacIntyre, H.L., Kana, T.M., 1998. A dynamic regulatory model of phytoplanktonic acclimation to light, nutrients, and temperature. *Limnology and Oceanography* 43, 679-694.

Gordon, H.R., McCluney, W.R., 1975. Estimation of the depth of sunlight penetration in the sea for remote sensing. *Applied Optics* 14, 413-416.

Hannachi, A., Jolliffe, I.T., Stephenson, D.B., 2007. Empirical orthogonal functions and related techniques in atmospheric science: A review. *International Journal of Climatology* 27, 1119-1152.

Hastenrath, S., 2002. Dipoles, temperature gradients, and tropical climate anomalies. *Bulletin of the American Meteorological Society* 83, 735-738.

Hermes, J.C., Reason, C.J.C., 2008. Annual cycle of the South Indian Ocean (Seychelles-Chagos) thermocline ridge in a regional ocean model. *Journal of Geophysical Research* 113, 04035.

- Huang, B., Kinter, J.L., 2002. Interannual variability in the tropical Indian Ocean. *Journal of Geophysical Research* 107, 3199.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187-211.
- Jury, M.R., Huang, B., 2004. The Rossby wave as a key mechanism of Indian Ocean climate variability. *Deep Sea Research Part I: Oceanographic Research Papers* 51, 2123-2136.
- Kirk, J.T.O., 1994. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge.
- Klein, S.A., Soden, B.J., Lau, N., 1999. Remote sea surface temperature variations during ENSO: Evidence for a tropical atmospheric bridge. *Journal of Climate* 12, 917-932.
- Koch-Larrouy, A., Lengaigne, M., Terray, P., Madec, G., Masson, S., 2009. Tidal mixing in the Indonesian Seas and its effect on the tropical climate system. *Climate Dynamics* 34, 891-904.
- Koné, V., Aumont, O., Levy, C., Resplandy, L., 2009. Physical and biogeochemical controls of the phytoplankton seasonal cycle in the Indian Ocean: A modeling study, in: Wiggert, J.D., Hood, R.R., Wajih, S., Naqvi, A., Brink, K.H., Smith, S.L. (Eds.), *Indian Ocean Biogeochemical Processes and Ecological Variability*, Geophysical Monograph Series. p. 350.
- Lawson, C., Hanson, R., 1974. Solving Least Square Problems. Prentice Hall, New Jersey.
- Lengaigne, M., Madec, G., Menkes, C., Alory, G., 2003. Impact of isopycnal mixing on the tropical ocean circulation. *Journal of Geophysical Research* 108, 3345.
- Lengaigne, M., Guilyardi, E., Boulanger, J., Menkes, C., Delecluse, P., Inness, P., Cole, J., Slingo, J., 2004. Triggering of El Niño by westerly wind events in a coupled general circulation model. *Climate Dynamics* 23, 601-620.
- Lengaigne, M., Menkes, C., Aumont, O., Gorgues, T., Bopp, L., André, J., Madec, G., 2007. Influence of the oceanic biology on the tropical Pacific climate in a coupled general circulation model. *Climate Dynamics* 28, 503-516.
- Li, T., Wang, B., Chang, C.P., Zhang, Y., 2003. A theory for the Indian Ocean dipole-zonal mode. *Journal of the Atmospheric Sciences* 60, 2119–2135.

- Madec, G., Delecluse, P., Imbard, M., Levy, C., 1998. OPA 8.1 general circulation model reference manual, in: Notes du Pole de Modelisation de l'Institut Pierre-Simon Laplace. France, p. 91.
- Masumoto, Y., Meyers, G., 1998. Forced Rossby waves in the southern tropical Indian Ocean. *Journal of Geophysical Research* 103, 27589-27602.
- Maury, O., 2010. An overview of APECOSM, a spatialized mass balanced "Apex Predators ECOSystem Model" to study physiologically structured tuna population dynamics in their ecosystem. *Progress In Oceanography* 84, 113-117.
- McClain, C.R., Signorini, S.R., Christian, J.R., 2004. Subtropical gyre variability observed by ocean-color satellites. *Deep Sea Research Part II: Topical Studies in Oceanography* 51, 281-301.
- McClain, E.P., Pichel, W.G., Walton, C.C., 1985. Comparative performance of AVHRR-based multichannel sea surface temperatures. *Journal of Geophysical Research* 90, 11587-11601.
- McPhaden, M.J., Zebiak, S.E., Glantz, M.H., 2006. ENSO as an Integrating Concept in Earth Science. *Science* 314, 1740-1745.
- Meyers, G., McIntosh, P., Pigot, L., Pook, M., 2007. The Years of El Niño, La Niña, and interactions with the tropical Indian Ocean. *Journal of Climate* 20, 2872-2880.
- Morel, A., Berthon, J., 1989. Surface pigments, algal biomass profiles, and potential production of the euphotic layer: relationships reinvestigated in view of remote-sensing applications. *Limnology and Oceanography* 34, 1545-1562.
- Murtugudde, R., Busalacchi, A.J., McCreary, J.P., 2003. Comment on "Dipoles, Temperature Gradients, and Tropical Climate Anomalies". *Bulletin of the American Meteorological Society* 84, 1422-1423.
- Murtugudde, R., Busalacchi, A.J., 1999. Interannual variability of the dynamics and thermodynamics of the tropical Indian Ocean. *Journal of Climate* 12, 2300-2326.
- Murtugudde, R.G., Signorini, S.R., Christian, J.R., Busalacchi, A.J., McClain, C.R., Picaut, J., 1999. Ocean color variability of the tropical Indo-Pacific basin observed by SeaWiFS during 1997-1998. *Journal of Geophysical Research* 104, 18351-18366.

- Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S and S-Plus. Springer, New York.
- Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., R Development Core Team, 2010. nlme: Linear and Nonlinear Mixed Effects MOdels.
- Pollehne, F., Klein, B., Zeitzschel, B., 1993. Low light adaptation and export production in the deep chlorophyll maximum layer in the northern Indian Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 40, 737-752.
- Pyper, B.J., Peterman, R.M., 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Canadian Journal of Fisheries and Aquatic Sciences 55, 2127-2140.
- Rao, S.A., Behera, S.K., 2005. Subsurface influence on SST in the tropical Indian Ocean: structure and interannual variability. Dynamics of Atmospheres and Oceans 39, 103-135.
- Rao, S.A., Behera, S.K., Masumoto, Y., Yamagata, T., 2002. Interannual subsurface variability in the tropical Indian Ocean with a special emphasis on the Indian Ocean Dipole. Deep Sea Research Part II: Topical Studies in Oceanography 49, 1549-1572.
- Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent, E.C., Kaplan, A., 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. Journal of Geophysical Research 108, 4407.
- R Development Core Team, 2009. R: A language and environment for statistical computing. Vienna, Austria.
- Reason, C., Allan, R., Lindesay, J., Ansell, T., 2000. ENSO and climatic signals across the Indian Ocean Basin in the global context: part I, interannual composite patterns. International Journal of Climatology 20, 1285-1327.
- Resplandy, L., Vialard, J., Lévy, M., Aumont, O., Dandonneau, Y., 2009. Seasonal and intraseasonal biogeochemical variability in the thermocline ridge of the southern tropical Indian Ocean. Journal of Geophysical Research 114, C07024.
- Rodgers, K.B., Aumont, O., Menkes, C., Gorgues, T., 2008. Decadal variations in equatorial Pacific ecosystems and ferrocline/pycnocline decoupling. Global Biogeochemical Cycles 22, GB2019.

- Saji, N.H., Goswami, B.N., Vinayachandran, P.N., Yamagata, T., 1999. A dipole mode in the tropical Indian Ocean. *Nature* 401, 360-363.
- Saji, N.H., Yamagata, T., 2003a. Structure of SST and surface wind variability during Indian Ocean Dipole Mode events: COADS observations. *Journal of Climate* 16, 2735-2751.
- Saji, N.H., Yamagata, T., 2003b. Possible impacts of Indian Ocean Dipole mode events on global climate. *Climate Research* 25, 151-169.
- Schott, F.A., Xie, S., Jr, J.P.M., 2009. Indian Ocean circulation and climate variability. *Reviews of Geophysics* 47, RG1002.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: The principles and practice of statistics in biological research*. WH Freeman, New York.
- Song, Q., Vecchi, G.A., Rosati, A.J., 2007. Indian Ocean variability in the GFDL coupled climate model. *Journal of Climate* 20, 2895-2916.
- Su, H., Neelin, J.D., Chou, C., 2001. Tropical teleconnection and local response to SST anomalies during the 1997-1998 El Niño. *Journal of Geophysical Research* 106, 20-025.
- Tourre, Y.M., White, W.B., 1995. ENSO Signals in Global Upper-Ocean Temperature. *Journal of Physical Oceanography* 25, 1317-1332.
- Trenberth, K.E., 1997. The definition of El Niño. *Bulletin of the American Meteorological Society* 78, 2771-2777.
- Uitz, J., Claustre, H., Morel, A., Hooker, S.B., 2006. Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll. *Journal of Geophysical Research* 111, C08005.
- Uppala, S.M., Kållberg, P.W., Simmons, A.J., Andrae, U., Bechtold, V.D.C., Fiorino, M., Gibson, J.K., Haseler, J., Hernandez, A., Kelly, G.A., Li, X., Onogi, K., Saarinen, S., Sokka, N., Allan, R.P., Andersson, E., Arpe, K., Balmaseda, M.A., Beljaars, A.C.M., Berg, L.V.D., Bidlot, J., Bormann, N., Caires, S., Chevallier, F., Dethof, A., Dragosavac, M., Fisher, M., Fuentes, M., Hagemann, S., Hólm, E., Hoskins, B.J., Isaksen, I., Janssen, P.A.E.M., Jenne, R., McNally, A.P., Mahfouf, J., Morcrette, J., Rayner, N.A., Saunders, R.W., Simon, P., Sterl, A., Trenberth, K.E., Untch, A., Vasiljevic, D., Viterbo, P., Woollen, J., 2005. The ERA-40 re-analysis. *Quarterly Journal of the Royal Meteorological Society* 131, 2961-3012.

- Venzke, S., Latif, M., Villwock, A., 1997. The coupled GCM ECHO-2. Part II: Indian Ocean response to ENSO (No. 246), Max-Planck Institut fur Meteorologie Report. Max-Planck Institut fur Meteorologie, Hamburg.
- Venzke, S., Latif, M., Villwock, A., 2000. Coupled GCM ECHO-2. Part II: Indian ocean response to ENSO. *Journal of Climate* 13, 1371-1383.
- Vialard, J., Menkes, C., Boulanger, J., Delecluse, P., Guilyardi, E., McPhaden, M.J., Madec, G., 2001. A model study of oceanic mechanisms affecting equatorial Pacific sea surface temperature during the 1997–98 El Niño. *Journal of Physical Oceanography* 31, 1649-1675.
- Vinayachandran, P.N., Iizuka, S., Yamagata, T., 2002. Indian Ocean dipole mode events in an ocean general circulation model. *Deep Sea Research Part II: Topical Studies in Oceanography* 49, 1573-1596.
- Wang, C., Fiedler, P.C., 2006. ENSO variability and the eastern tropical Pacific: A review. *Progress in Oceanography* 69, 239-266.
- Webster, P.J., Moore, A.M., Loschnigg, J.P., Leben, R.R., 1999. Coupled ocean-atmosphere dynamics in the Indian Ocean during 1997-98. *Nature* 401, 356-60.
- White, T.C.R., 2008. The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews* 83, 227-248.
- White, W.B., Gloersen, K.A., Marsac, F., Tourre, Y.M., 2004. Influence of coupled Rossby Waves on primary productivity and tuna abundance in the Indian Ocean. *Journal of Oceanography* 60, 531-541.
- Wiggert, J., Hood, R., Banse, K., Kindle, J., 2005. Monsoon-driven biogeochemical processes in the Arabian Sea. *Progress in Oceanography* 65, 176-213.
- Wiggert, J., Murtugudde, R., Christian, J., 2006. Annual ecosystem variability in the tropical Indian Ocean: Results of a coupled bio-physical ocean general circulation model. *Deep Sea Research Part II: Topical Studies in Oceanography* 53, 644-676.
- Wiggert, J., Vialard, J., Behrenfeld, M.J., 2009. Basinwide modification of dynamical and biogeochemical processes by the positive phase of the Indian Ocean Dipole during the SeaWiFS era, in: Wiggert, J.D., Hood, R.R., Wajih, S., Naqvi, A., Brink, K.H., Smith, S.L. (Eds.), *Indian Ocean Biogeochemical Processes and*

Ecological Variability, Geophysical Monograph Series. p. 350.

- Wilson, C., Adamec, D., 2002. A global view of bio-physical coupling from SeaWiFS and TOPEX satellite data, 1997-2001. *Geophysical Research Letters* 29, 1257.
- Wyrtki, K., 1973. An equatorial jet in the Indian Ocean. *Science* 181, 262-264.
- Xie, S., Annamalai, H., Schott, F.A., McCreary, J.P., 2002. Structure and mechanisms of south Indian Ocean climate variability. *Journal of Climate* 15, 864-878.
- Yamagata, T., Behera, S.K., Luo, J.J., Masson, S., Jury, M.R., Rao, S.A., 2004. Coupled ocean-atmosphere variability in the tropical Indian Ocean. *Geophysical Monograph* 147, 189–211.
- Yamagata, T., Behera, S.K., Rao, S.A., Guan, Z., Ashok, K., Saji, H.N., 2003. Comments on "Dipoles, temperature gradients, and tropical climate anomalies". *Bulletin of the American Meteorological Society* 84, 1418-1422.
- Yoder, J.A., Kennelly, M.A., 2003. Seasonal and ENSO variability in global ocean phytoplankton chlorophyll derived from 4 years of SeaWiFS measurements. *Global Biogeochemical Cycles* 17, 1112.
- Zelle, H., Appeldoorn, G., Burgers, G., van Oldenborgh, G.J., 2004. The relationship between sea surface temperature and thermocline depth in the eastern equatorial Pacific. *Journal of Physical Oceanography* 34, 643-655.
- Zhong, A., Hendon, H.H., Alves, O., 2005. Indian Ocean Variability and Its Association with ENSO in a Global Coupled Model. *Journal of Climate* 18, 3634-3649.

Appendix A

Table A1. Results of linear models fitted by least squares, which assumes independence of the response-variable samples and therefore does not account for autocorrelated errors. Models fitted for variables SST, CHL and Z20 in regions Indian Ocean (IO), southwest and southeast Indian Ocean (SWIO, SEIO respectively). Bold values are estimated coefficients, while below them in normal font are associated p-values (calculated from t-statistic). p-values for the F-statistic were <0.001 for all models. Coefficient units are in °C, mg/m² and m respectively.

Model Formula	Coefficients and p-values				Adjusted R-squared
	Intercept	IOZM	ENSO	IOZM* NINO	
$SST.IO_t = \beta_1 * ENSO_{t-6} + \epsilon_t$	25.601 <0.0001	-	0.138 <0.0001	-	0.396
$SST.SWIO_t = \beta_1 * ENSO_{t-2} + \epsilon_t$	27.721 <0.0001	-	0.242 <0.0001	-	0.369
$SST.SEIO_t = \beta_1 * ENSO_{t-8} + \epsilon_t$	28.564 <0.0001	-	0.134 <0.0001	-	0.082
$Z20.SWIO_t = \beta_1 * IOZM_{t-9} + \beta_2 * ENSO_{t-5} + \epsilon_t$	116.845 <0.0001	2.736 <0.0001	2.224 <0.0001	-	0.230
$Z20.SEIO_t = \beta_1 * IOZM_{t-1} + \beta_2 * ENSO_{t+1} + \beta_3 * (IOZM_{t-1} * ENSO_{t+1}) + \epsilon_t$	124.628 <0.0001	-1.813 <0.0001	-0.527 0.001	-0.299 0.004	0.242
$Chl.IO_t = \beta_1 * IOZM_{t+1} + \beta_2 * ENSO_{t-6} + \epsilon_t$	17.380 <0.0001	0.096 <0.0001	-0.051 <0.0001	-	0.235
$Chl.SWIO_t = \beta_1 * IOZM_{t-6} + \beta_2 * ENSO_{t-2} + \epsilon_t$	17.430 <0.0001	-0.470 <0.0001	-0.413 <0.0001	-	0.288
$Chl.SEIO_t = \beta_1 * IOZM_{t-1} + \beta_2 * ENSO_t + \epsilon_t$	18.720 <0.0001	1.031 <0.0001	0.226 <0.0001	-	0.509

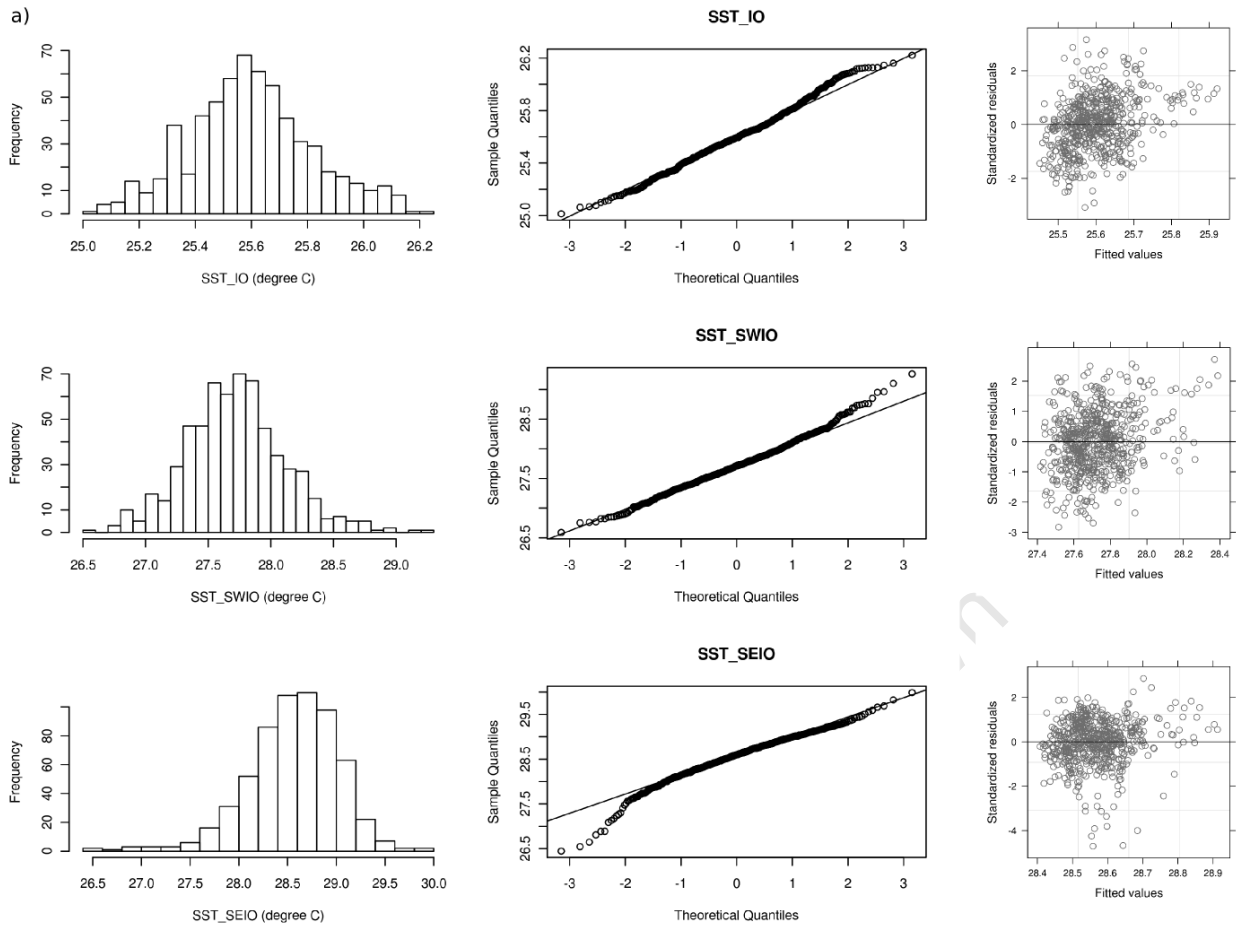
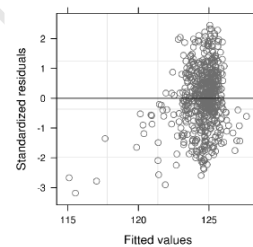
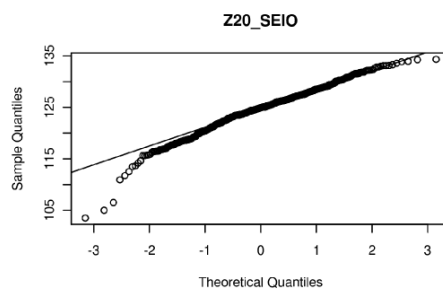
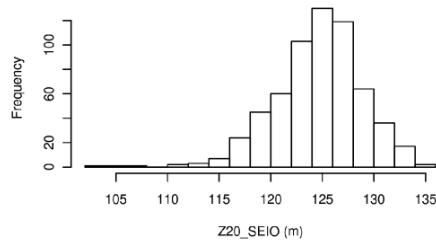
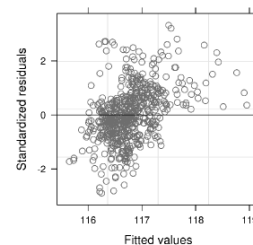
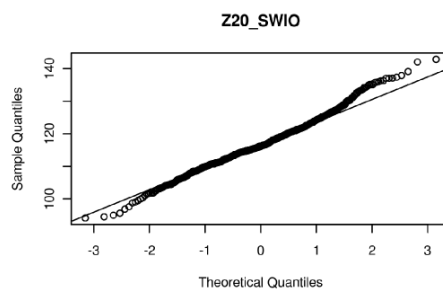
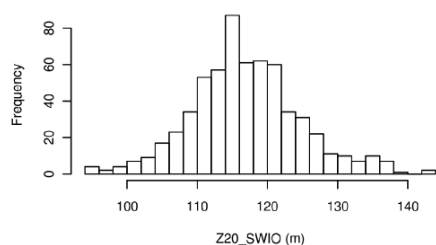
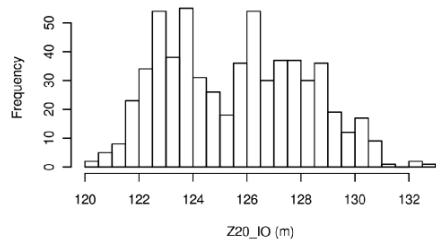
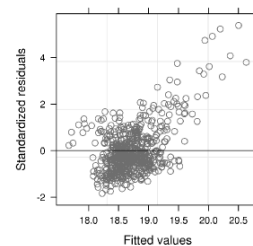
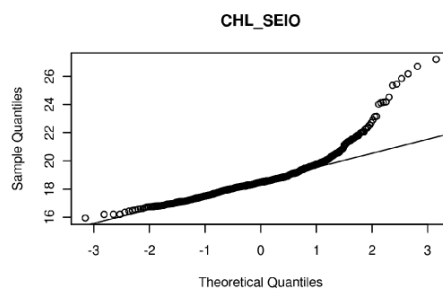
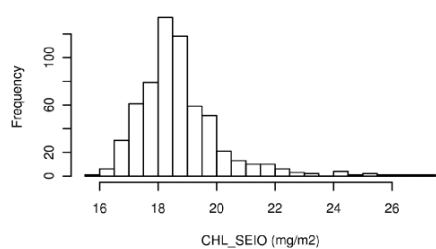
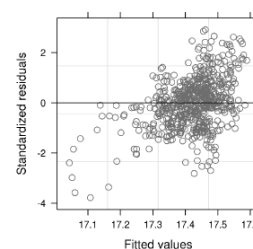
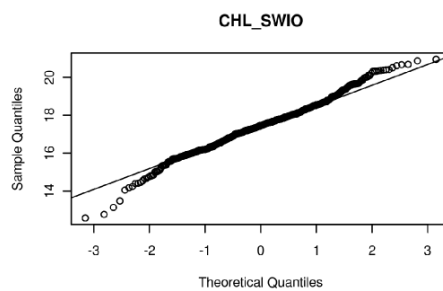
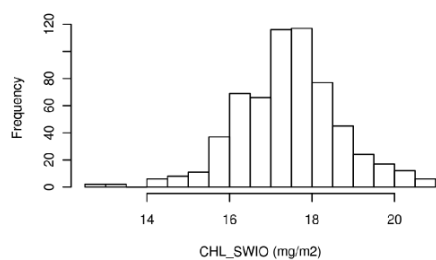
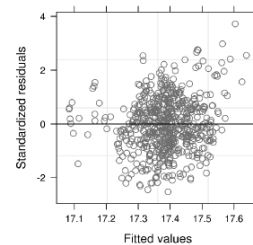
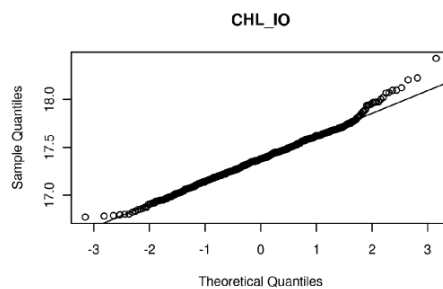
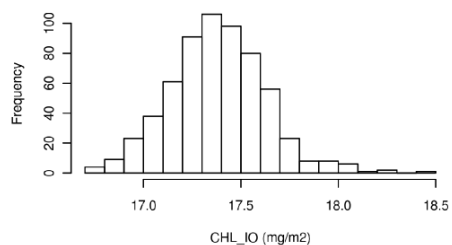


Figure A1. Histograms (left) and normal quantile-quantile plots (centre) of the response variables prepared for GLS-fitting of linear models, as well as scatterplots of model residuals versus fitted values (right) from the models reported in Table 3, Chapter 2. The variables are separated into a) SST, overleaf b) Z20 and c) CHL, while the relevant plots are ordered vertically by the region of interest (IO top, SWIO centre and SEIO bottom). Continued overleaf.

b)



c)



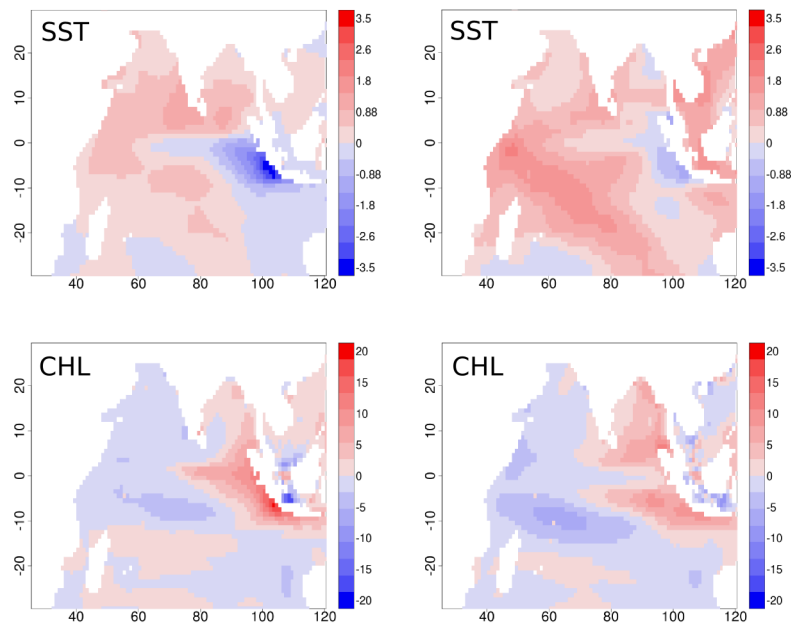


Figure A2. JJASON (left) and DJFMAM (right) anomalies of SST (top; °C) and CHL (bottom; mg/m²) for the 1997 IOZM – El Niño event.

Chapter 3

Tuna-Environment Relationships: Linking Indian Ocean Purse-Seine Catches of Skipjack (*Katsuwonus pelamis*) and Yellowfin Tuna (*Thunnus albacares*) to their Environment, Using Generalised Additive Models

Abstract

Growing fisheries datasets, together with ever-improving records of environmental variability, allow for increasingly useful descriptions of fish-environment relationships, that can provide valuable insights into the behaviour, ecology and habitat preferences of resource species. Here, historical (1981-2001) purse-seine catches of skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*), from French and Spanish fleets operating in the Indian Ocean, were compared to concomitant records of environmental variables using Generalised Additive Models (GAMs). The majority of environmental fields were provided from hindcasts of a state-of-the-art coupled bio-physical ocean model (NEMO-PISCES). A delta approach was used to handle the zero-inflated data, by which presence-absence models were evaluated, and thereafter, catch-per-unit-effort (CPUE) was modelled on condition that catches were positive (present). Results showed important differences between relationships obtained from catches made underneath fish aggregating devices (FADs), compared to those made on free-swimming schools. FADs efficiently congregate tuna from the surrounding environment, thereby apparently reducing catchability effects and allowing relationships that can be interpreted in terms of tuna abundances or habitat, to come to the fore. New ecological insights include the findings that deeper thermocline depths translate to greater skipjack and yellowfin tuna abundances, and that tuna densities seem to react to (a mesozooplankton proxy of) prey concentrations, by a Holling type II functional response, which has been assumed, but not shown empirically before. In addition to these insights, such tuna-environment relationships are valuable in their potential application to quasi real-time mapping of tuna habitats from data or simulations, thereby providing input for the adjustments of mobile no-take zones. In addition, the same relationships applied to forecast model outputs,

could provide best estimates of how tuna habitat might change with future climate change.

Introduction

Tuna stocks and other high-seas pelagic predators are in need of concerted research and political effort, to ensure that their exploitation and management is sustainable in future. Traditional management strategies that aim to maintain populations at certain threshold sizes (e.g. a stock biomass allowing the maximum sustainable yield, B_{MSY}) by controlling total catches or effort, have been largely ineffective and inadequate (Safina, 1993; Langley et al., 2009; Cullis-Suzuki and Pauly, 2010). These regional or ocean-basin-scale stocks are commonly exploited by a myriad of surrounding and distant fishing nations. Their catches typically exhibit high interannual catch variability, due to a combination of changes in gear and targeting strategies by the fishers (Sakagawa et al., 1987), as well as fluctuations in catch rates caused by environmental variability (e.g. Lehodey et al., 1997; Marsac and Le Blanc, 1998, 1999). One of the biggest challenges to understanding and effectively managing them is collation of complete and accurate fisheries data; a task which prompted the formation of several regional tuna fishery management organisations (RFMOs; e.g. Indian Ocean Tuna Commission, IOTC; Western Central Pacific Fisheries Commission, WCPFC; Inter-American Tropical Tuna Commission, IATTC; International Commission for the Conservation of Atlantic Tuna, ICCAT; Commission for the Conservation of the Southern Bluefin Tuna, CCSBT). Once the fisheries data have been collated nationally and gathered from cooperating countries by the RFMOs, uncertainties in the estimation of statistics and often-lacking knowledge of required parameters, result in very few examples of stock assessment models which allow adequate confidence in results to base management measures on (Safina, 2001). As a result, expert opinions are called upon to make judgements on collections of seemingly inconclusive assessments and statistics, following which there has been little evidence of management action effectively curbing fishing effort. An example is the Indian Ocean, where the status of albacore tuna is considered stable; bigeye tuna catches are considered to be close to MSY, although stock size indicators have declined since the 1970s; a reliable MSY for skipjack tuna is not available, but the stock size and fishing pressures are considered to be 'within acceptable limits'; yellowfin tuna are judged to be recently overexploited (Anon, 2009a); and southern bluefin tuna are believed to be

overexploited (Mori et al., 2001). While scientists meet regularly at international conferences and RFMO meetings in attempts to better understand and model tuna population dynamics and catch rates, unabated fishing, including illegal, unreported and unregulated fishing (IUU; Bray, 2000) carries on in a 'free-for-all' manner in most ocean basins.

Clearly, there is a pressing need to rethink management attempts, or at least add to them, so as to safeguard sustainable tuna stocks into the future. Spatial management strategies, such as setting aside a proportion of suitable tuna habitat for protection in no-take zones, could help address this problem (Mills and Carlton, 1998; Sumaila et al., 2007; Game et al., 2009). Such action would equally address the resolution (promoted by the Food and Agricultural Organisation, the World Summit on Sustainable Development and the IUCN Commission on Ecosystem Management, amongst others) to embrace ecosystem approaches to fishery management (Garcia and Cochrane, 2005) and should act to counter the erosion of pelagic predator diversity (Worm et al., 2005). Besides developing the legal framework and logistical challenges of enforcement, one of the main hurdles facing such spatial management of pelagic environments is identification of what constitutes 'good' habitat. Working towards the identification and description of tuna habitat preferences (and those of related pelagic predators) is therefore an important research priority and will be explored in this study by simultaneous interrogation of fisheries and environmental fields.

Tunas and other open ocean pelagic predators have evolved physiological and behavioural traits, convergently in some cases (e.g. Donley et al., 2004), that allow them to prosper in regions that are characteristically unproductive. Central to these specialisations is a highly active and efficient swimming mode (Dickson, 1995), which together with a suite of adaptations that make them proficient hunters of epi- and meso-pelagic prey, allows them to effectively integrate sparse and patchy prey densities. Regional endothermy, seen in very few other teleost species, allows several tuna species to tolerate ambient temperatures well below those required by their elevated metabolisms and thus to expand their habitat both latitudinally and vertically (Graham and Dickson, 2004). Coupled with their unique physiologies, specific behavioural strategies have resulted in niche-partitioning of wide-ranging pelagic habitats and allowed several tuna species to permeate global tropical and subtropical

oceans ($\sim 50^{\circ}\text{S}$ - 60°N ; Fonteneau, 1997), from surface layers down to more than 1000 m (Block et al., 2001; Dagorn et al., 2006).

Tunas are highly mobile predators that need to sustain a high metabolism (Sharp and Dizon, 1979) and are sensitive to specific physical and chemical thresholds (e.g. Neill et al., 1976; Block and Stevens, 2001; Graham and Dickson, 2004). As these mobile predators race through their three-dimensional environment, they frequently encounter gradients of environmental variables and prey densities, presumably adjusting their swimming trajectories and behaviour in response. These reactions to their surroundings, governed by physiological requirements and behavioural traits, are what define tuna habitat preferences. Although potentially overlapping in some cases, one should be able to describe and separate these multi-dimensional niches among different species (e.g. Graham and Dickson, 2004), using a combination of physical, chemical and biological factors that serve as their environmental cues (Hutchinson, 1957).

Tuna-Environment Investigations

Many authors have demonstrated environmental preferences or limitations of tuna at a variety of scales and using a variety of methods. Experiments with captive fish have been very useful in testing thresholds of environmental variables on tuna, as well as measuring physiological effects and responses (e.g. Dizon et al., 1977; Barkley et al., 1978; Sharp and Dizon, 1979; Bushnell et al., 1990). These experiments have been biased towards smaller species or sizes and require considerable infrastructure, skills and finances to perform. The information they provide, one could argue, provides indications of the outer limits or thresholds at which the fish can survive or show signs of stress, rather than providing information on habitat preferences in the natural environment.

The use of archival tags and acoustic telemetry methods have been successfully employed to obtain behavioural movements in relation to the environment and prey densities for tuna and other top predator species (e.g. Block et al., 1997; Josse et al., 1998; Dagorn et al., 2000; Musyl et al., 2003; Schaefer et al., 2007). Such field experiments are invaluable in understanding feeding strategies and small-scale behaviour employed by pelagic predators, besides having revealed the surprising depths to which some predators dive (e.g. Block et al., 2001; Dagorn et al., 2006).

However by their nature they are expensive experiments to conduct and the sample sizes (and number of such studies) have been limited. Furthermore the behavioural information gained from these studies is not easily scaled up to regional or basin habitat requirements.

Another strategy employed to describe environmental preferences of tuna has been to compare water-column measures of the environment to depth-specific long-line catch-rates from aboard long-lining vessels (e.g. Bertrand et al., 2002a; Song et al., 2008, 2009). Bertrand et al. (2002a) examined the stomach contents from tuna hooked on instrumented longlines, together with simultaneous acoustic measurements with which they tracked the prey communities in the water column. These approaches yield useful information on the depths, environmental conditions and/or prey densities at which tuna are caught, but they are still limited by certain time-frames and areas, and passive longlining gear potentially suffers biases related to the selectivity of the tuna, which seems to be influenced by prey densities (Bertrand et al., 2002a).

Lastly, several authors have compared large datasets of geo-referenced commercial fishery catches with gridded environmental fields. Although at a much coarser scale than the previous approaches, the vast datasets can complement finer-scale findings on habitat and behavioural preferences of tuna, and investigate their relevance at ocean-basin-scales. Multiple studies have followed this approach, employing a variety of statistical methods at different spatial and temporal scales, in the Indian (e.g. Marsac and Le Blanc, 1999; Romena, 2001; Chen et al., 2005) and other oceans (e.g. Evans et al., 1981; Bigelow et al., 1999; Maury et al., 2001a; Zainuddin et al., 2004, 2006, 2008; Zagaglia et al., 2004).

Besides limiting resolutions and quality of fisheries data, as well as a far-from-perfect knowledge of the senses and potential cues (or physiological limitations) of open-ocean predators such as tuna, one of the main challenges hampering progressive habitat descriptions from fishery data has commonly been a lack of environmental data at scales and resolutions necessary to describe a species' habitat. As a result of these lacking fields, historical studies relating catch data to the environment were based on long-term oceanographic averages (Laevastu and Rosa, 1962; Blackburn and Barnes, 1965) or short-term cruises or programs (e.g. Blackburn and Laurs, 1972; Blackburn and Williams, 1975; Ingham et al., 1977; Evans et al., 1981; Laurs

et al., 1984; Song et al., 2008, 2009). The former can provide only crude ranges of habitat descriptors and do not take into account the highly dynamic nature of the environment or fish and fishery movements (e.g. Marsac and Le Blanc, 1999), thereby overlooking much detail in the fish-environment relationships. The latter were again limited by cost and the amount of data that could be collected, being restricted to a relatively small sample in space and time. With the progression in ocean observations and numerical models however, there exists increasing opportunity to assess large fisheries datasets in terms of environmental variability, allowing informative and applicable advances to be made (e.g. Bigelow et al., 1999; Maury et al., 2001a).

Results from such investigations seem to be region-, species- and gear-specific. For example, Andrade (2003) investigated the pole-and-line skipjack tuna fishery in the south-western Atlantic Ocean and concludes that fishing effort is strongly related to the seasonal N-S migration of SST, further suggesting that oceanographic fronts and shallow thermoclines concentrate skipjack in reach of the surface fishery. Whereas investigating yellowfin purse-seine catches in the eastern and central Pacific during extreme climate events, De Anda-Montañez et al. (2004) conclude that surface temperature does not play a large role in the distribution of catches.

In the Indian Ocean, Chen et al. (2005) used stepwise discriminant analyses to investigate the explanatory power of surface and subsurface variables (including temperature, salinity, oxygen and chlorophyll concentrations) in separating above- and below-average albacore catches from the 1979-1985 Taiwanese longline fishery. Immature fish, mature non-spawning adults and spawning adults were distinguished on a combination of size and spatio-temporal considerations. The authors concluded that while only SST was significant in predicting CPUE of mature non-spawners, surface values of chlorophyll and salinity were additionally significant for immature fish, while surface salinity and subsurface temperature (at 100 m) and oxygen (at 200 m) were significant for spawning adult albacore tuna.

Song et al. (2008, 2009) estimated depths of successful tuna longline catches and related these to environmental variables (depth, temperature, salinity, chlorophyll concentration, dissolved oxygen concentration), measured concurrently from aboard two commercial longliners in the central, northern Indian Ocean in September – December 2005. Dividing the measured variables into categories and comparing CPUE

at different levels of these, Song et al. (2008) suggest that the highest catch rates of adult yellowfin tuna in the Indian Ocean occur in ranges of 160-179 m depth, 16-16.9°C water temperature, 35.4-35.49 psu salinity, 0.04-0.049 µg/l chlorophyll and 2.5-2.99 mg/l dissolved oxygen, although they acknowledge that salinity likely has a minimal effect on CPUE.

Maury et al. (2001a) used GAMs to investigate the effects of several environmental variables on yellowfin CPUE (both purse-seine and long-lining) across the Atlantic Ocean. The use of a three-dimensional ocean global circulation model allowed exploration of a host of variables, including surface and subsurface temperature, salinity, currents, thermocline depth and various indices of vertical and horizontal hydrological stability. Significant effects on CPUE of effort, wind strength, vertical current shear and thermocline depth and strength, were attributed to catchability effects (directly influencing gear efficacy and/or the vertical positioning of fish relative to gear depths), rather than changes in local abundances. Salinity, SST, temperature at 150 m depth and the horizontal SST gradient on the other hand, were interpreted to be significant environmental predictors of yellowfin tuna abundances, and were found to affect distributions at different spatial scales and with varying importance to different aged (sized) fish.

When attempting to describe species habitats or environmental preferences via the use of catch data, the limitations of the fisheries data need to be considered. A common measure of fishing performance is the catch per unit effort (CPUE), which is used as an explicit measure of relative abundance, under the assumption that catches remain a constant fraction of the population density (Maunder et al., 2006). However the fraction of the true abundance available to the fishery ("availability"; Marr, 1951), as well as the effectiveness of the fishing gear to capture that fraction ("catchability"; Arreguín-Sánchez, 1996), both potentially vary due to environmental impacts, either as a result of fish behavioural responses, or by affecting gear deployment or efficiency.

It follows that a vital consideration when investigating habitat relationships using fishery data, is to distinguish between catchability effects and those representative of the predator abundance or distribution (e.g. Maury et al., 2001a). GAMs are well suited to such applications. Although they do not separate the two sources explicitly,

the flexible non-linear relationships derived from GAMs can often aid identification of catchability or abundance effects, as long as they are carefully interpreted in terms of our understanding of behaviour and physiological limitations of the subject species, and how these interact with fishing gear (e.g. Bigelow et al., 1999; Maury et al., 2001a). GAMs do not require parametric assumptions of the input data and are said to be 'data-driven' in the way they allow the inputs to describe the relationships between explanatory and response variables, rather than assuming a certain functional relationship between them (Yee and Mitchell, 1991).

Evidence of how tuna forage modifies tuna behaviour and abundances has been sparse due to an almost complete lack of data on distributions of tuna prey (or related mid- and lower-trophic levels). Only on relatively small scales have authors successfully managed to relate tuna behaviour, and apparent distributions, to prey densities (e.g. Josse et al., 1998; Bertrand et al., 2002a, 2002b). Some authors have investigated time-lags of physical (e.g. Bigelow et al., 1999) and chlorophyll (e.g. Garcia and Cota, 1996) fields in order to account for the aggregation and/or trophic development of tuna forage, after certain oceanographic or phytoplankton (chlorophyll) features. However such methods, which do not account for passive (e.g. currents) and active (e.g. behavioural aggregative/dispersive) redistribution of the trophic energy, are unlikely to succeed, besides the difficulty of choosing a time-lag that would represent the development of tuna forage following certain physical or biological events. However such crude approximations of prey productivity, which are employed due to a lack of data on the densities of mid-trophic organisms in the oceans, can be superseded by the ever-improving development of accurate bio-physical ocean models (e.g. Lehodey et al., 1998; Aumont and Bopp, 2006; Maury, 2010), which model the trophic processes and redistribution of carbon available from primary productivity.

Environmental Preferences of Skipjack and Yellowfin Tuna

The bulk of Indian Ocean purse-seine catches are dominated by skipjack and yellowfin tuna. These two species feature minimally in coarser-resolution long-line catch data, unlike bigeye and albacore tuna, which together with several other commonly-targeted pelagic species, are mostly caught by long-lines. Skipjack and yellowfin tuna are well sampled by the purse-seine fleets across much of the Indian Ocean and are the two species that will be investigated here.

When attempting to describe environmental preferences of tuna from fisheries data, one needs to be aware of factors which may distort or confound these. In the present case, different life-stages of tuna could for example show different habitat preferences (e.g. Maury et al., 2001a). Spawning adults might for example respond differently to environmental cues, due to their reproductive requirements, as compared to non-spawners or juveniles. In addition, purse-seine fishers have two different modes of fishing: They can target either free-swimming schools, or those associated with fish aggregating devices (FADs). As FADs aggregate fish and therefore must modify their behaviour, the environmental preferences of the FAD-associated fish might be modified, and so likely require separate investigation to those of the free-swimming schools.

Skipjack Tuna (*Katsuwonus pelamis*)

Skipjack tuna are a relatively small tuna species (generally < 80 cm), which inhabit surface waters (<260 m) in the tropics and subtropics (Collette and Nauen, 1983). Due to their smaller size (greater surface to volume ratio), they are more sensitive to low temperatures than larger species, mostly inhabiting waters with surface temperatures of 20-30°C (Forsbergh, 1980), although large individuals have higher oxygen demands and are more efficient at conserving body heat, and thus may be caught at surface temperatures lower than 18°C (Barkley et al., 1978). Due to their oxygen demand and using experimental results, Barkley et al. (1978) suggest that 4-9 kg fish will require waters cooler than about 26°C, while individuals larger than this will remain in waters below 22°C. Vertical movements are usually limited to waters that are less than 8°C colder than surface temperatures (Brill et al., 2005). It is generally accepted that skipjack tuna require a minimum ambient oxygen concentration of ~3.5 ml/l (Barkley et al., 1978; Evans et al., 1981; Graham and Dickson, 2004).

In the Indian Ocean, the size at first maturity is 41-42 cm fork-length for females and 42-43 cm for males, which corresponds to an age of about 1.5 years (Stéquert and Ramcharrum, 1996). Skipjack spawn throughout the year, seemingly with a peak during the two monsoon seasons (November-March and June-August; Stéquert and Ramcharrum, 1996) and do so throughout most of their range, as long as waters are warmer than about 24°C (Schaefer, 2001). Their maximum reported age is 12 years (Collette and Nauen, 1983).

Yellowfin Tuna (*Thunnus albacares*)

Yellowfin tuna are a larger species (>200 cm, but commonly up to 150 cm), which inhabit the epi- and meso-pelagic zones of global tropical and subtropical waters (Collette and Nauen, 1983). Although mostly inhabiting surface layers above the thermocline, dives can reach depths of 300-350 m (Block et al., 1997; Bard et al., 1999) and sometimes over 1000 m (e.g. Dagorn et al., 2006). When oxygen concentrations are non-limiting, maximum depths seem to be restricted by temperature (Block et al., 1997) and (Brill et al., 1999) suggest that the relative difference between surface and deeper waters may be more important than absolute temperatures, with individuals generally keeping to waters that are within 8°C of surface values. The latter authors also note that tracked adult yellowfin tuna spent over 90% of their time in waters >22°C, only making brief dives into cooler (deeper) water. Oxygen concentrations <3.5 ml/l are limiting to yellowfin tuna (Brill, 1994) and thus play an important role in restricting vertical habitat.

In the Indian Ocean, a minimum length at sexual maturity was given as 101 and 110 cm for females and males respectively, while length at 50% maturity was estimated as ~114 and 120 cm respectively (Zhu et al., 2008). Yellowfin tuna will migrate to spawn in surface temperatures greater than 24°C (Schaefer, 2001; Schaefer et al., 2007) in broad tropical regions (between ~10°S-10°N in the Indian Ocean; Shung, 1973) and with a peak in January-March (Stéquert and Marsac, 1989). Their maximum reported age is nine years (Froese and Pauly, 2010).

Aim and Objectives

The aim of this study is to describe habitat preferences of skipjack and yellowfin tuna in the Indian Ocean, using historical purse-seine fisheries data and a suite of available environmental variables. This will be addressed by exploring non-linear relationships between geo-referenced catch-rates and environmental variables from a coupled bio-physical ocean model (NEMO-PISCES), using GAMs. With consideration of the uncertainties of inputs, the resultant relationships will then be identified and interpreted in terms of catchability or abundance effects, the latter of which are assumed to represent habitat preferences of the relevant species. While similar approaches can be used to standardise nominal CPUE statistics (Maunder and Punt, 2004), this is not the aim here. Rather, (non-linear) relationships that describe the response of tuna distributions to environmental conditions, are sought. Such

information is potentially vital for effectively managing tuna stocks in the future, by allowing identification of suitable habitat, of which a proportion can then be set aside for spatial protection. In addition, such relationships can advance predictions of how tuna habitats might change with future climate change.

Methods

Model Outputs and Data

Historical tuna purse-seine fisheries data compiled by the Indian Ocean Tuna Commission (IOTC) were sourced from the SARDARA database available at IRD (Institut de Recherche pour le Développement) in Sète, France. These data span the Indian Ocean and contain all the recorded tuna catches made by member countries of the IOTC (see <http://www.iotc.org/English/info/comstruct.php>). Data were chosen from the French and Spanish fleets, as they make up a large proportion of historical Indian Ocean catches, were among the earliest purse-seine fleets operating there (since 1981 and 1984 respectively) and are judged to be amongst the most-stringently controlled and reliable data (Anon, 2009a; A. Fonteneau, personal comment). These data include purse-seine catches for commonly caught species, as well as 'fishing days' which are a measure of fishing effort that is available at a monthly and 1° longitude by 1° latitude resolution. Fishing days are calculated by removing the time spent in ports, steaming time, and any time lost due to breakdowns, from the days at sea recorded in the captain's logbook. In addition, catches by size-class are available for the same fleets, although only at a 5° longitude by 5° latitude monthly resolution. These size data are obtained by observers sampling the fishing wells when the tuna boats land their catches in port, after which their measurements are extrapolated to the entire landed catch and aggregated over the 5° by 5° boxes. These catch-by-size data are recorded in 2-cm size classes.

Environmental variables were prepared on the same 1° by 1° monthly grid as the purse-seine catches. Most environmental variables were calculated from a 1958-2001 hindcast of NEMO-PISCES, a coupled bio-physical ocean model. The circulation model (NEMO-OPA8.2) simulates ocean physics and dynamics on a global numerical grid (ORCA0.5) at half a degree resolution and is based on OPA version 8.2 (Madec et al., 1998). The model has 31 depth levels, separated by 10 m in the upper 150 m and up to 500 m in the deep ocean. The outputs used here were forced using daily ERA40

surface winds (Uppala et al., 2005). For further details of the physical model, see Lengaigne et al. (2004), Rodgers et al. (2008) and references therein. The biogeochemical model (PISCES; Aumont and Bopp, 2006; Aumont et al., 2008) simulates chemical fluxes through 24 compartments including Fe, Si, PO₄, NO₃, NH₄, two phytoplankton and two zooplankton groups. Details of the Red-Green-Blue model, by which light penetration profiles are calculated, are given in Lengaigne et al. (2007). Phytoplankton chlorophyll and carbon are modelled by a method based on Geider et al. (1998). Further details of PISCES can be found in Aumont and Bopp (2006), while manuals for both NEMO and PISCES can be found at <http://www.nemo-ocean.eu/About-NEMO/Reference-manuals>.

The simulation used here has a spatial grid (ORCA0.5) that is 0.5° by 0.5° at the equator, with meridional resolution decreasing at higher latitudes. The outputs had been interpolated however and were provided on a 1° by 1° latitude-longitude grid and a temporal resolution of five days. Variables used from these outputs included temperature, salinity, photosynthetically available radiation (PAR), oxygen and mesozooplankton (zooplankton of 0.2-2 mm in size) concentration. Average monthly values were calculated for these fields, after which specific depth surfaces were used or derived variables were obtained as follows:

The depth of the 20°C isotherm (Z20) was used as a proxy for the thermocline depth, as is commonly done in tropical waters (e.g. Vinayachandran et al., 2002; Xie et al., 2002; Annamalai et al., 2003). These depths were estimated by linear interpolation of the temperature field. Similarly, the depths of specific oxygen concentrations (e.g. 3.5ml/l), indicated by the literature as limiting threshold values to tuna, were estimated from oxygen fields. After linear interpolation between depth levels (surfaces where model results are provided), the shallowest depth at which the oxygen concentration decreased below the selected threshold level was recorded. Vertically-integrated mesozooplankton concentrations between ~200 m and the surface, were calculated from the model outputs. In addition, average monthly pseudo wind stress (wind speed²) was calculated from daily surface wind speeds available from the ERA40 product (Uppala et al., 2005).

Three different tables of information, namely 'catches and effort', 'catches by size' and 'environmental variables' were imported into a relational database in PostgreSQL

(<http://www.postgresql.org/>) with geographic information systems ability added through PostGIS (<http://postgis.refractory.net/>). This allowed spatial manipulation and queries to be made, providing the tools to simply apply proportions of the lower resolution (5° by 5°) catch-by-size data, to the appropriate 1° by 1° resolution catch data.

Analyses

All analyses and data manipulation were performed with R programming language (R Development Core Team, 2009). The MGLM library (Wood, 2000) was used for fitting and assessing Generalised Additive Models. GAMs are a flexible extension of more-commonly used Generalised Linear Models, where a part of the linear predictor is specified as a sum of semi-parametric smooth functions of covariates (Wood, 2006). They allow multivariate exploration and analyses of data, without prior assumptions of linearity and with less-restrictive assumptions of the underlying distribution of errors, relative to multiple linear regression techniques (Hastie and Tibshirani, 1990). See Hastie and Tibshirani (1990) and Wood (2006) for an overview of GAMs, their technical background and (in Wood, 2006) their application in R.

Dealing with zero-inflated data is a common problem in fisheries science (Maunder and Punt, 2004). It was addressed here using a delta approach during the GAM analyses (e.g. Barry and Welsh, 2002). Within this framework, analyses were divided into two components: Firstly a presence-absence GAM was fitted to the environmental covariates of interest, assuming an underlying Bernoulli process (binomial distribution). Thereby the presence-absence variable y_i was modelled in terms of covariates using a logistic link function, after having been defined as:

$$y_i = \begin{cases} 1 & y_i > 0 \\ 0 & \text{otherwise} \end{cases}$$

Secondly, the non-null catches were subset and modelled separately as abundances, conditional on the catch being greater than zero (i.e. the tuna species being present). As the CPUE abundance measure is in weight (tonnes/fishing days) and after some initial exploration of results with different distributional assumptions, a continuous gamma distribution was chosen, rather than discretization of the data to be able to employ discrete distributions such as the zero-truncated Poisson or negative binomial.

Before running the GAM models, relationships among potential environmental

predictors were explored by pairwise scatterplots and non-parametric Kendall's tau correlation coefficients (e.g. Sokal and Rohlf, 1995). This allowed a priori identification of potentially redundant (highly correlated) variables and also provided insight as to linear or non-linear relationships among variables which would require exploration during model building.

Due to computational costs of working with large datasets, cubic regression splines (rather than thin plate regression splines) were used for one-dimensional smooth terms, and as the marginal bases to construct tensor products used for multivariate smoothing functions ('smoothing functions', 'smooth terms', and 'smooths' will be used interchangeably in the remainder of this study; Wood, 2006). Another parameter that needs to be chosen by the modeller is the basis dimension for each smooth (Wood, 2006). This parameter amounts to setting an upper limit to the degrees of freedom for each model term, which can act to limit the flexibility of the smooth in fitting the input data. During initial model exploration, the suggestion by Kim and Gu (2004) was followed in setting the basis dimension to $10 * n^{\frac{2}{9}}$ where n is the count of data. However in final models presented, basis dimensions were reduced in some cases, in order to reduce flexibility when smooths were otherwise too "wiggly" to allow meaningful interpretation.

As GAMs are a flexible semi-parametric technique and the use of large datasets favours statistical significance of variables, a stringent significance level of $\alpha=0.01$ was employed throughout the study. Non-significant variables were removed from models, while the Generalised Cross Validation score (GCV; Craven and Wahba, 1979) was used to choose among different model structures (Wood, 2006). Lastly, the motivation behind these analyses was to describe relationships between the environment and tuna catch data, which would be meaningful either in terms of catchability or habitat. With this in mind, smooths of environmental variables which were unstable among GAM models, or not meaningful in terms of tuna habitat or catchability, were additionally discarded.

Standardized deviance residuals were visually inspected for violations of model assumptions. Quantile-Quantile plots, histograms and scatter-plots of residuals versus the linear predictor, as well as response values versus fitted values, were plotted for abundance GAMs. Model checking with binary data is less straightforward, as the

distribution of their residuals will not be normal, even if the model is correct (Collett, 1991). Instead, a simple index plot of residuals was made to judge outliers and identify non-random trends over time. In addition, a bootstrapping method was used in which random binomial response fields were generated 100 times, with the same GAM fitted to these simulated data at each run, which allowed the estimation of confidence intervals of an empirical cumulative distribution function (CDF) of the (truly) binomial residuals (e.g. Wood, 2006). These simulations also allowed a variation of a runs test (Bradley, 1968) to be performed: As shown in Wood (2006), the number of runs in the model residuals were compared to those found in residuals from the 100 GAMs fitted to the simulated binomial fields, allowing assessment of whether these number of runs fell outside of the 3rd and 97th percentile, which would suggest a lack of randomness among residuals.

Results

Between 1981 and 2001 there were 18988 records of effort in combined French and Spanish purse-seine tuna fisheries data (aggregated per degree cell and month), which for skipjack and yellowfin tuna respectively, yielded 5660 and 6818 successful catch records of unassociated or free-swimming fish (referred to as FREE-schools or catches in the remainder of this study) and 16384 and 16249 successful catches of FAD-associated schools respectively. Here, and throughout the remainder of this thesis, a 'successful' catch refers to any non-null catch record for the species in question, for a given geographic cell and month.

Before exploration of GAMs, relationships between all pairs of environmental variables were explored: Scatter plots and correlation coefficients exposed some non-linear and linear relationships among variables (Figure 1), which exposes redundancy among highly correlated variables and potentially makes the model-fitting process numerically unstable and/or produces problems similar to over-fitting (Maunder and Punt, 2004). After exploration of many trial models, in which different covariates were included in combination or on their own, surface temperature, Z20, pseudo wind stress and mesozooplankton concentration were retained as the environmental variables included in the final models. The discarded variables were either correlated with one of these (but provided less convincing results than the kept variable), or produced unstable (among different models), non-significant or non-interpretable

smooths.

Results of GAMs containing only one-dimensional smooths (and associated with Figure 2-5), as well as their counterparts containing interaction factors, are summarised in Tables 1 and 2. By including interaction factors, the increase in deviance explained by models ranged between 0.7% and 3%.

Residual Checking

Residuals of presence-absence models adhere to the cumulative density function shape of simulated binary fields (Figure 2), although their residuals do not all fall within the 95% confidence intervals estimated from simulations. The confidence intervals in Figure 2 are very narrow due to the large dataset (N=18988) used in fitting the models. Index plots of deviance residuals do not show systematic patterns other than the intermittent clustering caused by annual fishing seasons. The number of runs in the residuals of presence-absence models reported, all fell between the 3rd and 97th percentile of those from the 100 simulated GAMs fit to the generated data, suggesting that the residuals of reported models were not significantly non-random.

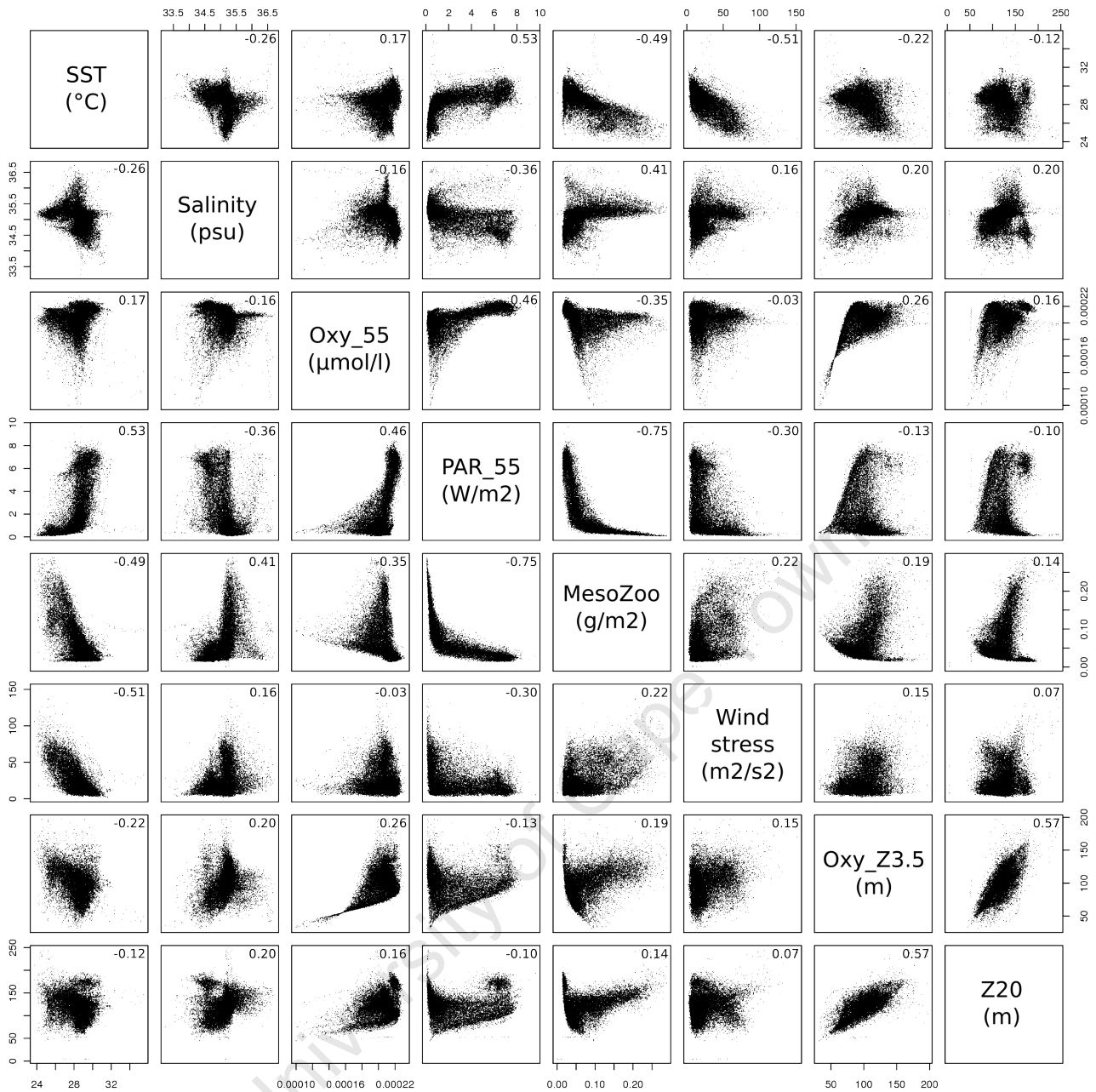


Figure 1. Pairwise scatterplots and Kendall tau rank correlation coefficients between environmental variables prepared for potential GAM exploration. Salinity=surface salinity; Oxy_55=oxygen concentration at 55 m; PAR_55=photosynthetically active radiation at 55 m; MesoZoo=integrated mesozooplankton concentration (to 200 m); Wind stress=pseudo wind stress; Oxy_Z3.5=depth of 3.5 ml/l oxygen threshold; Z20=depth of 20°C isotherm. N=18988 for surface values, less for variables at depth (due to bathymetry limits).

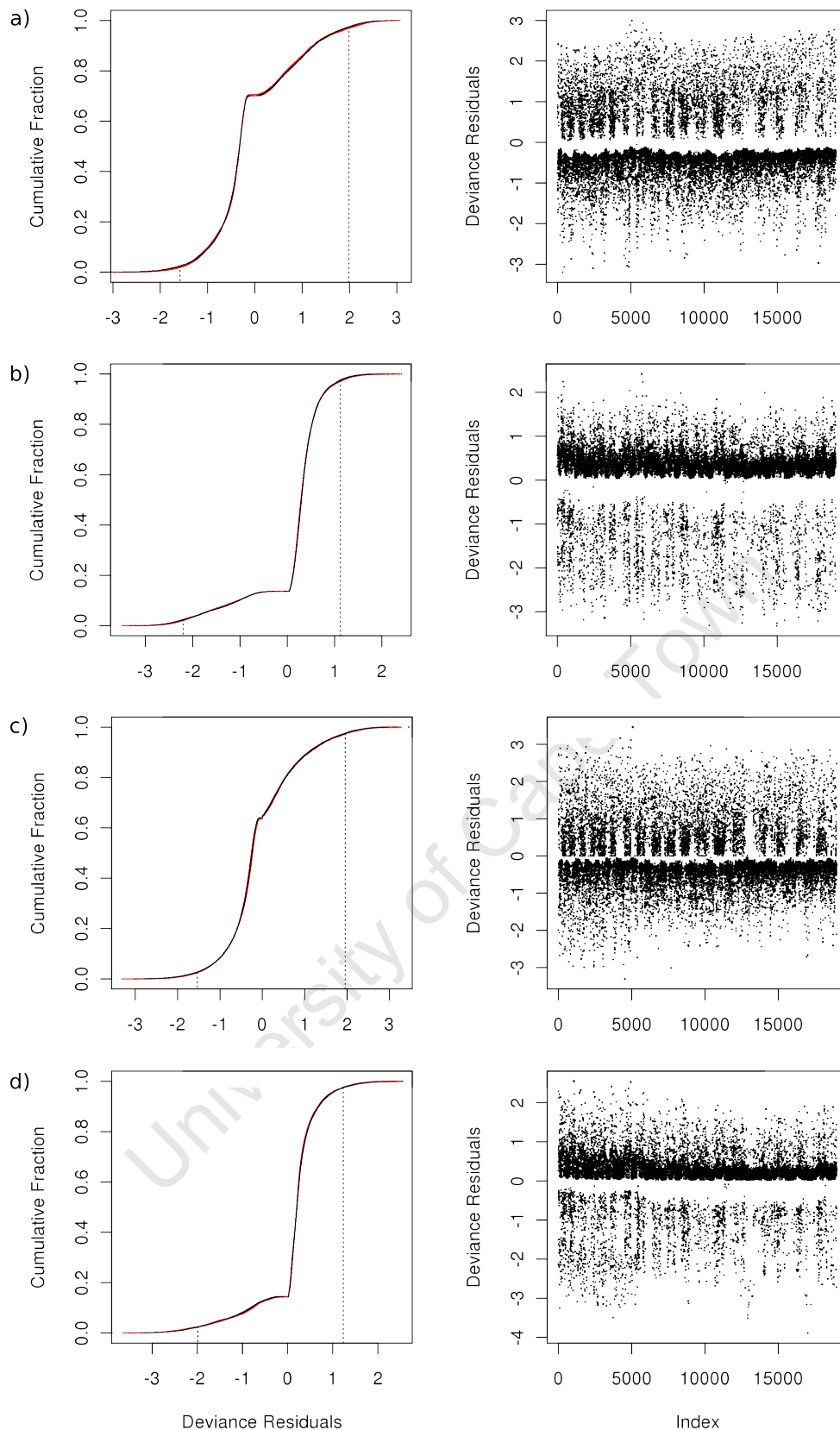


Figure 2. Residual checking of presence-Absence GAMs. On left are plotted empirical cumulative density functions showing simulated 95% confidence intervals (red lines) and deviance residuals (black points), while on right are index plots of deviance residuals, ordered by time. The residuals relate to models of skipjack a) FREE-schools

(sfree1p), b) FAD-schools (sfad1p) and yellowfin c) FREE-schools (yfree1p) and d) FAD-schools (yfad1p). Vertical dotted lines indicate the limits of 95% of residuals either side of the median. Black residual points and red confidence interval lines have been drawn with the same diameter.

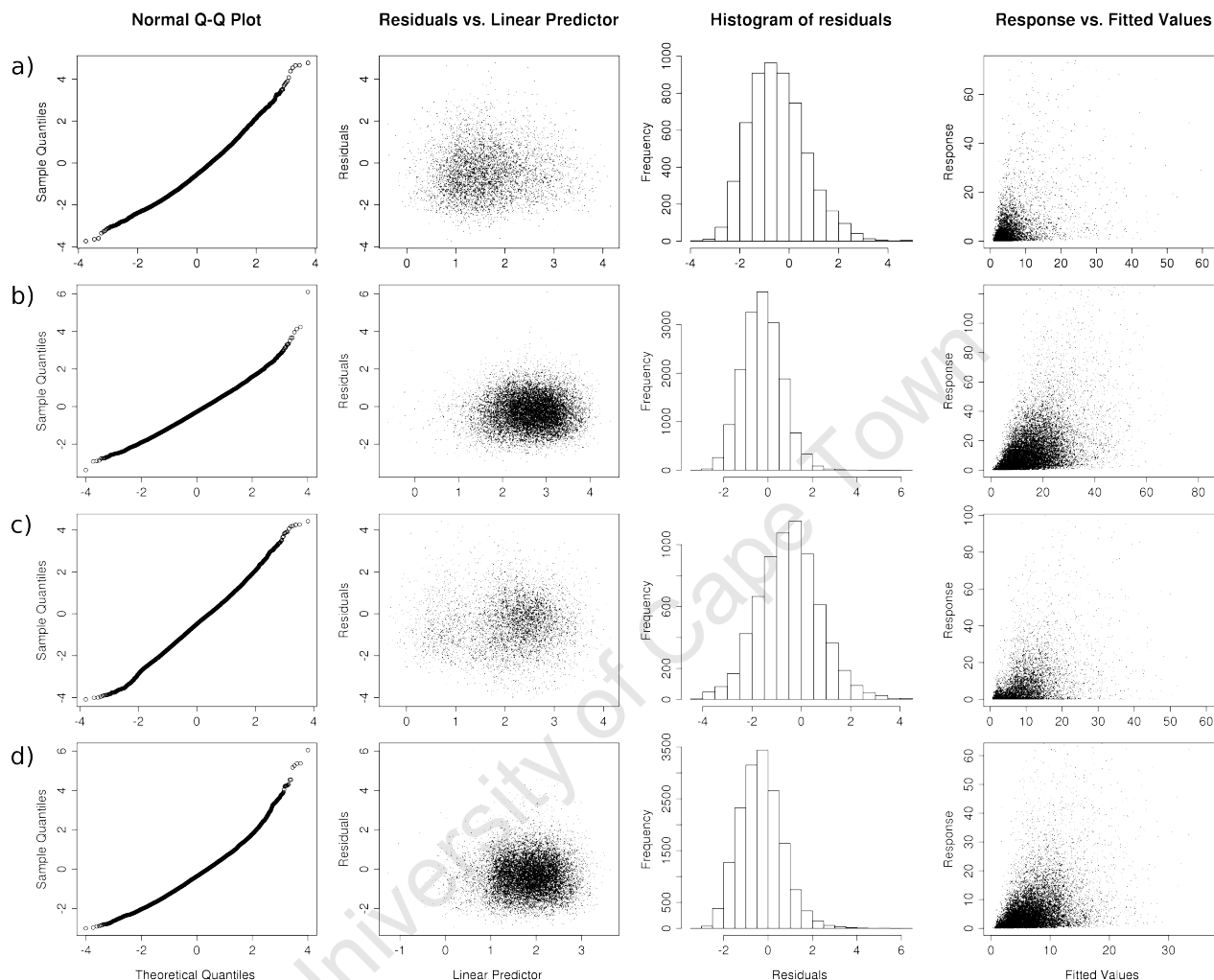


Figure 3. Residual plots for abundance GAMs of skipjack a) FREE-schools (sfree1a), b) FAD-schools (sfad1a) and yellowfin c) FREE-schools (yfree1a) and d) FAD-schools (yfad1a).

Similarly, residuals of abundance GAMs do not show obvious violations of assumptions, although they are slightly skewed and not perfectly normally distributed (Figure 3). They show no pattern in mean or variance when plotted against the linear predictor. Alternate distribution families (including discretization of the catch weights and use of discrete distributions) were explored, as well as a variety of link functions, however none of these efforts provided an improvement in residual diagnostics.

Table 1. Results of presence-Absence GAMs. Terms other than the intercept and error ($'+\beta_0+\epsilon'$) have been included. Statistics related to the fit are listed below each term. For example, 's(cov)' and 'te(cov1, cov2)' indicate a one-dimensional smooth and an interaction tensor product smooth of two covariates respectively; underneath them are reported the estimated degrees of freedom and F statistic. '+cov' indicates a parametric term, underneath which three coefficients are reported: the estimate, standard error and t-value respectively. *** p<0.001; ** p<0.01; temp5=surface temperature; Z20=depth of 20°C isotherm; wind=pseudo wind stress; mesoZoo=vertically integrated mesozooplankton concentration; fad-/free-catch=corresponding catch of FAD or FREE schools.

Model ID	Covariates and their statistics														Deviance Explained	Adjusted R-square	GCV score
sfree1p	s(SST)	+	s(Z20)	+	s(wind)	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	pA_fadcatch	36.2	0.41	0.78	
	3.11 5.05**		6.55 13.1***		6.97 2.84**		13.7 14.0***		11.4 365***		18.6 22.3***		-2.83 0.05 -52.9***				
sfree2p	te(SST,Z20)		+		te(wind,mesoZoo)		+		s(effort)	+	s(year)	+	pA_fadcatch	36.9	0.42	0.78	
	30.2 5.04***				76.6 3.25***				11.5 353***		18.7 22.9***		-2.84 0.05 -52.8***				
sfad1p	s(SST)	+	s(Z20)	+	s(wind)	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	pA_freecatch	27.4	0.29	0.58	
	7.35 8.70***		3.42 163***		8.00 10.7***		7.56 23.7***		9.39 185**		18.0 21.8***		-2.90 0.05 -61.3***				
sfad2p	te(SST,Z20)	+	te(wind,mesoZoo)	+	wind	+	mesoZoo	+	s(effort)	+	s(year)	+	pA_freecatch	29.5	0.30	0.58	
	90.3 8.84***		63.0 2.85***		-0.06 0.02 -3.26**		19.3 6.41 3.02**		9.49 186***		19.0 22.2***		-2.92 0.05 -61.2***				
yfree1p	SST	+	s(Z20)	+	s(wind)	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	pA_fadcatch	47.4	0.54	0.69	
	-0.12 0.03 -3.88***		12.5 42.0***		3.55 5.08***		8.26 40.7***		12.8 396***		18.7 35.1***		-4.30 0.07 -63.4***				
yfree2p	te(SST,Z20)		+		te(wind,mesoZoo)		+		s(effort)	+	s(year)	+	pA_fadcatch	48.8	0.55	0.68	
	101 7.75***				87.0 4.87***				13.1 381***		18.8 34.5***		-4.33 0.07 -63.2***				
yfad1p	s(SST)	+	s(Z20)	+	s(wind)	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	pA_freecatch	41.4	0.41	0.49	
	6.57 8.44***		5.64 37.1***		5.19 14.8***		8.12 9.70***		12.7 260***		17.6 71.3		-4.30 0.06 -75.9***				
yfad2p	te(SST,Z20)		+		te(wind,mesoZoo)		+		s(effort)	+	s(year)	+	pA_freecatch	44.4	0.43	0.48	
	162 3.68***				172 3.12***				12.7 262***		17.3 69.7***		-4.43 0.06 -75.5***				

Table 2. Same as for Table 1, but for abundance GAMs. N varies among different models and is listed in the table.

Model ID	Covariates and their statistics														Deviance Explained	Adjusted R-square	GCV score	N
sfree1a	s(SST)	+	s(Z20)	+	s(wind)	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	s(fadcatch)		25.4	0.16	1.56	5660
	7.36	3.23**	2.65	75.7***	9.40	4.19***	8.23	2.63**	10.3	54.0***	19.3	16.8***	5.37	11.2***				
sfree2a	te(SST,Z20)		+		te(wind,mesoZoo)		+		s(effort)	+	s(year)	+	s(fadcatch)		27.4	0.15	1.55	5660
	19.8	12.2***			56.4	3.67***			10.2	54.0***	19.4	17.1***	5.40	12.3***				
sfad1a	s(SST)	+	s(Z20)	+	wind	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	s(freecatch)		28.4	0.21	0.84	16384
	4.18	3.33**	9.38	65.3***	-0.01	.0006	-8.52***	13.1	32.6***	12.4	129***	18.9	34.7***	13.7	6.01***			
sfad2a	te(SST,Z20)		+		te(wind,mesoZoo)		+		s(effort)	+	s(year)	+	s(freecatch)		30.2	0.22	0.83	16384
	42.2	19.5***			79.0	10.2***			12.5	128***	18.9	33.7***	13.7	5.83***				
yfree1a			s(Z20)	+	s(wind)	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	s(fadcatch)		23.2	0.17	1.76	6818
			4.25	46.7***	8.51	9.64***	8.08	14.8***	9.79	24.3***	15.9	6.32***	10.6	16.0***				
yfree2a	te(SST,mesoZoo)	+	te(wind,Z20)	+	s(Z20)	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	s(fadcatch)		25.8	0.19	1.73	6818
	39.1	2.52***	35.5	3.42**	5.39	12.0***	8.10	2.95**	10.0	23.2***	15.1	7.36***	10.5	14.1***				
yfad1a	s(SST)	+	s(Z20)	+	s(wind)	+	s(mesoZoo)	+	s(effort)	+	s(year)	+	s(freecatch)		23.2	0.15	1.04	16249
	4.33	27.9***	4.28	37.2***	6.48	9.25***	12.0	23.0***	12.2	55.2***	19.2	40.1***	12.5	21.5***				
yfad2a	te(SST,Z20)		+		te(wind,mesoZoo)		+		s(effort)	+	s(year)	+	s(freecatch)		25.2	0.16	1.03	16249
	61.5	7.35***			91.7	5.92***			12.2	52.8***	18.5	42.43***	12.4	21.5***				

SST

French and Spanish purse-seine effort was recorded in surface temperatures ranging from ~ 24 - 32°C . Most of the SST plots (Figure 4, 5) suggest relatively flat or decreasing relationships with increasing temperature, except for the presence-absence models of FREE- and FAD-school skipjack, which suggest a peak at warmer temperatures (~ 28.5 and $\sim 30^{\circ}\text{C}$ respectively), with declines towards higher and lower temperatures.

Z20

The different models produced varying (and even opposing) Z20 relationships. All one-dimensional Z20 smooth terms involving FAD-associated schools were dominated by almost-monotonically-increasing slopes over the majority of well-sampled depths (Figure 4, 5). FREE-schools revealed the same increasing relationship for the skipjack abundance GAM (sfree1a), the opposite (monotonically decreasing relationship) for the yellowfin abundance GAM (yfree1a) and seemingly a mixture of the two relationships in presence-absence GAMs (sfree1p, yfree1p), with an inflection point at a Z20 depth of about 130-145 m.

Mesozooplankton

As with Z20 relationships, the shape of mesozooplankton smooths are more consistent among FAD- than FREE-schools. The former are dominated by an increasing relationship with greater mesozooplankton concentrations, although this levels off (and perhaps decreases slightly in yfad1a) at higher concentrations. FREE-school smooths differ between presence-absence models and those for abundance: Mesozooplankton smooths of presence-absence models suggest the highest chance of a successful catch at low concentrations and are dominated by a decreasing relationship as concentrations increase. Abundance smooths of mesozooplankton also suggest decreasing catch rates at higher concentrations, but only after an initial peak between about 0.03 and 0.05 g/m².

Wind

Wind smooths display a generally decreasing relationship between pseudo wind stress and CPUE, or probability of a successful catch, but with some variation in the detail of the shapes. Both presence-absence and abundance smooths for yellowfin FREE-schools rise to a peak at 20 - $40 \text{ m}^2/\text{s}^2$, before decreasing at higher values. The latter model's smooth is suggestive of increased abundances at high wind stress, although the widening confidence intervals do not allow confidence in this upward pattern.

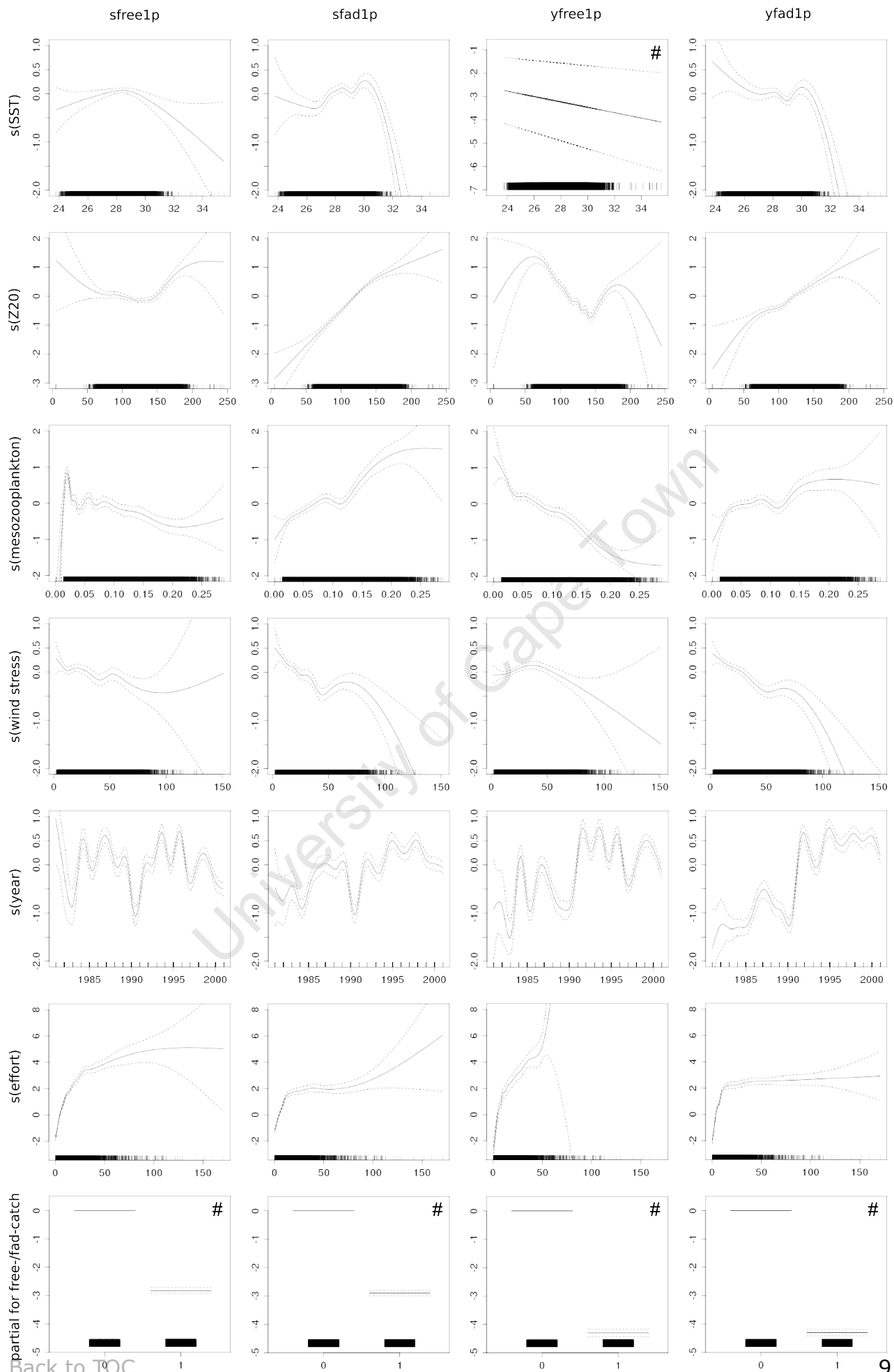


Figure 4. Smooths and parametric terms from fitted presence-absence models without interaction terms. Each column represents one model, identified by its name above. # identifies parametric terms, whose y-axis label should read "partial for cov" instead of the y-axis label for smooths, "s(cov)". X-axes represent covariate values with units of °C (SST), m (Z20), g/m² (mesozooplankton), m²/s² (wind stress), years, fishing days (effort) and binary value for null/positive catch (free-/fad-catch). Y-axes represent smooth function units, centered and on the scale of the linear predictor.

Effort

There is a clear difference between effort smooths of presence-absence GAMs and those of abundance, with additional differences between those of FAD- and FREE-schools. All presence-absence effort smooths suggest a steep initial increase, which then levels off. Abundance smooths on the other hand start with a steep initial decrease, after which FREE-school smooths suggest an increasing and thereafter leveling-off relationship, while FAD-school smooths show a continuing, though markedly less-steep, decline as effort increases.

FREE- Versus FAD-catch

Incorporation of a term describing the catch success of the fishing strategy not being modelled as the response term (i.e. including a FAD-catch explanatory term when modelling FREE-catches/CPUEs and vice versa), provided a marked decrease in GCV score and increase in the model deviance explained (more pronounced for presence-absence models). In addition, these model improvements were consistently greatest if the term was included in the form of a parametric categorical (presence-absence) term for presence-absence GAMs, and as a continuous term of catch values for abundance GAMs. All models point to a decreased CPUE (or chance of positive catch) as this explanatory FREE-/FAD-catch term becomes greater (or positive for binomial models; Figure 4, 5). This decrease is more pronounced in yellowfin models than in those of skipjack tuna.

Year Effect

Smooth functions of the year effect reveal clear interannual variability (Figure 4, 5). Sometimes this variability seems to be super-imposed on an increasing linear trend (e.g. all skipjack models except the FREE-school presence-absence GAM), or on a regime-shift-like step (e.g. yellowfin presence-absence GAMs).

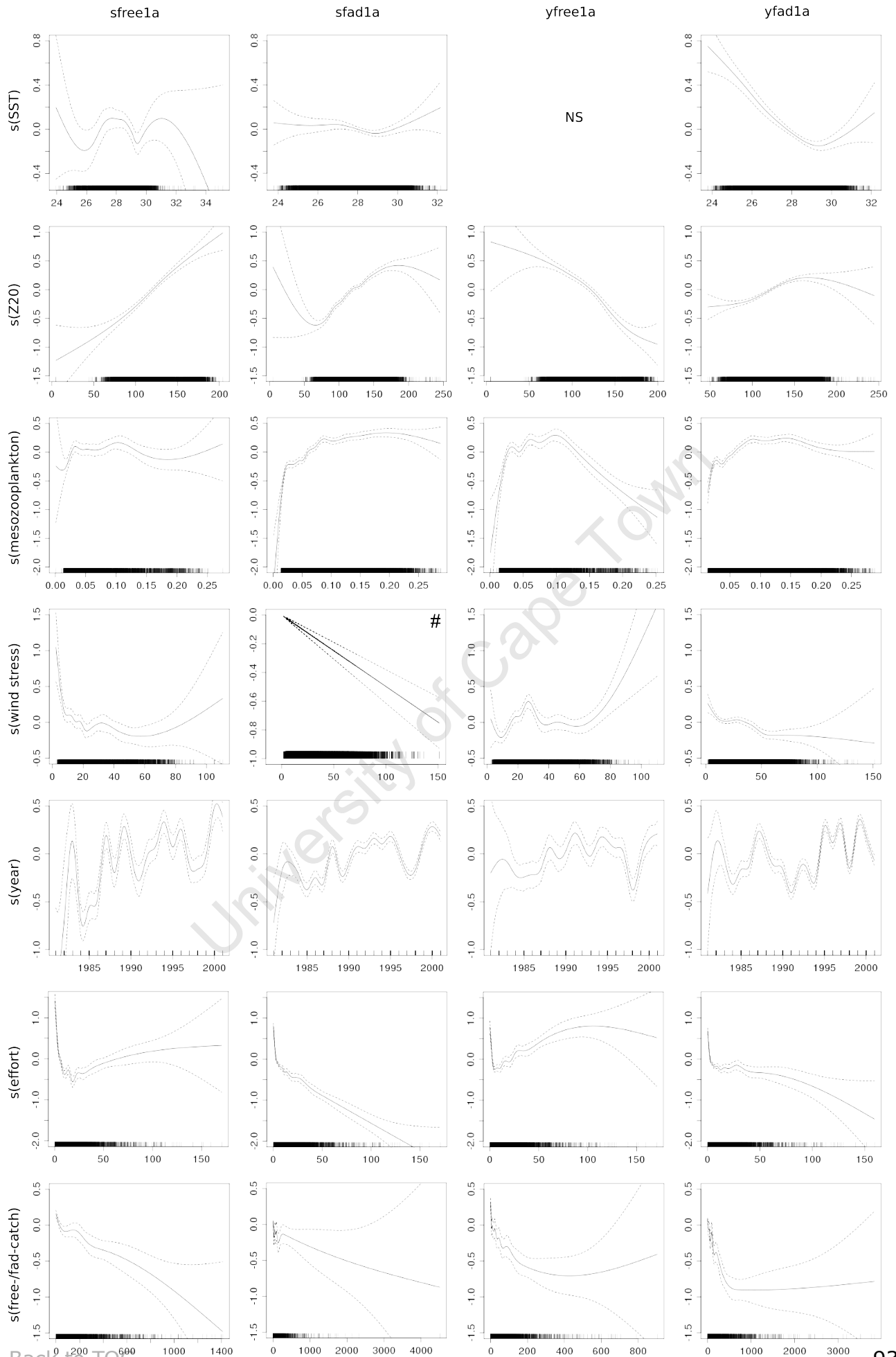


Figure 5. Same as for Figure 4, but smooths and terms are from abundance GAMs. NS=term not significant and thus removed.

Discussion

Model Fields, Fisheries Data, GAM Application and Assumptions

The NEMO-PISCES hindcasts used here were the most recent simulations run at the highest resolution available. The physics and near-surface dynamics of these models have been shown to compare well to observations, especially in tropical regions (e.g. Vialard et al., 2001; Lengaigne et al., 2003; Faure, 2007). In addition, the surface chlorophyll fields have been shown to agree well with estimates from SeaWiFS sensors in most parts of the Indian Ocean: Assessing the seasonality and the accumulated chlorophyll of phytoplankton blooms to isolate areas with specific bloom characteristics, Koné et al. (2009) showed that results compare well between the model and SeaWiFS, with discrepancies mainly in coastal areas and some northwestern parts of the Arabian Sea, as well as a region around southern Madagascar. Focusing on the Seychelles-Chagos ridge area, Resplandy et al. (2009) show that intra-seasonal, seasonal and interannual variability of surface chlorophyll is well simulated by the model relative to SeaWiFS records. Although the short overlap of model outputs (1958-2001) and SeaWiFS (October 1997 onwards) makes comprehensive comparisons difficult, the results in Koné et al. (2009), Resplandy et al. (2009) and Chapter 2, suggest that surface biogeochemical dynamics are being adequately simulated in the model to provide realistic estimates of regional chlorophyll changes. If biogeochemical dynamics are well simulated in hindcasts, it provides confidence to using outputs of mesozooplankton as a proxy of tuna prey (and their food), even though detailed validation of these fields has not taken place. Some previous comparisons of pelagic predator catches with the environment have attempted to include measures of available prey, by either applying a temporal lag to phytoplankton production (Garcia and Cota, 1996) or to physical fields (e.g. Bigelow et al., 1999; Maury et al., 2001a) which could represent the time needed for trophic transfers of energy and/or aggregation of prey organisms, following changes in the physical environment or productivity. Bertignac et al. (1998), Lehodey et al. (1998), Maury (1998) and Maury et al. (2001b) have shown how modelling the trophic conversion of primary productivity to secondary production, while taking into account its redistribution by currents and random diffusion, can provide estimates of potential

tuna forage which match up well to historical catch rates. The model used here is more detailed than these, explicitly modelling dynamics involved in physiological processes (including ingestion/assimilation, growth, maintenance, reproduction, mortality) and predator/prey relationships, that control the flow of energy to higher trophic levels, as well as the physics and three-dimensional redistribution of organisms. Such modelled fields are certainly our best estimates of zooplankton biomass at ocean-basin scales. Yet one has to acknowledge that the mesozooplankton outputs have not been adequately validated and so interpretations from their analysis need to be made with this uncertainty in mind.

French and Spanish catch statistics were used in this study, as they are among the purse-seine datasets that have been most thoroughly interrogated and are judged to be of reliable quality, make up a significant proportion of Indian Ocean catches, and provide good temporal and spatial coverage of historical purse-seine activity (A. Fonteneau, personal comment). The catch-by-size records available from the same fleets are at a coarser spatial resolution (5° by 5°), but were downscaled to the 1° by 1° cells in an a priori decision to separate mature (>1 m) and immature (<1 m) yellowfin tuna, as different life-stages could have differing habitat preferences. The initial results however showed no clear differences or advantage to making this distinction and therefore it was discarded. A difference in fishing strategy and gear (if artificial FADs are considered part of fishing gear) separates FAD-associated catches from those made on unassociated schools, and will likely modify the catchability constant (q ; e.g. Maunder and Punt, 2004). Therefore an a priori decision was taken to investigate FAD- and FREE-catches separately.

A common problem of analysing catches of oceanic predators, is the handling of a large number of zero- or null-catches (e.g. Bigelow et al., 1999; Punt et al., 2000; Shono, 2008). Simply discarding these zero-records can bias results (inflating catch rates), while adding a small constant to each catch value may be inappropriate and difficult to interpret, in that the size of this constant may influence results obtained (Maunder and Punt, 2004). When dealing with null-catches, it is important to consider the process that brought them about. If for example, the same process is responsible for both null-catches and non-null records, then the use of (discrete) distributions, which expect zero-values, or modified distributions that expect an inflated number of zero-values, may be appropriate (Maunder and Punt, 2004).

In the present study however, effort was recorded separately to catches and there is unfortunately no differentiation between effort directed at FAD-associated or FREE-schools. As a result, all FAD- and FREE-catch records, if assessed separately, are potentially associated with a proportion of 'indistinguishable' effort, that was actually directed at the 'other' fishing method not under consideration. This extra effort results in an artificial inflation of null-catches, as records of (undifferentiated) effort are recorded where there may have been no effort directed specifically at the FREE- or FAD-catch under assessment. The delta approach was therefore employed, so that the presence/absence response (containing the inflated zeroes) was modelled, and thereafter abundances (CPUE) were modelled separately, on condition that a positive catch was present.

GAMs are highly flexible relative to linear regression techniques and as a result require special care in their application. Redundant (highly correlated) environmental variables and those that were unstable (among different model designs), were discarded. Residual plots, as well as the GCV score and total deviance explained, were consulted throughout the development of models, with the ambition towards optimizing these. The models presented above, are however not those that could explain the highest deviance possible with all available significant covariates included. Rather, they represent those which explain the highest deviance, while limited to relationships (and interactions) of covariates that are meaningful to interpret in terms of tuna abundance or catchability effects.

Residual plots, and comparisons with simulated (true) random binary residuals, were employed to assess presence-absence models. As is commonly the case with biological and environmental data (Bakun, 1996), efforts to find the best distribution, link function and model design, did not yield perfectly distributed residuals. The presence-absence residuals lie partially outside the simulated 95% confidence intervals of the empirical CDF (Figure 2), while those from abundance models suggest a slight skewness (Figure 3). However none of the residual checks identified an alarming feature, which would identify a clear violation of assumptions. Therefore the model results should be interpreted cautiously and interpretative emphasis has been reserved for covariate patterns that are highly significant and/or consistent among different models.

The inclusion of two species, separate examination of FAD- versus FREE-catches and the use of a delta approach to investigate both presence-absence as well as abundance models, has resulted in a multitude of models, residual plots and covariate relationships to report on. However this strategy has allowed the results and covariate relationships to be approached from a number of different perspectives and led to productive comparisons yielding insights that would not have been forthcoming from only one model or perspective. As it is the shape of the tuna-environment relationships that are of greatest interest here, and in order to discuss interpretations of the covariate relationships efficiently, a strategy has been taken to do so one covariate at a time, rather than to report and discuss each model separately and potentially repeat similar discussions several times.

Comparison of FREE- Versus FAD-results

An a priori hypothesis was that FAD-associated catches would not be as instructive as FREE-catches in describing tuna habitat, as FADs modify the free-swimming behaviour of open-ocean predators (Dempster and Taquet, 2004) and therefore might bias or cloud the environmental preferences of fish caught underneath them. FREE-schools, on the other hand, are caught roaming their habitat in an unrestricted manner. Surprisingly, results revealed the opposite: FREE-school catches or CPUE seem to be largely influenced by catchability effects, while those of FAD-associated schools mostly show environmental relationships indicative of habitat preferences. This unexpected result can be explained in terms of spatial scales.

A FAD undoubtedly modifies tuna behaviour and attracts or aggregates them, as evidenced by tracking experiments (e.g. Ohta and Kakuma, 2005; Dagorn et al., 2007) and their widespread adoption to augment catches (Fonteneau et al., 2000; Moreno et al., 2007). Fish aggregate underneath the FADs, within the ~200-300 m reach of purse-seine nets, frequently in dense schools near the surface (Josse et al., 2000). This aggregating behaviour under the FADs seems to reduce the importance of catchability effects, which are often related to the vertical escape of fish or a reduced efficiency of fishing gear (e.g. Evans et al., 1981; Maury et al., 2001a). However FADs can act only on the available background tuna abundance and attract fish from a finite (and relatively small) area. If habitat conditions are unsuitable, then there would be a smaller pool of background tuna abundance for FADs to act on and these FADs would

attract proportionately fewer tuna than those in areas of 'good habitat'. The FADs thus act to filter out much of the catchability signal, bringing to the fore the environmental preferences or abundance relationships, which are otherwise masked by the former.

In addition to likely accumulating greater numbers of tuna, the FADs drifting in 'good habitat' (tuna-rich waters) will replenish aggregations faster after having been fished, simply due to the greater rate of encounters between FADs and higher densities of tuna. Therefore one is likely able to successfully fish FADs in rich tuna grounds more frequently, in addition to obtaining larger yields per set. So although they modify fish behaviour at small spatio-temporal scales, at the larger scales of consideration here (1° by 1° and monthly), FAD catches effectively remove (some) catchability factors seen in FREE-schools, seemingly acting as efficient 'samplers' of the background tuna environment and thereby revealing habitat or abundance relationships.

SST

Temperature is the environmental variable most commonly compared to tuna catch rates or tracked movements, likely because it is one of the most well-sampled variables in the ocean. It is also well-established as having important physiological implications to tuna (Dizon et al., 1977; Barkley et al., 1978; Sharp and Dizon, 1979) and thereby imposes restrictions on their horizontal and vertical distribution ranges.

Barkley et al. (1978) experimentally determined the temperature range of captive skipjack tuna to be about 18-30°C. The authors suggest smaller fish would be comfortable in the upper part of this range, often swimming near the surface in warm tropical waters, while large individuals would prefer temperatures as low as 20°C and therefore would inhabit greater depths in the same tropical regions (see also Neill et al., 1976). Consistent with those estimates, Andrade and Garcia (1999) showed that off the Brazilian coastline, Japanese pole and line catches of skipjack took place in waters of 17-30°C with highest CPUEs common in 22-26.5°C. Within the Indian Ocean, there seem to have been no published studies using tracking data or employing fisheries catches, which have compared skipjack distributions or movements to their SST environment.

Yellowfin tuna inhabit tropical waters similarly to skipjack, although with their larger thermal inertia (size) and more sophisticated thermoregulatory abilities, are able to

extend their ranges to cooler waters than do skipjack (Graham and Dickson, 2004). Inspection of Japanese longlining data in Wise et al. (2002) show that catches of yellowfin have been made at SSTs of $\sim 14\text{--}32^{\circ}\text{C}$ in the Indian Ocean, although the extremities of this range are perhaps slightly exaggerated by the coarse resolution (5° by 5°) of the catch and effort data. Maury et al. (2001a) suggest that the majority of yellowfin catches in the Atlantic Ocean take place in surface waters of $25\text{--}30^{\circ}\text{C}$, while adult fish prefer surface temperatures of $26\text{--}29^{\circ}\text{C}$ and juveniles appear to favour those warmer than 27°C .

Taking into account the above ranges, one could expect a dome-shaped response of purse-seine catches to surface temperature, with the peak corresponding to the preferred temperature range of the species under consideration (though perhaps shifted slightly to the right, as caught fish are not necessarily inhabiting only the very surface), as seen in Andrade and Garcia (1999) and for larger yellowfin in Maury et al. (2001a). However this was not the case here. Only skipjack presence-absence models (sfree1p and sfad1p, Figure 4) suggested peaks of successful catches (at $\sim 27\text{--}30^{\circ}\text{C}$), with decreases above and below. The remaining temperature smooths were relatively inconclusive, or for yellowfin catches suggested decreasing relationships as temperature increased (Figure 4, 5). The lack of expected temperature relationships is however not surprising, given the fact that only a relatively narrow (and warm) range of tropical waters was sampled by the purse-seine fleets ($\sim 24\text{--}32^{\circ}\text{C}$). The coldest surface waters fished are above those recognised as representing a limit to either skipjack or yellowfin tuna (Graham and Dickson, 2004). The highest temperatures are however above the upper limits of both species (e.g. Barkley et al., 1978; Sharp and Dizon, 1979) and congruently, three of the four presence-absence models suggest relatively steep decreases at highest surface temperatures. The lack of meaningful SST relationships with Brazilian longline catches in the equatorial Atlantic (Zagaglia et al., 2004), may similarly be due to the narrow SST range ($25\text{--}29^{\circ}\text{C}$) sampled and its correspondence with SSTs typically associated with yellowfin distributions (e.g. Maury et al., 2001a).

When comparing SSTs to tuna catches, one has to bear in mind that outside of the coolest extremities of their range, the actual surface temperature is likely less consequential compared to the vertical temperature profile, considering that tuna would rarely be swimming right at the surface, unless there is a constraint forcing

them upwards from below (such as a steep, shallow oxycline). From a habitat suitability point of view, it is the vertical temperature profile which potentially limits a tuna's habitat volume (e.g. Maury, 2005), and perhaps more importantly, access to below-surface prey resources. This point is supported by the fact that interactions of surface temperature and Z20 were found to be highly significant and frequently led to the greatest explanation of model deviance (Table 2).

Z20

As touched on above, thermocline depth plays a potentially important role in controlling the vertical behaviour of tropical tuna (e.g. Brill et al., 1999). As a result, it can limit their habitat volume (e.g. Bertrand et al., 2002b), as well as affecting their catchability due to the depth-specificity of fishing gear. A shallow thermocline for example should concentrate yellowfin and skipjack tuna closer to the surface; an effect that has been demonstrated by negative relationships between surface gear catch rates and thermocline depth (e.g. Maury et al., 2001a). Deeper-targeting longline gear on the other hand, would likely produce the opposite (increasing) relationship between catch rate and thermocline depth, as confirmed by Maury et al. (2001a).

A mixture of positive and negative Z20 relationships emerged from the current analyses (Figure 4, 5), even though only purse-seine (surface) catches were being investigated. As a (concentration of fish in upper layers) catchability effect, should drive a negatively-sloping Z20 relationship, the positively-sloping smooths seen in all models of FAD-associated catches, as well as the skipjack abundance model of FREE-catches, are interpreted as a greater local abundance of fish in a deeper habitat. All other things being equal, a deeper thermocline should allow better access to prey resources which attempt to escape predation by avoiding sunlit surface layers. Supporting this line of thought, Lehodey et al. (1997) showed that skipjack catches in the western Pacific were greatest in the equatorial warm pool, which has warm surface temperatures and a deep thermocline. The above finding has important implications in the assessment of tuna habitat quality, both in terms of management and predictive ability, as it suggests that deeper thermoclines (or greater habitat volumes) are beneficial to skipjack and yellowfin tuna. The limit of a 'habitat volume', as related to vertical profiles of temperature and oxygen, has been applied to in situ data (e.g. Bertrand et al., 2002b) and in modelling studies (e.g. Dueri and Maury,

2010). However the GAM relationships presented here are the first empirical evidence (as far as the author is aware) that greater tuna abundances are related to a deeper thermocline.

Abundance GAMs of unassociated (FREE) yellowfin catches showed a negative Z20-CPUE relationship, indicative of a catchability (concentrating) effect of Z20. Presence-absence models of both skipjack and yellowfin suggest a mixture of the decreasing catchability effect, and dominating at deeper Z20 depths, the increasing habitat/abundance relationship. Why do the different models express the catchability or habitat effect to differing degrees? One obvious feature is that all FAD-associated models reveal a positive habitat effect of Z20, while FREE-catches produced variable and a mixture of relationships (Figure 4, 5). As discussed previously, catchability effects seem to be expressed more strongly in GAMs of unassociated (FREE) catches, while such effects are largely filtered by the modified behaviour of FAD-associated tuna, thereby revealing the abundance/habitat effects.

Why do skipjack and yellowfin FREE-school CPUEs reveal opposite relationships with Z20? Due to their lesser thermoregulatory abilities and smaller thermal inertia compared to larger yellowfin tuna (Graham and Dickson, 2004), skipjack distributions may react more strongly to habitat volume (Z20 depth) than do yellowfin, which have a capacity to dive well below the thermocline for brief periods (Dagorn et al., 2006; Schaefer et al., 2007). Comparing the remaining models, the positive habitat relationship does seem to be more pronounced for skipjack tuna than for yellowfin. In addition, there could feasibly be a difference in the flight behaviour of the two species. Due to their greater diving abilities, yellowfin may have a strong downward-fleeing escape instinct when they sense danger (e.g. in the form of enclosing nets and engine noise), whereas skipjack may behave differently in their flight response. If the diving (e.g. thermoregulatory or low-light sight) abilities of their predators are more advanced than those of skipjack, there would be less evolutionary pressure to flee downwards, which might explain a weaker catchability relationship seen with thermocline depths.

The presence-absence model of yellowfin FREE-schools (and to a lesser degree skipjack) show an interesting mixture of the negative catchability effect and positive habitat effect, with a clear inflection at just under 150 m. Considering that purse-seine

nets have a finite depth limit, it is quite likely that there would be a threshold thermocline depth, above which a shallower tendency would increasingly concentrate fish within surface layers, increasing chances of a successful catch, while below the threshold depth, there would be no further decrease in catchability and a positive habitat effect might become the dominant factor as the thermocline depth increases further.

Mesozooplankton

Forage is recognised as one of the environmental parameters that is potentially most important to tuna distributions and is likely to impact their behaviour and distribution on a wide range of spatio-temporal scales (e.g. Blackburn and Laurs, 1972; Lehodey et al., 1998; Lehodey, 2001; Maury et al., 2001b; Bertrand et al., 2002a; Fonteneau et al., 2008; Dueri and Maury, 2010). Tracking experiments together with coincidental acoustic surveys of the water column, have revealed how tuna adjust their swimming depths and diving behaviour in order to exploit prey aggregations (e.g. Josse et al., 1998), commonly leading to diel patterns in their vertical positioning as they track the movements of the deep sound-scattering layer (e.g. Musyl et al., 2003; Weng et al., 2009). Stomach content analyses are useful to shed light on prey preferences (e.g. Ménard et al., 2000; Potier et al., 2007) and together with the use of acoustic and experimental longline surveys, Bertrand et al. (2002a) managed to describe the pelagic prey environment, together with behavioural and trophic interactions of three tuna species in French Polynesia. As was concluded in the same paper, the passive longlining gear used was providing biased samples of mostly unsatiated individuals, and seemingly not sampling tuna in dense prey patches effectively, suggestive that longlining data may not be suitable for describing tuna forage relationships.

Due to an almost complete lack of data on tuna prey abundances or distributions, evidence of broadly-applicable functional relationships between pelagic predators and their forage have similarly been lacking. Authors have attempted to incorporate estimates of trophic productivity in comparisons with fisheries data, by including chlorophyll (or primary production; e.g. Zagaglia et al., 2004; Zainuddin et al., 2006; Song et al., 2009), sometimes with a time-lag (e.g. Garcia and Cota, 1996). However none of these studies succeeded in providing a convincing functional response of tuna catches to productivity.

In the current analyses, mesozooplankton smooths showed notable similarities within FAD-associated models, less so within FREE-associated relationships, and only slight differences between species (Figure 4, 5). All FAD-associated models suggest an increasing, and then levelling off, relationship between catch rate (or chances of positive catch) and mesozooplankton concentrations. Assuming tuna follow an ideal free distribution (Fretwell and Lucas, 1969; i.e. that tuna density is proportional to the GAM smooth), the shape of these relationships are suggestive of a Holling type II functional response to tuna forage (Holling, 1959), which is assumed in theory (Gamblin et al., 2004; Dueri and Maury, 2010), but for which empirical evidence has not been shown before (as far as the author is aware).

Considering the importance of food resources to the high metabolism of tuna, the initial increasing slopes seen in the mesozooplankton relationships of FAD-associated models are not surprising: Areas with higher tuna forage would be expected to sustain higher tuna densities. However this increasing relationship then levels off and even shows signs of decreasing at highest mesozooplankton levels (Figure 4, 5). The levelling-off and decreasing parts of the relationship might be explained by the fact that highly productive waters may often be hostile to tuna in respect to other environmental variables. Surface-feeding tuna such as yellowfin and skipjack are visual predators (Lehodey, 2001) and thus likely avoid turbid productive waters. In addition, highly productive regions are commonly fuelled by cold upwelling waters and/or may exhibit low oxygen concentrations near the surface, both of which would provide hostile environments to tropical tunas.

Presence-absence models of FREE-catches suggest that the chance of a successful catch decreases as mesozooplankton concentrations increase (Figure 4). Corresponding abundance models (sfree1a, yfree1a; Figure 5) also suggest a decreasing relationship at mesozooplankton concentrations higher than $\sim 0.1 \text{ g/m}^2$. These negative slopes could be interpreted as a modification in behaviour by unassociated schools, which reduces their catchability as mesozooplankton increase (despite the assumedly greater tuna abundances as interpreted from the FAD-associated smoothing functions).

For example, the negative slope could be explained if the large FREE-schools targeted by purse-seiners, are predominantly made up of spawning adults (as is believed for

yellowfin catches; A. Fonteneau, personal comment), which are made more vulnerable as a result of their spawning behaviour. Spawning aggregations likely respond differently to mesozooplankton densities than non-spawning schools. As put by Blackburn and Williams (1975): "Skipjack may be distributed according to the environmental requirements of their larvae when spawning and according to their own feeding requirements when not spawning". Spawning individuals might for example, search out regions of low mesozooplankton concentrations, as these likely provide lower predation pressures on developing eggs. Evolutionary development of such a strategy would, of course, require that once hatched, larvae would find adequate food resources in these unproductive regions to survive, or perhaps more likely, that the eggs would encounter more productive downstream food resources (e.g. oceanographic fronts or eddies) by the time that hatched larvae required food intake. Evidence supportive of the above theory, is the fact that average tuna sizes caught from FREE-schools are indeed notably larger for yellowfin (and slightly larger for skipjack), than are FAD-associated catches (Anon, 2009b).

The interesting non-linear smooths shown here between purse-seine catches and the mesozooplankton proxy of forage abundance, are (to the author's knowledge) the first time such predator-prey functional relationships have been shown from commercial tuna catches. Of course they need to be treated with appropriate caution, considering the uncertainties of mesozooplankton fields. Zagaglia et al. (2004) did show a marginally significant negative relationship between catch rates of yellowfin and remotely sensed chlorophyll using Brazilian longline data in the equatorial Atlantic. Although suggesting this relationship was not key in affecting yellowfin distribution, the authors noted that it might be caused by a preference for clearer waters. Given the low range of chlorophyll values in their study (mostly $<0.4 \text{ mg/m}^3$) however, this explanation seems unlikely.

Wind

Evans et al. (1981) showed how wind speeds in excess of 8 m/s were accompanied by a reduced success of purse-seine sets in the eastern tropical Pacific. Subsequently other authors have included wind in their assessment of fishery data (e.g. Maury et al., 2001a; Zagaglia et al., 2004; Bigelow et al., 2006), due to its potential effect on gear or fishing efficiency. The effect of pseudo wind stress on CPUE and probabilities of a positive catch in GAMs reported here, was generally negative, although the shape

of non-linear smooths was not consistent among models (Figure 4, 5). Not surprisingly, most presence-absence models showed sharply declining chances of a positive catch at highest values of pseudo wind stress (Figure 4), although the same effect is not seen in abundance models (Figure 5).

Even though strong winds (and accompanying rough seas) very likely have a significant effect on fishing efficiency (thereby catchability), and also the ability to visually detect surface schools of tuna, an accurate description of these effects is unlikely to come from comparisons with monthly-aggregated wind fields. A case in point is that abundance models are based on only successful monthly 'samples' of purse-seine activity, and yet the range of pseudo wind stress values recorded is similar in abundance FAD-school models to those of presence-absence models (which have many unsuccessful records, of which some could be expected to be due to bad weather; Figure 4, 5). Wind strengths are commonly highly variable and extreme events occur on the order of days or shorter. Therefore average wind stress over a month will give only a very rough guide as to how many 'fishable days' there were, or how the efficiency of fishing attempts might have been affected during that month. This lack of adequate resolution, combined with the fact that the fishing fleets largely target certain species and fishing modes (FAD-/FREE-schools) in specific regions and during certain seasons (with specific wind regimes), might explain some of the unaccounted patterns seen in pseudo wind stress smooths, such as the unexpected (increasing) relationship seen in yellowfin FREE-school CPUEs (yfree1a).

Additional Variables

Although several additional environmental variables were initially explored (e.g. Figure 1), they were correlated with and superseded by those discussed above, or did not provide meaningful relationships interpretable in terms of catchability or habitat. The lack of results are of some interest in themselves, while some of the discarded variables did show potentially interesting relationships.

Although salinity has been suggested to play a potential role in tuna distributions (e.g. Bigelow et al., 1999; Maury et al., 2001a), the smooths emanating from analyses here (not shown), though significant, were not consistent among models and did not provide any indication of being interpretable in terms of tuna behaviour or catchability. Their significance was likely due to the spatially structured fisheries catches occurring

on background basin-scale salinity patterns.

Oxygen undoubtedly plays an important role in limiting the vertical habitat of tuna (e.g. Barkley et al., 1978; Brill, 1994), at least in low-oxygen regions (Stramma et al., 2008). However smooths of oxygen concentration at 55 m were relatively flat and did not offer meaningful insights (not shown). On the contrary, the threshold depth of 3.5 ml/l oxygen (estimated to provide a lower limit to both yellowfin and skipjack tuna; Barkley et al., 1978; Evans et al., 1981; Brill, 1994) provided some significant and meaningful relationships (not shown). However as the thermocline is involved in stratification, which in turn affects the oxycline (Ingham et al., 1977), the depth of the oxygen limit was highly correlated to Z20 depth (Figure 1). The smooth of the oxygen threshold often became far more meaningful and significant only after removal of the Z20 term, and almost invariably showed a similar shape as had Z20 before removal. On the contrary, inclusion or removal of the oxygen threshold covariate did not impact much on the Z20 smooths, hence these were retained as the more stable and preferred explanatory covariates. The effect of Z20 and the depth of the oxygen threshold seem similar, but due to the correlation of these two covariates, confident separation of their individual role on fisheries catches may be difficult and provides a potential avenue for future research.

Effort

Presence-absence models suggest that chances of a successful catch sharply increase with increasing effort, although this effect quickly levels off (Figure 4). A very similar effort smooth was shown by Maury et al. (2001a) for young yellowfin tuna in the Atlantic Ocean. Using an advection-diffusion-reaction model and simulating fishing effort, Maury and Gascuel (2001) subsequently demonstrated how the heightened efficiency in locating fish aggregations due to cooperation (and/or spying) among fishing vessels, could be responsible for such non-linear relationships between CPUE and effort. The patchy nature of tuna aggregations (e.g. Fonteneau et al., 2008) means that one vessel searching a region of ocean will be less effective at finding a concentration of tuna than (for example) five vessels searching the same region. If the vessel which finds the concentration, immediately attracts the other vessels towards the tuna aggregation, the average 'unsuccessful' searching time of vessels will be dramatically shortened, compared to if each vessel carried on searching based on its own (spatially-limited) intelligence. Such cooperative (and/or spying) behaviour

of vessels is clearly demonstrated by the example documented in Fonteneau et al. (2008) and likely leads to hyperstability of the stock (Gaertner and Dreyfus-Leon, 2004), a situation in which CPUE indices would decrease more slowly than true abundances (Hilborn and Walters, 2004).

As FADs aggregate tuna from the surrounding background population and are monitored or tracked by vessels (Fonteneau et al., 2000), they help tuna fleets locate and fish the available tuna concentrations in an area, thereby saturating (or levelling-off) the effort curve sooner than would be seen for FREE-school smoothing functions, where searching time is of greater importance. The effort smooths of FAD-catch models support such reasoning, as they level off more abruptly and earlier than those of the corresponding FREE-catches (Figure 4).

Inclusion of effort covariates in models of a CPUE response is not common, although it has been done before (e.g. Maury et al., 2001a; Fonteneau and Richard, 2003). Catch rate is commonly used as a measure of abundance and assumes that catches are proportional to the product of effort and fish density: $C = qEN$ (1), where C is catch, E is effort, q is the catchability (or the fraction of abundance caught by one unit of effort) and N is the resource abundance (Maunder and Punt, 2004). CPUE is then

rewritten as $\frac{C}{E} = qN$ (2) and including an effort covariate when modelling CPUE, therefore implies a remaining effort term on the right side of equation (2) and/or a quadratic effort term in (1). What abundance GAM results shown here and elsewhere (Maury et al., 2001a) suggest, is that catchability (q) is not independent of the effort term and that even after catch has been standardised (divided) by effort, there remains a non-linear effect of effort in the catchability constant, which is ignored by most fisheries scientists.

All abundance models show a very steep initial decline in effort smooths (Figure 5), which is likely caused by exceptionally high CPUE values at lowest effort values (causing inflated average CPUE at low effort; not shown). These exceptionally large CPUE values might be due to the stochastic nature of purse-seine catches, together with the temporal structuring of effort into calendar months: There will occasionally be a degree square and month sample, where very low effort (perhaps a single purse-seiner crossing a relatively small area/corner of a grid square) happens to result in

one or more successful purse-seine sets, causing an exceptionally high CPUE for that month and cell. However in an unbiased sampling design, such a stochastic effect would be counter-balanced by a proportionately greater number of small or zero-catches at low effort values. The fact that this is not the case, strongly suggests there might be either a) an under-reporting of small effort values when catches are insignificant or unsuccessful, or b) a bias towards under-estimating effort at small values, so that average CPUEs are artificially inflated at the low effort values. Whatever the cause may be, this artificial bias should be taken into account in the use of these data and its importance to stock assessments and other statistical investigations of CPUE should be further evaluated. Models that excluded low-effort CPUEs (not shown) revealed very similar smooths to those shown in Figure 4, except that they lacked the initial steep decline in effort smooths. It seems therefore, that the non-linear effort smooths in Figure 4 are adequately describing, and thereby accounting for, the CPUE bias at low effort values.

If one ignores (or removes) the initial declines in effort smooths discussed above, the remainder of each smooth is more comparable to those of presence-absence models. The same cooperation and/or spying effect could explain unassociated abundance smooths, which suggest a positive, but levelling-off relationship of CPUE with effort, similar to, though not as steep as those seen in presence-absence models. FAD-associated abundance models however point to a decreasing CPUE with greater effort, which seems more pronounced for skipjack than yellowfin CPUE. As FADs act to concentrate fish from the surrounding environment and equally concentrate purse-seine sets spatio-temporally around themselves, a local overfishing effect (decreasing slope in effort smooths; Maury and Gascuel, 2001) is more likely to emerge from these catch data by two potential means: 1) As the density of vessels increases within a region, the frequency of purse-seine sets on FADs in that area is likely to rise and the FAD-associated fish community has less time to recover between sets, resulting in lower yields per set. 2) As the FADs efficiently aggregate fish from the surrounding environment, in effect greatly increasing the tuna catchability and therefore efficiency of purse-seiners, overfishing or depletion of local (or even regional) tuna abundances is likely to take place at far lower effort of fishing days than for FREE-catches. Unfortunately the difference in average CPUE between FAD-associated and FREE-school fishing, cannot be accurately calculated from the current dataset, due to the unspecified effort. This is undoubtedly a great disadvantage to making comparisons

between FREE- and FAD-associated catch statistics and such details need to be secured from the fishery in future.

Year Effect

GAMs and GLMs (generalised linear models) are commonly used to standardize nominal CPUE, in order to produce CPUE time-series that are more representative of true stock abundances, by accounting for spatio-temporal, gear-related and/or environmental biases (e.g. Maunder and Punt, 2004; Su et al., 2008). However standardisation of CPUE was not the aim here and would have demanded more rigorous attention to statistical details, different priorities in model design and covariate selection, besides greater attention to the difficulties in using CPUE as a measure of stock abundance (e.g. Harley et al., 2001; Maunder et al., 2006; Rouyer et al., 2008). Instead, a year-effect was included in the GAMs, specifically allowing for the greatest degrees of freedom for this covariate, so that the most flexible smoothing function is allowed to emerge from the fitting procedure, in an attempt to remove inter-annual biases that could otherwise confound the environmental relationships of interest. Effects of interannual environmental variability, changes in targeting strategy, as well as changes in the efficiency of fleets and their gear, should largely be accounted for by this strategy.

FREE- or FAD-catch

Due to the lack of differentiation between effort directed at FAD- or FREE-schools, the total effort recorded has to be applied to both FAD- and FREE-catches. Besides causing an over-estimation of effort, this lack of resolution likely introduces a bias to results, as the proportion of effort directed at each of the two types of schools is unlikely to remain constant throughout the dataset.

To counter such a potential bias as best as possible, catches of FAD-schools (FREE-schools) were included as an explanatory covariate when modelling FREE-school (FAD-school) catch success or CPUE. In this way, the covariate provides information on the amount of effort attributable to each of the two fishing strategies, based on the basic assumption that catches are related to the amount of effort exerted to accomplish them. Similar approaches have been taken before in multi-species fisheries (e.g. Andrade et al., 2005; Su et al., 2008), in order to account for potentially unstable targeting strategies by fishers. As might be expected, the results of these covariates

pointed to highly significant decreases in the CPUE (or chances of positive catch) as the predictor variable increased (or became positive; Figure 4, 5). The inclusion of these predictor FREE- or FAD-catch covariates improved the fit and deviance explained by the models notably and acted to remove at least a proportion of the potential bias caused by the unspecified targeting of effort.

Insights into Tuna Ecology and Behaviour

The results from this investigation and their comparison with previous studies have allowed interesting insights into tuna ecology and behaviour and their interaction with purse-seine fisheries. Although tuna distributions can be related to surface temperature measurements (Maury et al., 2001a), such relationships likely only become clear when sampled SSTs extend to the limits (or beyond) of tuna temperature ranges. The vertical temperature profile is likely of far greater consequence to tuna behaviour and distributions: A shallower thermocline can act to trap skipjack and yellowfin tuna within vertical reach of the purse-seine nets - a catchability effect emerging mainly from FREE-school catches in this study. Countering this catchability effect however, it seems a deeper thermocline will on average mean greater vertical habitat and greater access to prey resources, leading to greater tuna abundances, as seen mainly in models of FAD-associated catch data. What is not seen in thermocline relationships shown here, is that the latter habitat effect likely has a maximum thermocline depth threshold, beyond which abundances would level-off and perhaps decrease again, due to the fact that the deepest thermocline depths are found in the unproductive oceanic gyre regions, which do not seem to support significant populations of yellowfin or skipjack tuna (Fonteneau, 1997). In certain low-oxygen regions of the oceans, the vertical oxygen profile likely plays a similar, but perhaps more critical role, to that of temperature and is expected to produce similar relationships in these regions (e.g. Prince and Goodyear, 2006).

For the first time (as far as the author is aware), a proxy of mid-trophic productivity has resulted in meaningful functional relationships in comparison with commercial fisheries data. These GAM relationships are suggestive of a Holling type II response curve, which has been employed in the modelling of tuna and other predator abundances (Gamblin et al., 2004; Maury et al., 2007), but up to now has not been demonstrated empirically. Certainly one has to acknowledge that the uncertainties in the mesozooplankton outputs have not been quantified and could therefore be

providing a biased picture. Phytoplankton fields seem to provide realistic views of the primary trophic level (e.g. Koné et al., 2009; Resplandy et al., 2009; Chapter 2), yet there are not comparable in situ datasets to verify basin-wide zooplankton fields and verification by cruise or station data were beyond the temporal scope of this dissertation. Instead, trust in the zooplankton relationships are based on confidence in phytoplankton fields and the model's skill at predicting the zooplankton biomass, by explicitly simulating physiological processes, predation and (active as well as passive) redistribution of biomass. As collection of basin-scale zooplankton data at high spatio-temporal resolutions is not yet a reality, simulated fields are likely to play a large role in future and concerted effort in their development and verification is vital for marine and fisheries science.

Besides the improved understanding of interactions between tuna catches and their environment, the kind of non-linear relationships described here can potentially provide very practical applications to resource management and conservation of open-ocean ecosystems. By isolating the environmental relationships that are interpreted as affecting abundances and applying them to environmental fields (measured in quasi real-time or simulated by forecast models), current or future changes in tuna habitat can be mapped. Such real-time (or forecast) habitat mapping could provide a vital tool for management of mobile no-take reserves, besides providing best estimates of how future climate change may impact on tuna habitats and distributions.

Conclusion and Recommendations

Contrasting FAD- and FREE-catch responses to environmental variables has been very useful in understanding and interpreting non-linear relationships revealed by GAMs. To the author's knowledge, this comparative approach has not been employed before and has demonstrated the value in assessing fisheries data from a range of perspectives, and of using flexible, non-linear modelling techniques in doing so. Future work on purse-seine catches needs to take into account the important differences between catches of FREE- and FAD-schools and how these impact on analyses and hypotheses being examined. Results presented here show that these two different fishing strategies can lead to greater differences in results and interpretations within a species, than the differences emerging between skipjack and yellowfin tuna.

Indian Ocean purse-seine catches investigated here, seem to confirm the importance

of three-dimensional habitat to skipjack and yellowfin tuna: The thermocline (and hence vertical thermal structure) can play an important role in catchability, as shown previously (e.g. Maury et al., 2001a). If this catchability effect is removed (by FADs) however, yellowfin and skipjack tuna abundances respond positively to thermocline depth, assumedly because colder sub-thermocline waters limit habitat depth and thereby access to food resources. This finding, together with the novel relationships between tuna catches (CPUE) and the mesozooplankton forage proxy, provide exciting new insights to tuna ecology and behaviour from commercial fisheries data.

In addition, this study has helped demonstrate the value in using realistic bio-physical ocean models in such investigations. Together with ever-increasing resolution and more accurate hindcasts of physical and biogeochemical dynamics, primary productivity and higher trophic levels, similar analyses promise to be an exciting and productive avenue of research in coming decades. However to match the increased access to more finer-scale environmental fields in future, and to allow increasingly accurate descriptions of tuna-environment relationships therewith, there is an urgent need for the collection and dissemination of detailed fisheries data at high resolutions (such as detailed set-by-set catch, effort, size and species information).

With ailing fish stocks globally (Worm et al., 2009) and the inherent difficulties in assessing and managing open-ocean fish resources (e.g. Miller, 2007; Cullis-Suzuki and Pauly, 2010), spatial protection of suitable habitats in no-take areas may be a promising sustainable solution that deserves attention (Game et al., 2009). Identifying or mapping these habitats in real time, or from forecasts, is one of the potential valuable applications of non-linear methods applied here, besides providing further insight into tuna ecology and behaviour. Furthermore, together with longer-term forecast simulations, these functional relationships might provide the best estimates of how habitats are likely to respond to future changes in climate. With growing food demands and greater pollution impacts from expanding human populations, our understanding of tuna habitat and how abundances and distributions are impacted by the environment, is likely a vital component in attempts to sustainably manage these resources over coming decades.

References

- Andrade, H.A., Garcia, C.A., 1999. Skipjack tuna fishery in relation to sea surface temperature off the southern Brazilian coast. *Fisheries Oceanography* 8, 245-254.
- Andrade, H.A., 2003. The relationship between the skipjack tuna (*Katsuwonus pelamis*) fishery and seasonal temperature variability in the south-western Atlantic. *Fisheries Oceanography* 12, 10-18.
- Andrade, H.A., Tozetto, A.L., Santos, J.A.T., 2005. The effect of environmental factors and of the fishermen strategy on the skipjack tuna (*Katsuwonus pelamis*) CPUE in the southwest Atlantic. *Collective Volume Science Papers, ICCAT* 58, 350-358.
- Annamalai, H., Murtugudde, R., Potemra, J., Xie, S.P., Liu, P., Wang, B., 2003. Coupled dynamics over the Indian Ocean: spring initiation of the Zonal Mode. *Deep Sea Research Part II: Topical Studies in Oceanography* 50, 2305-2330.
- Anon, 2009a. IOTC Report of the Eleventh Session of the Scientific Committee. IOTC, Victoria, Seychelles.
- Anon, 2009b. IOTC Report of the Eleventh Session of the IOTC Working Party on Tropical Tunas. IOTC, Mombasa, Kenya.
- Arreguín-Sánchez, F., 1996. Catchability: a key parameter for fish stock assessment. *Reviews in Fish Biology and Fisheries* 6, 221-242.
- Aumont, O., Bopp, L., 2006. Globalizing results from ocean in situ iron fertilization studies. *Global Biogeochemical Cycles* 20, GB2017.
- Aumont, O., Bopp, L., Schulz, M., 2008. What does temporal variability in aeolian dust deposition contribute to sea-surface iron and chlorophyll distributions? *Geophysical Research Letters* 35, L07607.
- Bakun, A., 1996. Patterns in the ocean: Ocean processes and marine population dynamics. California Sea Grant College System, National Oceanic and Atmospheric Administration in cooperation with Centro de Investigaciones Biologicas del Noroeste, La Paz, Mexico.
- Bard, F.X., Yen, S., Stein, A., 1999. Habitat of deep swimming tuna (*Thunnus obesus*, *T. albacares*, *T. alalunga*) in Central South Pacific. *Collective Volume Science Papers, ICCAT* 49, 309-317.
- Barkley, R.A., Neill, W.H., Gooding, R.M., 1978. Skipjack tuna, *Katsuwonus pelamis*, habitat based on temperature and oxygen requirements. *Fishery Bulletin* 76,

653-662.

- Barry, S.C., Welsh, A.H., 2002. Generalized additive modelling and zero inflated count data. *Ecological Modelling* 157, 179-188.
- Bertignac, M., Lehodey, P., Hampton, J., 1998. A spatial population dynamics simulation model of tropical tunas using a habitat index based on environmental parameters. *Fisheries Oceanography* 7, 326-334.
- Bertrand, A., Bard, F., Josse, E., 2002a. Tuna food habits related to the micronekton distribution in French Polynesia. *Marine Biology* 140, 1023-1037.
- Bertrand, A., Josse, E., Bach, P., Gros, P., Dagorn, L., 2002b. Hydrological and trophic characteristics of tuna habitat: Consequences on tuna distribution and longline catchability. *Canadian Journal of Fisheries and Aquatic Sciences* 59, 1002-1013.
- Bigelow, K., Musyl, M.K., Poisson, F., Kleiber, P., 2006. Pelagic longline gear depth and shoaling. *Fisheries Research* 77, 173-183.
- Bigelow, K.A., Boggs, C.H., HE, X., 1999. Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. *Fisheries Oceanography* 8, 178-198.
- Blackburn, M., Barnes, H., 1965. Oceanography and the ecology of tunas. *Oceanography and Marine Biology: An Annual Review* 3, 299-322.
- Blackburn, M., Laurs, M.R., 1972. Distribution of forage of skipjack tuna (*Euthynnus pelamis*) in the eastern tropical Pacific. NOAA Technical Report No. SSRF-649, 1-16.
- Blackburn, M., Williams, F., 1975. Distribution and ecology of skipjack tuna, *Katsuwonus pelamis*, in an offshore area of the eastern tropical Pacific Ocean. *Fishery Bulletin* 73, 382-411.
- Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L., Seitz, A., Walli, A., Fudge, D., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293, 1310-1314.
- Block, B.A., Keen, J.E., Castillo, B., Dewar, H., Freund, E.V., Marcinek, D.J., Brill, R.W., Farwell, C., 1997. Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Marine Biology* 130, 119-132.
- Block, B.A., Stevens, E.D., 2001. Tuna: physiology, ecology, and evolution. Academic Press.
- Bradley, J.V., 1968. Distribution-free statistical tests. Prentice Hall.
- Bray, K., 2000. A global review of illegal, unreported and unregulated (IUU) fishing.

FAO paper AUS:IUU/2000/6, 1-52.

- Brill, R.W., 1994. A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fisheries Oceanography* 3, 204-216.
- Brill, R.W., Bigelow, K.A., Musyl, M.K., Fritsches, K.A., Warrant, E.J., 2005. Bigeye tuna (*Thunnus obesus*) behavior and physiology and their relevance to stock assessments and fishery biology. *Collective Volume of Scientific Papers ICCAT* 57, 142-161.
- Brill, R.W., Block, B.A., Boggs, C.H., Bigelow, K.A., Freund, E.V., Marcinek, D.J., 1999. Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Marine Biology* 133, 395-408.
- Bushnell, P.G., Brill, R.W., Bourke, R.E., 1990. Cardiorespiratory response of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) to acute reductions of ambient oxygen. *Canadian Journal of Zoology* 68, 1857-1865.
- Chen, I.C., Lee, P.F., Tzeng, W.N., 2005. Distribution of albacore (*Thunnus alalunga*) in the Indian Ocean and its relation to environmental factors. *Fisheries Oceanography* 14, 71–80.
- Collett, D., 1991. *Modelling binary data*. Chapman Hall, London.
- Collette, B.B., Nauen, C.E., 1983. *Scombrids of the world: an annotated and illustrated catalogue of tunas, mackerels, bonitos, and related species known to date*, FAO Fisheries Synopsis. FAO, Rome, Italy.
- Craven, P., Wahba, G., 1979. Smoothing noisy data with spline functions. *Numerische Mathematik* 31, 377-403.
- Cullis-Suzuki, S., Pauly, D., 2010. Failing the high seas: A global evaluation of regional fisheries management organizations. *Marine Policy* 34, 1036-1042.
- Dagorn, L., Bach, P., Josse, E., 2000. Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* 136, 361-371.
- Dagorn, L., Holland, K., Itano, D., 2007. Behavior of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna in a network of fish aggregating devices (FADs). *Marine Biology* 151, 595-606.
- Dagorn, L., Holland, K.N., Hallier, J., Taquet, M., Moreno, G., Sancho, G., Itano, D.G.,

- Aumeeruddy, R., Girard, C., Million, J., Fonteneau, A., 2006. Deep diving behavior observed in yellowfin tuna (*Thunnus albacares*). *Aquatic Living Resources* 19, 85-88.
- De Anda-Montañez, J.A., Amador-Buenrostro, A., Martínez-Aguilar, S., Muhlia-Almazán, A., 2004. Spatial analysis of yellowfin tuna (*Thunnus albacares*) catch rate and its relation to El Niño and La Niña events in the eastern tropical Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography* 51, 575-586.
- Dempster, T., Taquet, M., 2004. Fish aggregation device (FAD) research: gaps in current knowledge and future directions for ecological studies. *Reviews in Fish Biology and Fisheries* 14, 21-42.
- Dickson, K.A., 1995. Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Environmental Biology of Fishes* 42, 65-97.
- Dizon, A.E., Neill, W.H., Magnuson, J.J., 1977. Rapid temperature compensation of volitional swimming speeds and lethal temperatures in tropical tunas (Scombridae). *Environmental Biology of Fishes* 2, 83-92.
- Donley, J.M., Sepulveda, C.A., Konstantinidis, P., Gemballa, S., Shadwick, R.E., 2004. Convergent evolution in mechanical design of lamnid sharks and tunas. *Nature* 429, 61-65.
- Dueri, S., Maury, O., 2010. Application of the APECOSM-E model to the skipjack tuna (*Katsuwonus pelamis*) fisheries of the Indian Ocean, in: IOTC Proceedings. Presented at the Twelfth Session of the IOTC Working Party on Tropical Tunas, Victoria, Seychelles, pp. 1-36.
- Evans, R.H., McLain, D.R., Bauer, R.A., 1981. Atlantic skipjack tuna: influences of mean environmental conditions on their vulnerability to surface fishing gear. *Marine Fisheries Review* 43, 1-11.
- Faure, V., 2007. Validation of physical simulations: Outputs interpolations (No. 2), GLOBEC: Climate and Fishing Impacts on the Spatial Population Dynamics of Tunas. OCEANOMOD, GLOBEC.
- Fonteneau, A., 1997. Atlas of tropical tuna fisheries. ORSTOM Editions, Paris.
- Fonteneau, A., Pallares, P., Pianet, R., 2000. A worldwide review of purse seine fisheries on FADs, in: Le Gall, J.Y., Cayre, P., Taquet, M. (Eds.), *Pêche thonière et dispositifs de concentration de poissons*. Ifremer, Martinique, pp. 15-35.
- Fonteneau, A., Lucas, V., Tewkai, E., Delgado, A., Demarcq, H., 2008. Mesoscale exploitation of a major tuna concentration in the Indian Ocean. *Aquatic Living Resources*

Resources 21, 109.

- Fonteneau, A., Richard, N., 2003. Relationship between catch, effort, CPUE and local abundance for non-target species, such as billfishes, caught by Indian Ocean longline fisheries. *Marine Freshwater Research* 54, 383-392.
- Forsbergh, E.D., 1980. Synopsis of biological data on the skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758), in the Pacific Ocean, in: Bayliff, W.H. (Ed.), Synopsis of biological data on eight species of scombrids. Special Report 2. Inter-American Tropical Tuna Commission, La Jolla, California, pp. 295-360.
- Fretwell, S.D., Lucas, H.L., 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19, 16-36.
- Froese, R., Pauly, D., 2010. FishBase. World wide web electronic publication. URL <http://www.fishbase.org/>
- Gaertner, D., Dreyfus-Leon, M., 2004. Analysis of non-linear relationships between catch per unit effort and abundance in a tuna purse-seine fishery simulated with artificial neural networks. *ICES Journal of Marine Science* 61, 812-820.
- Gamblin, G., Maury, O., Fonteneau, A., Hallier, J., 2004. Simulation of tag-recapture experiments in the Indian Ocean: A habitat based model applied to the Skipjack population. 6th Working party on Tropical Tunus, IOTC, Victoria, Seychelles 14, 1-13.
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P., Richardson, A.J., 2009. Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology and Evolution* 24, 360-369.
- Garcia, S.M., Cochrane, K.L., 2005. Ecosystem approach to fisheries: a review of implementation guidelines. *ICES Journal of Marine Science* 62, 311-318.
- Garcia, S.O., Cota, S.L., 1996. Relative yellowfin tuna abundance distribution and its relationship to environmental features as observed from satellites, in: Proceedings of the 47th Tuna Conference. Lake Arrowhead, California.
- Geider, R.J., MacIntyre, H.L., Kana, T.M., 1998. A dynamic regulatory model of phytoplanktonic acclimation to light, nutrients, and temperature. *Limnology and Oceanography* 43, 679-694.
- Graham, J.B., Dickson, K.A., 2004. Tuna comparative physiology. *Journal of Experimental Biology* 207, 4015-4024.
- Harley, S.J., Myers, R.A., Dunn, A., 2001. Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1760-1772.

- Hastie, T., Tibshirani, R., 1990. Generalized additive models. Chapman Hall/CRC.
- Hermes, J.C., Reason, C.J.C., 2008. Annual cycle of the South Indian Ocean (Seychelles-Chagos) thermocline ridge in a regional ocean model. *Journal of Geophysical Research* 113, 04035.
- Hilborn, R., Walters, C., 2004. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Springer.
- Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91, 385-398.
- Hutchinson, G.E., 1957. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22, 415 -427.
- Ingham, M.C., Cook, S.K., Hausknecht, K.A., 1977. Oxycline characteristics and skipjack tuna distribution in the southeastern tropical Atlantic. *Fisheries Bulletin* 75, 857-865.
- Josse, E., Bach, P., Dagorn, L., 1998. Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* 371/372, 61-69.
- Josse, E., Dagorn, L., Bertrand, A., 2000. Typology and behaviour of tuna aggregations around fish aggregating devices from acoustic surveys in French Polynesia. *Aquatic Living Resources* 13, 183-192.
- Kim, Y., Gu, C., 2004. Smoothing spline Gaussian regression: more scalable computation via efficient approximation. *Journal of the Royal Statistical Society (B)* 66, 337-356.
- Koné, V., Aumont, O., Levy, C., Resplandy, L., 2009. Physical and biogeochemical controls of the phytoplankton seasonal cycle in the Indian Ocean: A modeling study, in: Wiggert, J.D., Hood, R.R., Wajih, S., Naqvi, A., Brink, K.H., Smith, S.L. (Eds.), *Indian Ocean Biogeochemical Processes and Ecological Variability*, *Geophysical Monograph Series*. p. 350.
- Laevastu, T., Rosa, H., 1962. Distribution and Relative Abundance of Tunas in Relation to Their Environment, *FAO Fisheries Report*, No 6. Food and Agriculture Organization of the United Nations.
- Langley, A., Wright, A., Hurry, G., Hampton, J., Aqorua, T., Rodwell, L., 2009. Slow steps towards management of the world's largest tuna fishery. *Marine Policy* 33, 271-279.
- Laurs, R.M., Fiedler, P.C., Montgomery, D.R., 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-sea research*.

Part A. Oceanographic research papers 31, 1085-1099.

- Lehodey, P., André, J., Bertignac, M., Hampton, J., Stoens, A., Menkes, C., Memery, L., Grima, N., 1998. Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical biogeochemical model. *Fisheries Oceanography* 7, 317-325.
- Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., Picaut, J., 1997. El Niño Southern Oscillation and tuna in the western Pacific. *Nature* 389, 715-718.
- Lehodey, P., 2001. The pelagic ecosystem of the tropical Pacific Ocean: dynamic spatial modelling and biological consequences of ENSO. *Progress In Oceanography* 49, 439-468.
- Lengaigne, M., Guilyardi, E., Boulanger, J., Menkes, C., Delecluse, P., Inness, P., Cole, J., Slingo, J., 2004. Triggering of El Niño by westerly wind events in a coupled general circulation model. *Climate Dynamics* 23, 601-620.
- Lengaigne, M., Madec, G., Menkes, C., Alory, G., 2003. Impact of isopycnal mixing on the tropical ocean circulation. *Journal of Geophysical Research* 108, 3345.
- Lengaigne, M., Menkes, C., Aumont, O., Gorgues, T., Bopp, L., André, J., Madec, G., 2007. Influence of the oceanic biology on the tropical Pacific climate in a coupled general circulation model. *Climate Dynamics* 28, 503-516.
- Madec, G., Delecluse, P., Imbard, M., Levy, C., 1998. OPA 8.1 general circulation model reference manual, in: *Notes du Pole de Modelisation de l'Institut Pierre-Simon Laplace*. France, p. 91.
- Marr, J.C., 1951. On the use of the terms abundance, availability and apparent abundance in fishery biology. *Copeia* 1951, 163-169.
- Marsac, F., Le Blanc, J.L., 1998. Interannual and ENSO-associated variability of the coupled ocean-atmosphere system with possible impacts on the yellowfin tuna fisheries of the Indian and Atlantic oceans. *Collective Volume Science Papers, ICCAT* 50, 345-377.
- Marsac, F., Le Blanc, J.L., 1999. Oceanographic changes during the 1997-1998 El Niño in the Indian Ocean and their impact on the purse seine fishery. *IOTC Proceedings* 2, 147-157.
- Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research* 70, 141-159.
- Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., Harley, S.J., 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES Journal of Marine Science* 63, 1373-1385.

- Maury, O., 1998. Modélisation spatiale en halieutique. Approche par simulateur sous SIG. Application à la modélisation hiérarchique de la population de thons albacore (*Thunnus albacares*) de l'Atlantique tropical (Ph.D. thesis).
- Maury, O., 2005. How to model the size-dependent vertical behaviour of bigeye (*Thunnus obesus*) tuna in its environment. Collective Volume Science Papers, ICCAT 57, 115-126.
- Maury, O., Gascuel, D., 2001. 'Local overfishing' and fishing tactics: theoretical considerations and applied consequences in stock assessment studied with a numerical simulator of fisheries. Aquatic Living Resources 14, 203-210.
- Maury, O., Gascuel, D., Fonteneau, A., 2001b. Spatial modeling of Atlantic yellowfin tuna population dynamics: a habitat based advection-diffusion-reaction approach with application to the local overfishing study, in: Spatial Processes and Management of Marine Populations. Alaska Sea Grant College Program, pp. 105-122.
- Maury, O., Gascuel, D., Marsac, F., Fonteneau, A., De Rosa, A.L., 2001a. Hierarchical interpretation of nonlinear relationships linking yellowfin tuna (*Thunnus albacares*) distribution to the environment in the Atlantic Ocean. Canadian Journal of Fisheries and Aquatic Sciences 58, 458-469.
- Maury, O., 2010. An overview of APECOSM, a spatialized mass balanced "Apex Predators ECOSystem Model" to study physiologically structured tuna population dynamics in their ecosystem. Progress In Oceanography 84, 113-117.
- Maury, O., Faugeras, B., Shin, Y., Poggiale, J., Ari, T.B., Marsac, F., 2007. Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 1: The model. Progress In Oceanography 74, 479-499.
- Ménard, F., Stéquert, B., Rubin, A., Herrera, M., Marchal, É., 2000. Food consumption of tuna in the Equatorial Atlantic ocean: FAD-associated versus unassociated schools. Aquatic Living Resources 13, 233.
- Miller, K.A., 2007. Climate variability and tropical tuna: Management challenges for highly migratory fish stocks. Marine Policy 31, 56-70.
- Mills, C.E., Carlton, J.T., 1998. Rationale for a system of international reserves for the open ocean. Conservation Biology 12, 244-247.
- Moreno, G., Dagorn, L., Sancho, G., Itano, D., 2007. Fish behaviour from fishers knowledge: the case study of tropical tuna around drifting fish aggregating devices (DFADs). Canadian Journal of Fisheries and Aquatic Sciences 64, 1517-

1528.

- Mori, M., Katsukawa, T., Matsuda, H., 2001. Recovery plan for an exploited species, southern bluefin tuna. *Population Ecology* 43, 125-132.
- Musyl, M.K., Brill, R.W., Boggs, C.H., Curran, D.S., Kazama, T.K., Seki, M.P., 2003. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fisheries Oceanography* 12, 152-169.
- Neill, W.H., Chang, R.K., Dizon, A.E., 1976. Magnitude and ecological implications of thermal inertia in skipjack tuna, *Katsuwonus pelamis* (Linnaeus). *Environmental Biology of Fishes* 1, 61-80.
- Ohta, I., Kakuma, S., 2005. Periodic behavior and residence time of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa Islands, as identified with automated listening stations. *Marine Biology* 146, 581-594.
- Potier, M., Marsac, F., Cherel, Y., Lucas, V., Sabatie, R., Maury, O., Ménard, F., 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fisheries Research* 83, 60-72.
- Prince, E.D., Goodyear, C.P., 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography* 15, 451-464.
- Punt, A.E., Walker, T.I., Taylor, B.L., Pribac, F., 2000. Standardization of catch and effort data in a spatially-structured shark fishery. *Fisheries Research* 45, 129-145.
- R Development Core Team, 2009. R: A language and environment for statistical computing. Vienna, Austria.
- Resplandy, L., Vialard, J., Lévy, M., Aumont, O., Dandonneau, Y., 2009. Seasonal and intraseasonal biogeochemical variability in the thermocline ridge of the southern tropical Indian Ocean. *Journal of Geophysical Research* 114, C07024.
- Rodgers, K.B., Aumont, O., Menkes, C., Gorgues, T., 2008. Decadal variations in equatorial Pacific ecosystems and ferrocline/pycnocline decoupling. *Global Biogeochemical Cycles* 22, GB2019.
- Romena, N., 2001. Factors affecting distribution of adult yellowfin tuna (*Thunnus albacares*) and its reproductive ecology in the Indian Ocean based on Japanese tuna longline fisheries and survey information. *IOTC Proceedings* 4, 336-389.
- Rouyer, T., Fromentin, J., Ménard, F., Cazelles, B., Briand, K., Pianet, R., Planque, B., Stenseth, N.C., 2008. Complex interplays among population dynamics,

- environmental forcing, and exploitation in fisheries. *Proceedings of the National Academy of Sciences* 105, 5420-5425.
- Safina, C., 1993. Bluefin tuna in the west Atlantic: negligent management and the making of an endangered species. *Conservation Biology* 7, 229-234.
- Safina, C., 2001. Tuna conservation, in: Block, B.A., Stevens, E.D. (Eds.), *Tuna: Ecological Physiology and Evolution*. Academic Press, pp. 413-459.
- Sakagawa, G.T., Coan, A.L., Bartoo, N.W., 1987. Patterns in longline fishery data and catches of bigeye tuna, *Thunnus obesus*. *Marine Fisheries Review* 49, 57-66.
- Schaefer, K.M., 2001. Reproductive biology of tunas, in: Block, B.A., Stevens, E.D. (Eds.), *Tuna: physiology, ecology and evolution*. Academic Press, pp. 225-269.
- Schaefer, K., Fuller, D., Block, B., 2007. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. *Marine Biology* 152, 503-525.
- Sharp, G.D., Dizon, A.E., 1979. *The physiological ecology of tunas*. Academic Press, New York.
- Shono, H., 2008. Application of the Tweedie distribution to zero-catch data in CPUE analysis. *Fisheries Research* 93, 154-162.
- Shung, S.H., 1973. The sexual activity of yellowfin tuna caught by the longline fishery in the Indian Ocean based on the examination of ovaries. *Bulletin Far Seas Fisheries Research Laboratory* 9, 123-142.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: The principles and practice of statistics in biological research*. WH Freeman, New York.
- Song, L., Zhou, J., Zhou, Y., Nishida, T., Jiang, W., Wang, J., 2009. Environmental preferences of bigeye tuna, *Thunnus obesus*, in the Indian Ocean: an application to a longline fishery. *Environmental Biology of Fishes* 85, 153-171.
- Song, L.M., Zhang, Y., Xu, L.X., Jiang, W.X., Wang, J.Q., 2008. Environmental preferences of longlining for yellowfin tuna (*Thunnus albacares*) in the tropical high seas of the Indian Ocean. *Fisheries Oceanography* 17, 239-253.
- Stéquert, B., Marsac, F., 1989. *Tropical tuna - surface fisheries in the Indian Ocean*, FAO Technical Fisheries Paper, No 282. Rome.
- Stéquert, B., Ramcharrum, B., 1996. Reproduction of skipjack tuna (*Katsuwonus pelamis*) from the western Indian Ocean. *Aquatic Living Resources* 9, 235-248.
- Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V., 2008. Expanding oxygen-minimum zones in the tropical oceans. *Science* 320, 655-658.
- Sumaila, U.R., Zeller, D., Watson, R., Alder, J., Pauly, D., 2007. Potential costs and

benefits of marine reserves in the high seas. *Marine Ecology Progress Series* 345, 305-310.

- Su, N.J., Yeh, S.Z., Sun, C.L., Punt, A.E., Chen, Y., Wang, S.P., 2008. Standardizing catch and effort data of the Taiwanese distant-water longline fishery in the western and central Pacific Ocean for bigeye tuna, *Thunnus obesus*. *Fisheries Research* 90, 235-246.
- Uppala, S.M., K  llberg, P.W., Simmons, A.J., Andrae, U., Bechtold, V.D.C., Fiorino, M., Gibson, J.K., Haseler, J., Hernandez, A., Kelly, G.A., Li, X., Onogi, K., Saarinen, S., Sokka, N., Allan, R.P., Andersson, E., Arpe, K., Balmaseda, M.A., Beljaars, A.C.M., Berg, L.V.D., Bidlot, J., Bormann, N., Caires, S., Chevallier, F., Dethof, A., Dragosavac, M., Fisher, M., Fuentes, M., Hagemann, S., H  lm, E., Hoskins, B.J., Isaksen, I., Janssen, P.A.E.M., Jenne, R., McNally, A.P., Mahfouf, J., Morcrette, J., Rayner, N.A., Saunders, R.W., Simon, P., Sterl, A., Trenberth, K.E., Untch, A., Vasiljevic, D., Viterbo, P., Woollen, J., 2005. The ERA-40 re-analysis. *Quarterly Journal of the Royal Meteorological Society* 131, 2961-3012.
- Vialard, J., Menkes, C., Boulanger, J., Delecluse, P., Guilyardi, E., McPhaden, M.J., Madec, G., 2001. A model study of oceanic mechanisms affecting equatorial Pacific sea surface temperature during the 1997-98 El Ni  o. *Journal of Physical Oceanography* 31, 1649-1675.
- Vinayachandran, P.N., Iizuka, S., Yamagata, T., 2002. Indian Ocean dipole mode events in an ocean general circulation model. *Deep Sea Research Part II: Topical Studies in Oceanography* 49, 1573-1596.
- Weng, K.C., Stokesbury, M.J.W., Boustany, A.M., Seitz, A.C., Teo, S.L.H., Miller, S.K., Block, B.A., 2009. Habitat and behaviour of yellowfin tuna (*Thunnus albacares*) in the Gulf of Mexico determined using pop-up satellite archival tags. *Journal of Fish Biology* 74, 1434-1449.
- Wise, B., Bugg, A., Barratt, D., Barry, S., Nishida, T., Shono, H., Kalish, J., 2002. Standardisation of Japanese longline catch rates for yellowfin tuna in the Indian Ocean using GAM analyses, IOTC Proceedings, 5, IOTC WPTT-02-11.
- Wood, S.N., 2006. Generalized additive models: an introduction with R. Chapman Hall/CRC.
- Wood, S.N., 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. *Journal of the Royal Statistical Society (B)* 62, 413-428.
- Worm, B., Sandow, M., Oschlies, A., Lotze, H.K., Myers, R.A., 2005. Global patterns of predator diversity in the open oceans. *Science* 309, 1365-1369.

- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., Zeller, D., 2009. Rebuilding global fisheries. *Science* 325, 578-585.
- Xie, S., Annamalai, H., Schott, F.A., McCreary, J.P., 2002. Structure and mechanisms of south Indian Ocean climate variability. *Journal of Climate* 15, 864-878.
- Yee, T.W., Mitchell, N.D., 1991. Generalized additive models in plant ecology. *Journal of Vegetation Science* 2, 587-602.
- Zagaglia, C.R., Lorenzzetti, J.A., Stech, J.L., 2004. Remote sensing data and longline catches of yellowfin tuna (*Thunnus albacares*) in the equatorial Atlantic. *Remote Sensing of Environment* 93, 267-281.
- Zainuddin, M., Kiyofuji, H., Saitoh, K., Saitoh, S.I., 2006. Using multi-sensor satellite remote sensing and catch data to detect ocean hot spots for albacore (*Thunnus alalunga*) in the northwestern North Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography* 53, 419-431.
- Zainuddin, M., Saitoh, K., Saitoh, S.E., 2008. Albacore (*Thunnus alalunga*) fishing ground in relation to oceanographic conditions in the western North Pacific Ocean using remotely sensed satellite data. *Fisheries Oceanography* 17, 61-73.
- Zainuddin, M., Saitoh, S., Saitoh, K., 2004. Detection of potential fishing ground for albacore tuna using synoptic measurements of ocean color and thermal remote sensing in the northwestern North Pacific. *Geophysical Research Letters* 31, 20311.
- Zhu, G., Xu, L., Zhou, Y., Song, L., 2008. Reproductive biology of yellowfin tuna *T. albacares* in the west-central Indian Ocean. *Journal of Ocean, University of China* 7, 327-332.

Chapter 4

General Conclusion

Managing Ecosystems Sustainably in a Changing World

The aim of applied marine science, as with many other scientific disciplines, is to provide sound scientific evidence and develop robust constructs, which ultimately will inform decisions of how best to manage the interaction of humans with their marine environment. Due to the population explosion and the concomitant development of technologies that have allowed encroachment, exploitation and engineering of environments globally, people effectively interact with most of the biosphere (and many physical processes), reflecting an anthropocene epoch (Crutzen, 2002). Human-environment interactions are however mostly measured and/or managed at regional, national or even smaller scales. The spatial scale of this interaction, together with the economic incentives related to it, are likely some of the biggest factors that influence how challenging it is to successfully effect procedures that attempt to curb damaging or unsustainable practices. The greater the numbers of stakeholders, especially if they include different countries, cultures and associated priorities, the more difficult this management challenge becomes, as firstly consensus, and thereafter adherence or enforcement, needs to be achieved. A classic example of such a challenge is that of the global crisis of anthropogenic climate change. The management of tuna stocks, which range over entire ocean basins, is another large-scale and similarly challenging example (Miller, 2007).

In order to achieve the ideal, of basing on sound science, the decisions of how best to conserve ecosystems and manage resources in a variable and rapidly changing climate, two goals need to be addressed: 1) Changes in the physical environment need to be understood and predicted, and 2) the responses and interactions in biogeochemistry and ecosystems or resources, need to be described. While the two goals are commonly dealt with separately, they are in fact inextricably linked. Climate and physical variability impact heavily on biology (e.g. Bakun, 1996; Brander, 2010; Drinkwater et al., 2010), while there are also feedbacks on a wide range of scales, between the biogeochemistry or biology and the physical environment (e.g. De La Rocha and Passow, 2007; Lengaigne et al., 2007; Rodgers et al., 2008; Cermeño et

al., 2008). Due to these complex linkages and interactions, there is a need to consider systems with a more holistic approach; a strategy that has frequently been limited by a lack of data. As such, well-structured and carefully parameterised, coupled bio-physical numerical models can help fill existing data gaps, providing an invaluable and rapidly-improving arsenal of tools and numerical fields, for understanding and predicting variability in environments and ecosystems.

Throughout this dissertation, hindcast outputs from a coupled bio-physical ocean model (NEMO-PISCES; Aumont and Bopp, 2006) were employed to provide a record of past environmental variability, much of which is not available from in situ datasets alone. As has been demonstrated here, such models allow (and are going to allow increasingly in future) exciting and novel avenues of research in marine science (and other realms), previously bounded by a lack of in situ data.

Interannual Climatic Impacts

Within the Indian Ocean, a large proportion of interannual variability is driven by the ocean-atmosphere interactions that characterise ENSO and IOZM events. These two climatic modes (and different combinations of their events) produce different patterns of predictable anomalies in large parts of the Indian Ocean, as seen in chapter two. While IO surface temperatures are largely controlled by ENSO-related dynamics, the thermocline (as estimated by Z20) is largely under IOZM influence. Because of the strong impact that thermocline depth has on primary productivity, IOZM equally has a dominant control on IO chlorophyll concentrations, causing regional and basin-scale re-arrangements of the basal trophic level, as shown in chapter two. These anomalous patterns of productivity assumedly filter through the food chains, influencing ecological processes in many different ways and impacting on resource populations. Therefore better descriptions and understanding of these anomaly patterns, together with models that are becoming more skilful at predicting the climatic events that cause them (e.g. Wang et al., 1999; Luo et al., 2007), can ultimately feed into meaningful pre-emptive management action and mitigation efforts.

Certainly the most novel and interesting results in chapter two, from a biological point of view, are the predictable patterns of chlorophyll anomalies. As phytoplankton form the base of food chains and direct the flow of energy through the ecosystem (Bakun, 1996), thereby affecting export production and carbon cycling (e.g. Cermeño et al.,

2008), understanding their responses to climatic events is crucial to many different aspects of resource management, conservation planning, and in predicting changes to the biological carbon pump (De La Rocha and Passow, 2007). Developing a more confident and detailed understanding of the regional phytoplankton responses to ENSO/IOZM events, such as investigating the changes in phytoplankton communities and quantifying changes in primary production, is an exciting and potentially valuable avenue for future research.

Tuna and their Environmental Responses

Their highly mobile lifestyle, demanding metabolism (Dickson, 1995) and well-documented physiological limitations (e.g. Neill et al., 1976; Block and Stevens, 2001; Graham and Dickson, 2004), mean that tuna are likely highly reactive to perturbations of their environment, perhaps especially to those that influence forage availability. Due to its strong influence on both thermocline depth and primary productivity, IOZM events likely have significant impacts on IO tuna. Notable changes in Indian Ocean purse-seine catches of tuna were seen in response to the 1997 El Niño-positive IOZM event (Marsac and Le Blanc, 1999), although to what extent these observed changes were driven by catchability effects or real changes in distributions, is difficult to ascertain. Similar zonal displacements in skipjack catches were shown in the western Pacific by Lehodey et al. (1997) and are interpreted as regional movements of tuna abundances in reaction to the ENSO-driven displacement of their preferred habitat of the warm pool. The results in chapter three reiterated how important the third dimension is to tuna habitat preferences and it is perhaps their preference of a deeper thermocline (shown in chapter three) that causes the skipjack stocks to follow the zonal changes in the western Pacific warm pool. Lehodey et al. (1997) note that the warm pool itself is relatively unproductive, however they reason that significant tuna forage is likely provided from the more productive upwelling region of the adjacent Pacific cold tongue.

However if an adjacent source of higher productivity were not available, how does one reconcile the two relationships, interpreted as habitat preferences, of greater tuna abundances with deeper thermocline depths and also with higher tuna forage concentrations? As seen in chapter two, a deeper thermocline largely translates to decreased chlorophyll productivity (see also Wiggert et al., 2009). However these two effects are not necessarily opposing, due to the fact that increased thermocline depths

and the resultant decrease in tuna forage (that assumedly follows a decrease in chlorophyll concentrations) will be temporarily displaced. Lehodey et al. (1998) and Maury (1998) for example, suggest time-frames of three to seven months for the conversion of primary productivity into tuna forage.

The differences between tuna-environment relationships gained from FAD-associated catches and free-swimming tunas in chapter three, highlight how FADs modify the tuna-fishery interaction via their effects on tuna behaviour. Fortunately for analyses here, this modification seems to act to remove (to a large extent), catchability effects that likely cloud habitat preferences in analyses of free schools. This finding has not been shown or discovered before (to the author's knowledge) and has important implications to any similar investigations that deal with similar purse-seine datasets. Even though they might be beneficial to analyses of catch data, there are multiple concerns of how FADs impact negatively on the ecology of target species, as well as that of the many by-catch species (e.g. Bromhead et al., 2000; Marsac et al., 2000; Taquet et al., 2007; Hallier and Gaertner, 2008). In addition, FADs greatly increase fishing mortality (raise efficiency) and heighten the likelihood of recruitment overfishing in larger species such as yellowfin and bigeye tuna (Bromhead et al., 2000). Therefore the continued wide-spread and largely unregulated use of FADs is a pressing issue, of which the effects on target species and ecosystems are not well researched and need greater attention (Dempster and Taquet, 2004).

Future Research and Outlook

An obvious next step to tuna-environment relationships described in chapter three, but which was not possible in the time-frame available, would be to apply the functional relationships that describe tuna habitat, to environmental fields of a different time-period and assess how such habitat suitability estimates compare to abundance indices. In addition, and especially if the prior comparisons provide confidence that habitat suitability is being adequately described by these functional relationships, application thereof in the same way, but to forecasts of NEMO-PISCES forced by IPCC SRES (Intergovernmental Panel on Climate Change, Special Reports on Emission Scenarios) predictions, could provide useful estimates of how tuna habitat will likely change under future climate change scenarios.

Of course these tuna-environment relationships can only aid forecasts of what

environmental changes might mean to tuna habitat, providing one part of the equation describing the future health and sustainability of tuna stocks. The other component consists of direct human impacts, chief among them fishing pressure. The human population and its anthropogenic impacts will continue to grow for decades to come, requiring ever greater efforts to maintain resources and ecosystems in a sustainable state. Therefore besides global climate change and the management of resources and conserving biodiversity, one of the greatest challenges facing our generation is to reduce and reverse population growth. In the mean time, one hopes that with an improved understanding and predictability of how climate variability will impact tuna populations, managers and politicians will have improved tools to make better decisions toward the long-term sustainability of ecosystems and resources, including how best to manage or curb fishing and other anthropogenic impacts. One concrete example by which these GAM relationships could aid such decisions, is by identifying favourable tuna habitat, in quasi real-time or from forecast models, which would allow the effective management of mobile protected areas in the open ocean environment. Trials of such ecosystem approaches to fishery management are overdue in the pelagic ocean (Game et al., 2009) and require urgent attention.

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References

- Aumont, O., Bopp, L., 2006. Globalizing results from ocean in situ iron fertilization studies. *Global Biogeochemical Cycles* 20, GB2017.
- Bakun, A., 1996. Patterns in the ocean: Ocean processes and marine population dynamics. California Sea Grant College System, National Oceanic and Atmospheric Administration in cooperation with Centro de Investigaciones Biologicas del Noroeste, La Paz, Mexico.
- Block, B.A., Stevens, E.D., 2001. Tuna: physiology, ecology, and evolution. Academic Press.
- Brander, K., 2010. Impacts of climate change on fisheries. *Journal of Marine Systems* 79, 389-402.
- Bromhead, D., Foster, J., Attard, R., Findlay, J., Kalish, J., 2000. A review of the impact of fish aggregating devices (FADs) on tuna fisheries. Bureau of Rural Sciences, Australia.
- Cermeño, P., Dutkiewicz, S., Harris, R.P., Follows, M., Schofield, O., Falkowski, P.G., 2008. The role of nutricline depth in regulating the ocean carbon cycle. *Proceedings of the National Academy of Sciences* 105, 20344-20349.
- Crutzen, P.J., 2002. Geology of mankind. *Nature* 415, 23.
- De La Rocha, C.L., Passow, U., 2007. Factors influencing the sinking of POC and the efficiency of the biological carbon pump. *Deep Sea Research Part II: Topical Studies in Oceanography* 54, 639-658.
- Dempster, T., Taquet, M., 2004. Fish aggregation device (FAD) research: gaps in current knowledge and future directions for ecological studies. *Reviews in Fish Biology and Fisheries* 14, 21-42.
- Dickson, K.A., 1995. Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Environmental Biology of Fishes* 42, 65-97.
- Drinkwater, K.F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R.I., Pörtner, H., Polovina, J.J., Takasuka, A., 2010. On the processes linking climate to ecosystem changes. *Journal of Marine Systems* 79, 374-388.
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P., Richardson, A.J., 2009. Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology and Evolution* 24, 360-369.

- Graham, J.B., Dickson, K.A., 2004. Tuna comparative physiology. *Journal of Experimental Biology* 207, 4015-4024.
- Hallier, J.P., Gaertner, D., 2008. Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series* 353, 255-264.
- Lehodey, P., André, J., Bertignac, M., Hampton, J., Stoens, A., Menkes, C., Memery, L., Grima, N., 1998. Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical biogeochemical model. *Fisheries Oceanography* 7, 317-325.
- Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., Picaut, J., 1997. El Niño Southern Oscillation and tuna in the western Pacific. *Nature* 389, 715-718.
- Lengaigne, M., Menkes, C., Aumont, O., Gorgues, T., Bopp, L., André, J., Madec, G., 2007. Influence of the oceanic biology on the tropical Pacific climate in a coupled general circulation model. *Climate Dynamics* 28, 503-516.
- Luo, J.J., Masson, S., Behera, S., Yamagata, T., 2007. Experimental forecasts of the Indian Ocean Dipole using a coupled OAGCM. *Journal of Climate* 20, 2178-2190.
- Marsac, F., Fonteneau, A., Ménard, F., 2000. Drifting FADs used in tuna fisheries: an ecological trap? *Peche thoniere et dispositifs de concentration de poissons*. Edition Ifremer. Actes Colloq 28, 36-54.
- Marsac, F., Le Blanc, J.L., 1999. Oceanographic changes during the 1997-1998 El Niño in the Indian Ocean and their impact on the purse seine fishery. *IOTC Proceedings* 2, 147-157.
- Maury, O., 1998. Modélisation spatiale en halieutique. Approche par simulateur sous SIG. Application à la modélisation hiérarchique de la population de thons albacore (*Thunnus albacares*) de l'Atlantique tropical (Ph.D. thesis).
- Miller, K.A., 2007. Climate variability and tropical tuna: Management challenges for highly migratory fish stocks. *Marine Policy* 31, 56-70.
- Neill, W.H., Chang, R.K., Dizon, A.E., 1976. Magnitude and ecological implications of thermal inertia in skipjack tuna, *Katsuwonus pelamis* (Linnaeus). *Environmental Biology of Fishes* 1, 61-80.
- Rodgers, K.B., Aumont, O., Menkes, C., Gorgues, T., 2008. Decadal variations in equatorial Pacific ecosystems and ferrocline/pycnocline decoupling. *Global Biogeochemical Cycles* 22, GB2019.
- Taquet, M., Dagorn, L., Gaertner, J., Girard, C., Aumerruddy, R., Sancho, G., Itano, D.,

2007. Behavior of dolphinfish (*Coryphaena hippurus*) around drifting FADs as observed from automated acoustic receivers. *Aquatic Living Resources* 20, 8.
- Wang, H., Zhang, R., Cole, J., Chavez, F., 1999. El Niño and the related phenomenon Southern Oscillation (ENSO): The largest signal in interannual climate variation. *Proceedings of the National Academy of Sciences* 96, 11071-11072.
- Wiggert, J., Vialard, J., Behrenfeld, M.J., 2009. Basinwide modification of dynamical and biogeochemical processes by the positive phase of the Indian Ocean Dipole during the SeaWiFS era, in: Wiggert, J.D., Hood, R.R., Wajih, S., Naqvi, A., Brink, K.H., Smith, S.L. (Eds.), *Indian Ocean Biogeochemical Processes and Ecological Variability*, Geophysical Monograph Series. p. 350.

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