Changements démographiques chez les petits pélagiques du Golfe du Lion : y a-t-il un contrôle bottom-up ?
Elisabeth van Beveren

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Population changes in small pelagic fish of the Gulf of Lions: a bottom-up control?

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Defended on the 14th of December 2015 before the jury composed of:

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2. Christian Möllmann  reporter
3. Paul Marchal  reporter
4. Olivier le Pape  examinator
5. Claire Saraux  PhD supervisor
6. Jean-Marc Fromentin  PhD supervisor
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Abstract

Knowledge on population dynamics is key to the improvement of management and the understanding of ecosystem functioning. Since 2007, the size of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Gulf of Lions (NW Mediterranean) has severely decreased, which has strongly affected the fisheries. Simultaneously, the commercially uninteresting sprat population increased remarkably. As the economic and ecological stakes are high, the EcoPelGol project of which this PhD is part was established. We first analysed the sardine, anchovy and (partially) sprat population for changes in body condition, growth and size and age structure over the last 20 years. We concluded that sardine and anchovy have had from 2008 onwards a distinctively poor body condition and size, and that sardine have also showed a concurrent decrease in age and growth. In contrast, both species were in optimal and average “health” during 2005-2007 and 1992-2004, respectively. Subsequently, historical landings of sardine, anchovy and mackerel were considered (1865-2013), of which the fluctuations were characterised and statistically related to environmental variables. The recent dramatic landings decrease was put into perspective, as for example sardine is now for the first time landed less than before the 1960s, when a big probably effort-related upsurge occurred. Despite most of the variability being explained by what looks like changes in fishing effort, a link was found between the sardine and anchovy landings and the Atlantic Multidecadal Oscillation and the anchovy landings and the Western Mediterranean Oscillation. Next, as a management associated bluefin tuna increase also happened since 2007, its predation pressure on all three small pelagic species was estimated. We concluded that although sardine and anchovy are bluefin tuna’s main prey items, less than 2% of each population (including sprat) was consumed annually during 2011-2013 and that there was no clear size selectivity. Thus, tuna could not have had a noticeable impact on the population abundance or size structure of the small pelagics. In the last chapter, an epizootic disease was considered. An all-embracing approach directed towards the all-year round detection of both general and specific parasites, bacteria and viruses revealed the mostly temporal and not necessarily high occurrence of only three groups: microparasites, *Vibrio* spp. (sometimes determined as *Vibrio alginolyticus*) and bacteria of the genus *Tenacibaculum*. Although we could not exclude their pathogenicity, significant tissue damage at a cellular or macroscopic level was never observed, making the disease hypothesis less likely. Thus, we considered several hypotheses and indicated that top-down control (through Bluefin tuna predation), pathogens and fisheries are unlikely to be main drivers. In contrast, some environmental parameters explained a part of the variability in fish condition and landings. After a final discussion on all probable theories we concluded that a bottom-up control, such as especially a planktonic change in quantity and/or quality, might be on the basis of the observed changes. Although this work is a great step towards the understanding of the small pelagic dynamics in the Gulf of Lions, further investigations will still be needed to confirm our main hypothesis and to estimate the potential synergetic effect of other drivers.

**Key words:** sardine, anchovy, sprat, population dynamics, historical landings, predation pressure, fish disease
Résumé

La compréhension et la gestion des écosystèmes requièrent un maximum de connaissances sur les dynamiques de populations. Depuis 2007, la taille de la sardine (*Sardina pilchardus*) et de l’anchois (*Engraulis encrasicolus*) dans le Golfe du Lion a chuté tandis qu’au même moment, la population de sprat, qui a une faible valeur commerciale, a fortement augmenté. Les très forts enjeux économiques autour de ces espèces ont conduit au projet de recherche « EcoPelGol » dans lequel se situe cette étude portant sur les changements observés. La condition corporelle, la croissance ainsi que la structure en âge et en taille des sardines, des anchois et en partie des sprats ont été analysées sur les vingt dernières années. Alors qu’en 2005-2007, la situation semblait optimale pour les anchois et les sardines (taille et condition élevées), celle-ci s’est considérablement dégradée depuis 2008, l’anchois et la sardine étant significativement plus petits et plus maigres. De plus, une diminution de l’âge et de la croissance a été observée chez la sardine. Nous avons ensuite caractérisé les fluctuations des débarquements historiques (1865-2013) de l’anchois, de la sardine et du maquereau. La chute récente des débarquements a été mise en exergue, avec une situation inédite où la sardine est actuellement moins débarquée qu’avant les années 60, date à laquelle les débarquements ont fortement augmenté suite à un accroissement conséquent de l’effort de pêche. Bien que la majorité de la variance dans les séries de débarquements semble être engendrée par les changements de l’effort de pêche, nous avons également observé une relation entre les débarquements et l’indice « Atlantic Multidecadal Oscillation » pour l’anchois et la sardine et avec le « Western Mediterranean Oscillation » pour l’anchois. Dans une troisième analyse, la pression de prédation du thon rouge sur l’anchois, la sardine et le sprat a été estimée pour voir si l’accroissement de la population du thon depuis 2007 lié à de nouvelles mesures de gestion a pu impacté les poissons petits pélagiques. Mais bien que la sardine et l’anchois soient les proies principales du thon, moins de 2% de leurs populations ont été consommés chaque année entre 2011-2013, et ce, sans sélectivité sur la taille de ces proies de la part du thon. Ainsi, le thon rouge n’a pas pu avoir un impact significatif sur la structure en taille ou les abondances des petits pélagiques. Dans le chapitre final, nous avons considéré la possible influence de pathogènes. Des analyses globales dirigées vers la détection des parasites, des bactéries et des virus ont été effectuées tout au long de l’année et ont révélées la présence ponctuelle et relativement faible de bactéries des genres *Tenacibaculum* et *Vibrio* et celle systématique de microparasites. Malgré l’impossibilité d’exclure leur pathogénicité, aucune lésion tissulaire n’a été attribuée à ces organismes, réduisant fortement la probabilité d’une épidémie. Nos travaux indiquent que les mécanismes « top-down », des pathogènes ou encore la pêche ne sont probablement pas les facteurs clés pour expliquer les changements observés chez les poissons petits pélagiques. À l’opposé, certains paramètres environnementaux ont expliqué une partie de la variabilité dans la condition corporelle des poissons et leurs débarquements. Nous concluons donc qu’un contrôle « bottom-up », et particulièrement un changement dans la quantité et/ou qualité du zooplancton, peut être la cause des phénomènes dans les populations des poissons petits pélagiques. Si cette thèse permet une avancée dans la compréhension de leur dynamique, des analyses complémentaires seront nécessaires pour confirmer notre hypothèse principale et pour estimer l’influence des autres facteurs agissant potentiellement en synergie.

**Mots clés:** sardine, anchois, sprat, dynamique des populations, débarquements historiques, pression de prédation, épidémiologie des poissons
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# Table of contents

Abstract ................................................................................................................................................... iii  
Résumé ..................................................................................................................................................... v  
Acknowledgments .................................................................................................................................. vii  
Table of contents..................................................................................................................................... ix  
Synthèse en Français ............................................................................................................................... 1  
   Introduction......................................................................................................................................... 1  
   Les petits pélagiques sur une échelle mondiale................................................................................. 2  
   Changements de croissance, condition, taille et âge .......................................................................... 3  
   L’historique des débarquements ....................................................................................................... 5  
   La pression de prédatation du thon ................................................................................................. 7  
   Les agents infectieux de la sardine ...................................................................................................... 9  
   Discussion et conclusion .................................................................................................................... 11  
General introduction ............................................................................................................................. 15  
   Population dynamics ......................................................................................................................... 15  
   Processes ........................................................................................................................................... 15  
   Drivers ............................................................................................................................................... 16  
Small pelagic population dynamics ................................................................................................... 18  
   The dynamics of the small pelagics of the Gulf of Lions ................................................................... 18  
   Project outline ................................................................................................................................... 21  
   References ......................................................................................................................................... 22  
Chapter 1: The status and dynamics of small pelagics in the world ..................................................... 29  
   Boundary currents ............................................................................................................................. 30  
   Benguela (Namibia and South-Africa) ........................................................................................... 30  
   Humboldt (South American west coast) ........................................................................................ 32  
   California (North American west coast) ........................................................................................ 33  
   Canary (between Guinea and Morocco) ........................................................................................ 34  
   Kuroshio-Oyashio (Japan) .............................................................................................................. 34  
   South Australia .................................................................................................................................. 35  
   NE Atlantic ......................................................................................................................................... 36
# Table of contents

Introduction ....................................................................................................................................... 88
Material and methods ....................................................................................................................... 89
Data ............................................................................................................................................... 89
Statistical analyses ......................................................................................................................... 90
Results ............................................................................................................................................... 93
Landings description ...................................................................................................................... 93
Patterns, periodicity and breakpoints ........................................................................................... 94
Relationship with the environment ............................................................................................... 95
Discussion .......................................................................................................................................... 98
Acknowledgments ........................................................................................................................... 101
References ....................................................................................................................................... 101
Supplementary material .................................................................................................................. 105
Appendix S1 Description of the environmental time series ....................................................... 105
Figure S1 ...................................................................................................................................... 109
Figure S2 ...................................................................................................................................... 110
Table S1 ....................................................................................................................................... 111

## Chapter 4: Prey predator interactions in the face of effective management strategies: changes in Mediterranean small pelagics are not due to increased tuna predation

Abstract ........................................................................................................................................... 114
Introduction ..................................................................................................................................... 115
Material and methods ..................................................................................................................... 116
Estimating predator abundance: ABFT census ............................................................................ 116
Estimating ingestion rates of ABFT using a Dynamic Energy Budget model ............................... 117
Tuna diet from stomach content analyses .................................................................................. 117
Estimating prey abundance: small pelagic fish census................................................................. 118
Predation pressure on small pelagic fish..................................................................................... 119
Results ............................................................................................................................................. 120
Tuna diet and selectivity .............................................................................................................. 120
Predation pressure on small pelagics .......................................................................................... 121
Discussion ........................................................................................................................................ 123
Effect on the abundance ............................................................................................................. 123
Effect on the size distribution ..................................................................................................... 123
Tuna energy requirement ............................................................................................................. 124
Atlantic bluefin tuna diet............................................................................................................. 124
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>References</td>
<td>174</td>
</tr>
<tr>
<td>Annex</td>
<td>183</td>
</tr>
<tr>
<td>Publications</td>
<td>183</td>
</tr>
<tr>
<td>Conference presentations</td>
<td>184</td>
</tr>
<tr>
<td>International Statistical Ecology Conference</td>
<td>184</td>
</tr>
<tr>
<td>Colloque de l’Association Française d’Halieutique</td>
<td>185</td>
</tr>
</tbody>
</table>
Introduction
La compréhension des fluctuations des populations est un des objectifs majeurs en écologie. Par exemple, pour comprendre le fonctionnement d’un écosystème, il est indispensable d’identifier les facteurs responsables des fluctuations de ses différents compartiments. Hormis l’intérêt évident pour l’écologie, le sujet est aussi intéressant d’un point de vue de gestion des stocks exploités. Cette connaissance est en effet nécessaire à la mise en place des stratégies, avec des conséquences positives sur le plan du fonctionnement des écosystèmes comme sur le plan économique. Avec une bonne compréhension de ces fluctuations, il est par exemple possible d’identifier les stratégies de gestion les plus adaptées, d’évaluer leur efficacité et d’anticiper ou d’estimer le temps de rétablissement des stocks.

Les poissons petits pélagiques sont particulièrement connus pour leurs grandes fluctuations naturelles. Par exemple, le taux de déposition d’écaillles des sardines et des anchois de Californie pendant 1700 années montre que ces fluctuations sont inhérentes aux populations. A l’échelle d’une décennie, la biomasse de leurs populations peut chuter de plusieurs milliers de tonnes, un phénomène qui est bien visible au travers des débarquements. Ceci a des vastes conséquences pour les pêcheries, du fait que ces espèces sont commercialement très importantes. Par exemple en 2009, les poissons petits pélagiques ont contribué à 22% des débarquements mondiaux des pêches commerciales.

Ces fluctuations prononcées sont en grande partie le résultat d’une biomasse importante à des niveaux trophiques intermédiaires (« wasp-waist control ») et d’un mode de vie rapide (reproduction précoce, forte fertilité, courte durée de vie, etc.). Du fait de leur mode de vie rapide, la dynamique de leur population est très instable et surtout déterminée par le recrutement. Ce dernier dépend de plusieurs facteurs biologiques et environnementaux, amplifiant sa variabilité. Par ailleurs, la position centrale des petits pélagiques dans le réseau trophique les expose à plusieurs éléments qui agissent comme des contrôles « bottom-up » (la productivité, etc.), lorsque la population est contrôlée par ses ressources (proies, espace ou lumière), ou « top-down » (la prédation), lorsque la population est régulée par ses consommateurs. De plus, du fait de l’importance de ces débarquements, la pêche peut encore accroître l’intensité des fluctuations de populations de petits pélagiques.

Cette étude s’intéresse aux petits pélagiques du Golfe du Lion (GOL), une zone du plateau continental située au nord-ouest de la Méditerranée et connue pour ses upwellings locaux. Depuis les années 2007-2008, les espèces de petits pélagiques dominantes, la sardine et l’anchois, ont subi un changement brutal de leur structure en taille et une chute dans le ratio biomasse /abondance de la population. La biomasse et l’abondance ont fluctué considérablement au cours des deux dernières décennies, mais n’ont pas chuté drastiquement, contrairement à ce qui a pu être observé dans plusieurs autres écosystèmes. En revanche, la diminution brutale de la taille des sardines et des anchois a entraîné une diminution très nette des débarquements. La plupart des chaluts et des lamparos (sennes tournantes coulissantes qui utilisent la lumière pour agréger le poisson avant de le pêcher) se sont tournés vers la pêche d’espèces à plus forte valeur commerciale, ou ont dû mettre fin
à leur activité. En outre, la population de sprat, dont la biomasse était habituellement faible, a pris une place de plus en plus importante dans l’écosystème. Mais cette espèce a une très faible valeur commerciale, du fait de sa petite taille et des habitudes locales de consommation. Malgré les très forts enjeux économiques, les mécanismes expliquant ces changements restent inconnus.

Deux hypothèses principales sont souvent avancées pour expliquer les causes des fluctuations des populations de petits pélagiques. Premièrement, ces fluctuations sont généralement liées à une chute du recrutement, ce facteur étant clé pour les fluctuations des populations des petits pélagiques mondiales. Cependant, le recrutement de la sardine et de l’anchois dans le GOL semblent s’être maintenu à des niveaux élevés, comme le montrent les niveaux relativement élevés d’abondance de ces populations. Cette observation est particulièrement remarquable et rend la situation encore plus énigmatique sur le plan scientifique. Deuxièmement, la pêche peut être aussi un facteur important, éventuellement en synergie avec d’autres éléments. Mais la pêche non plus ne semble pas être la clé des changements observés dans le cas du Golfe du Lion, les taux d’exploitation observés restant relativement faibles (généralement < 20%). Cependant, la faible pression de pêche actuelle ne nous permet pas de l’exclure comme élément syngrique. Puisque les changements observés sont si particuliers et ne peuvent être expliqués par les mécanismes classiques, d’autres hypothèses doivent être formulées pour les comprendre.

Le projet EcoPelGol (écosystème pélagique du golfe du Lion) a été créé pour répondre aux questions posées par cette crise de la pêche des petits pélagiques. Cette thèse est une partie de ce projet, avec pour but l’amélioration de la connaissance des fluctuations dans le GOL, et des éléments contrôlant ces fluctuations.

**Les petits pélagiques sur une échelle mondiale.**

Pour mieux comprendre les fluctuations du GOL, il est d’abord indispensable de les comparer avec celles des autres écosystèmes dans lesquelles la sardine et l’anchois sont présents. Ces deux espèces ont une distribution presque mondiale et sont particulièrement connus pour leur prévalence dans les systèmes d’upwelling: le Humboldt (côte Ouest d’Amérique du Sud), la Californie (côte Ouest d’Amérique du Nord), le Kuroshio-Oyashio (Japon), le Benguela (Namibie et Afrique du Sud) et les Canaries (entre la Guinée et le Maroc). De plus, leurs débarquements sont également importants dans l’Atlantique Nord-Ouest, le Sud-Ouest d’Australie, la Méditerranée et la mer Noire. Un examen de chacun de ces systèmes permet d’identifier les grandes différences et similitudes entre tous ces systèmes. En termes de mécanismes, les changements de productivité, en liaison avec des variations environnementales, apparaissent de manière constante comme une cause majeure des fluctuations de ces espèces. Par conséquent, l’importance des éléments qui contribuent à la productivité planctonique des océans, comme les apports terrigènes par les fleuves et les upwellings, sont aussi fréquemment avancés. Mais beaucoup d’autres facteurs peuvent également jouer un rôle, comme la pêche, la prédation, ou les effets liés à la densité de la population et les maladies.

Même si le contrôle « bottom-up » apparaît globalement important et ne devrait surtout pas être ignoré, des arguments sont aussi avancés sur la nécessité de considérer les mécanismes qui peuvent avoir un effet syngrique. De ce fait, un ensemble d’éléments ont été testés dans le cadre de cette thèse.
Changements de croissance, condition, taille et âge

Le premier chapitre avait pour but de mieux comprendre les fluctuations de la dynamique et de la structure des populations, de pouvoir proposer des paramètres potentiellement importants pour ces changements et de savoir pourquoi le ratio biomasse/abondance était plus faible depuis les dernières années. Au regard de ce dernier point, plusieurs hypothèses non-exclusives ont été proposées. Premièrement, les petits poissons pélagiques peuvent grandir plus lentement, de telle manière qu’en moyenne, leur taille et leur poids diminuent. Deuxièmement, dans une certaine mesure, les vieux et grands poissons peuvent avoir disparu de la population (par émigration et/ou décès). Troisièmement, une diminution de la condition corporelle des poissons peut engendrer des individus de poids inférieur au poids attendu quant à leur taille. En fonction des hypothèses effectivement valides, des processus alternatifs entraînant des changements dans la population (comme la survie vs. la reproduction) peuvent être indiqués. Par exemple, ces analyses peuvent pointer vers un contrôle «bottom-up», un contrôle «top-down», ou même un autre processus.

Pour tester ces hypothèses, la condition corporelle, la croissance et la structure en âge et en taille ont été examinés. Ces paramètres sont fréquemment considérés dans la recherche halieutique, mais rarement rapportés simultanément pour une période de plusieurs années et pour plusieurs espèces. Selon la directive-cadre «stratégie pour le milieu marin» (DCSMM), un stock en «bonne santé» est une population qui se situe dans les limites de sécurité biologique en présentant une répartition de la population par âge et par taille qui témoigne de la bonne santé du stock, bien qu’une définition exacte d’une telle répartition ne soit pas aisée. Malgré cela, une meilleure connaissance de la structure en âge et de la structure taille des populations contribue à une meilleure compréhension de la démographie des populations et de leurs fluctuations. En outre, nous avons aussi étudié la croissance et la condition corporelle des individus. Cette dernière était basée sur une relation taille-poids (l’indice de Le Cren), qui est corrélée avec le contenu en gras des individus. Même si la croissance et la condition corporelle sont toutes les deux basées sur la longueur des poissons, elles fournissent des informations différentes et complémentaires.

Afin de vérifier si un changement dans ces quatre paramètres clés s’est produit, de mieux comprendre les fluctuations, et de poser des hypothèses concernant les éléments moteurs, nous avons analysé des données d’une campagne scientifique (PELMED, «PElagiques MEDiterranée») dirigée vers les petits pélagiques dans le Golfe de Lion. Cette campagne est organisée en un volet acoustique et un volet biologique, et est réalisée chaque année au mois de Juillet depuis 1992, après deux années exploratoires (1984 et 1985). De plus, pour obtenir des données taille-âge, des otolithes d’anchois et de sardines ont été collectés durant la période 2002-2012 (et 1993, 1998 et 1999 pour les anchois) lors de la campagne PELMED, d’une autre campagne scientifique (MEDITS) et auprès des pêcheurs. La structure en âge a été obtenue grâce à un modèle de mélange gaussien Bayésien innovant, qui décompose une structure en tailles en incorporant a priori une clé taille-âge indépendante. Finalement, pour définir l’état de santé des populations pendant les différentes années d’une façon objective, nous avons fait une analyse en composante principale (ACP), prenant en compte séparément pour l’anchois et la sardine leurs valeurs annuelles d’abondance, de biomasse, de condition corporelle, de tailles moyennes et d’âges moyens.

Premièrement, nous avons constaté que pour la sardine et l’anchois les quatre paramètres fluctuaient indépendamment de leur biomasse et de leur abondance. Pour la sardine uniquement, une relation faible et inverse est apparue vis-à-vis de son abondance. De plus, l’abondance et la biomasse de la
La sardine n’était pas corrélée. De grands nombres de poissons dans l’écosystème ne sont donc pas toujours indicateurs d’une grande biomasse, et vice versa. De ce fait, notre étude montre que la seule considération des fluctuations de biomasse peut être trompeuse, puisque ces altérations peuvent refléter différents états de santé des populations.


L’anomalie observée pendant les dernières années pourrait être potentiellement reliée à des changements environnementaux ou à la pêche. Étant donnés les niveaux d’exploitation pendant les dernières années (ratio débarquements/biomasse faible et généralement <20% même quand la biomasse était faible ou commençait à augmenter) pour les trois espèces et la nature des changements observés (pratiquement en parallèle pour l’anchois, la sardine et le sprat: cette dernière espèce n’étant pas exploitée), il est peu probable que la surexploitation soit le forçage principal causant ces changements au sein des populations de poissons petits pélagiques. Néanmoins, l’effet de la pêche ne peut pas être exclu, puisqu’une interaction avec d’autres facteurs est possible. La condition et la croissance étant affectées, nous suggérons les processus « bottom-up » comme hypothèses principales. Par exemple, des facteurs environnementaux peuvent influencer la productivité et la biomasse de la communauté planctonique, limitant l’apport énergétique des espèces de petits pélagiques. Ce type de changement a déjà été observé dans d’autres écosystèmes. Enfin, la disparition des classes d’âge les plus élevées dans la population de sardine pointe vers une surmortalité adulte, dont les causes restent à définir. Ainsi, nous n’exclurons pas la possibilité d’une épidémie touchant principalement les adultes, phénomène ayant déjà touché une population de sardines au large de l’Australie.
L’historique des débarquements

A la suite des résultats présentés dans le premier chapitre qui suggéraient un contrôle bottom-up dans le golfe du Lion, nous nous sommes intéressés à l’effet de l’environnement sur la sardine, l’anchois et le sprat. Etant donné que les fluctuations des populations peuvent se produire avec une périodicité étendue, que les effets environnementaux peuvent être long à se répercuter sur l’écosystème et que l’effet de la pêche peut avoir un effet chronique (déplacement de la ligne de référence), les séries temporelles courtes ne sont pas toujours adéquates pour examiner des changements substantiels dans la biomasse, l’abondance ou les débarquements des populations. C’est pourquoi il faut regarder des périodes aussi longues que possible. Malheureusement, les séries d’abondance et de la biomasse disponibles étaient limitées à 20 années, rendant leur exploitation délicate. Nous nous sommes donc tournés vers les séries de débarquements, pour lesquelles les statistiques nationales françaises nous ont permis de compiler une série temporelle d’une longueur exceptionnelle (1865-2013). Ces données nous ont permis de vérifier si des situations similaires aux dernières années ont déjà eu lieu (notamment par la création d’un scenario de référence) et si la variabilité des débarquements hors changement d’effort important peut être reliée aux changements environnementaux.


Bien que des données sur les débarquements soient disponibles, ni les causes de leurs fluctuations fondamentales ni leur ampleur ne sont connues. Ainsi on a compilé des séries de débarquements pour l’anchois, la sardine et le maquereau sur le long terme pour plusieurs quartiers de la côte Méditerranéenne Française. Nous avons testé la relation entre les débarquements et la température de surface, le débit du Rhône et des indices climatiques comme l’oscillation nord-atlantique (NAO), l’oscillation Méditerranée occidentale (WeMO) et l’oscillation atlantique multidécennale (AMO). Pour cela, nous avons comparé les patterns, les cycles et les points de rupture de ces séries avec ceux des séries environnementales. En plus, nous avons évalué par espèces les relations débarquements-environnement avec des modèles additifs généralisés (GAMs).

Dans l’ordre décroissant, les trois espèces les plus importantes dans les débarquements de petits pélagiques sont la sardine, l’anchois et le maquereau. Les débarquements maximum dans la région ont atteint 22 090 t pour la sardine (1970), 9 593 t pour l’anchois (1988) et 1 693 t pour le
maquereau (2007). Pendant la période étudié (1865-2013), la sardine a été l’espèce la plus débarquée dans chaque quartier maritime (Port-Vendres, Sète, Marseille et l’ensemble de Nice/Toulon/Martigues). En général, les débarquements de l’anchois et de la sardine ont fortement augmenté (au moins cinq fois) au début des années 60 mais sont actuellement redescendus vers des niveaux similaires à ceux des années antérieures à 1960. Etonnamment, les débarquements de la sardine sont maintenant même plus faibles que pendant tout la période, mettant en exergue la singularité de la situation actuelle. L’anchois était peu débarqué avant 1960, d’où un contraste moins impressionnant. Les fluctuations du maquereau sont moins importantes, probablement parce que cette espèce est moins ciblée. Etant donné que la grande tendance dans les débarquements de l’anchois et de la sardine correspond au pattern d’effort connu qualitativement, et que des changements similaires ont été observés dans plusieurs pays Méditerranéens, nous estimons la probabilité que cette tendance soit créée par des changements d’effort comme très grande.

Cependant, les changements observés ne semblent pas liés uniquement à l’évolution de l’effort de pêche et à la demande du marché. Même si en termes de patterns, de cyclicité et de points de rupture, aucune similarité forte n’a été trouvée entre les séries des débarquements et des indices environnementaux, l’utilisation des GAMs par espèces a montré que l’effet de WeMO était statistiquement significatif pour l’anchois et que de l’AMO était significatif pour l’anchois et la sardine, mais avec un effet opposé pour les deux espèces. L’effet positif de l’AMO sur une population, comme la sardine, est généralement associé avec une élévation du recrutement et de la croissance, résultant d’un réchauffement des eaux. L’effet négatif de L’AMO sur l’anchois peut s’expliquer sur la base des différences alimentaires entre les deux espèces. En général, l’anchois se nourrit avec du zooplancton plus grand que la sardine. L’AMO agissant indirectement sur les communautés planctonique peut favoriser l’une ou l’autre espèce. Spécifiquement, l’AMO positive peut avoir un effet négatif sur les grands copépodes et subséquemment sur l’anchois. L’effet des autres paramètres environnementaux n’a pas pu être démontré, peut-être du fait qu’ils étaient trop faible pour être détectés, ou qu’ils agissent à des échelles temporelles différentes (comme par exemple des saisons au lieu des années).

Jusqu’à maintenant, nous n’avions pas considéré la pêche comme l’élément principal pouvant expliquer les changements récents. Cependant, cette idée était basée sur l’information venant des deux dernières décennies. Nos analyses montrent que la plus grande partie de la variabilité dans les débarquements est expliquée par une tendance à long terme, très probablement liée à des changements d’effort comme l’indique la synchronicité des points de rupture au niveau des espèces. De cette façon, la mortalité des petits pélagiques induite par la pêche a dû fortement augmenter depuis les années 1960, effet se répercutant éventuellement encore dans les observations faites aujourd’hui. Néanmoins, malgré l’effet indéniable de la pêche, son effet doit être mis en perspective. En fait, la biomasse de la sardine et de l’anchois a atteint pendant les années récentes (1993-2015) des niveaux dix fois plus élevés que les plus hauts débarquements historiques. Ceci montre que malgré la pression de pêche précédente, les populations d’aujourd’hui peuvent encore se régénérer et donner des biomasses importantes. Ainsi, cette étude soutient l’idée que la surpêche seule ne peut pas être la cause des changements actuels.

En résumé, la compilation et l’analyse des séries des débarquements historiques des sardines, des anchois et des maquereaux pour la partie Méditerranéenne Française a mis en lumière des facteurs environnementaux importants pour les fluctuations des populations pélagiques, sans pouvoir
toujours conclure sur les changements récents. De plus, les données de débarquement ont été mises en perspective avec l’histoire de la pêche sur cette façade maritime. Pour ces raisons, cette étude peut bénéficier à la compréhension de l’écosystème pélagique du Golfe de Lion et à la bonne gestion des stocks de poisson.

La pression de prédation du thon
Plusieurs hypothèses pouvant expliquer les changements observés au niveau des populations de petits pélagiques ont été proposées au début de ce travail. Cependant, celles-ci ne sont pas nécessairement exclusives puisque plusieurs éléments agissant en synergie peuvent impacter les populations en même temps. Dans ce chapitre, nous avons étudié l’existence potentielle d’un « top-down control ». De ce fait, nous nous sommes principalement intéressés à l’effet possible de la prédation par la population de thon rouge (*Thynnus thynnus*).

La compréhension des relations prédateur-proie est cruciale dans une optique de gestion écosystémique. Un des aspects clés de ces relations est l’estimation de l’intensité de la prédation, sachant que celle-ci peut être affectée par des mesures de gestion de la pêche. Cependant, l’évaluation de cette intensité requiert beaucoup de données, lesquelles sont particulièrement difficiles à obtenir pour des espèces marines, de par la contrainte pratique liée à leur observation. Nous avons donc élaboré une méthode originale pour estimer la pression de prédation du thon rouge sur les populations des petits pélagiques, en combinant des techniques modernes et des études de terrain.

Le thon rouge est un prédateur connu des petits pélagiques. Des juvéniles de cette espèce résident plusieurs mois dans le Golfe du Lion (de début Mars jusqu’à fin Mai et Fin Juillet jusqu’à fin Octobre) et peuvent alors représenter une source potentiellement importante de prédation pour la sardine, l’anchois et le sprat. D’autres prédateurs, tel que les dauphins, sont également présents, mais ces derniers se nourrissent principalement d’autres espèces de proie et leur biomasse se concentre généralement dans des eaux plus profondes que celle des petits pélagiques. Ces dernières années (2009-2012), l’abondance de juvéniles de thons a fortement augmenté, suite à un plan de reconstitution de cette population mis en place en 2007, qui incluait, en autres choses, des restrictions sur la saison de pêche, des quotas très restrictifs et un poids minimal de débarquements de 30 kg. De ce fait, l’augmentation d’abondance de juvéniles de thons s’est déroulée simultanément à la diminution de biomasse et de taille des sardines et des anchois. Une question s’est alors imposée : est-ce que l’accroissement de l’abondance du thon, en provoquant une intensification de la pression de prédation, peut être la cause des changements dans les populations de petits pélagiques ? Actuellement, la plupart des approches de gestion se focalisent sur une seule espèce, sans tenir compte de l’impact que celle-ci peut avoir sur d’autres parties de l’écosystème. Pourtant, si ces approches ont des répercussions sur d’autres espèces, les stratégies de gestion devront être adaptées.

Nous avons donc étudié la pression de prédation du thon sur les trois espèces de petits pélagiques entre 2011 et 2013 en termes d’abondance et de distribution en taille. La proportion annuelle de chaque population de petits pélagiques consommée par le thon, ainsi que la sélectivité du thon pour certaines classes de taille ont été estimées en utilisant comme entrées principales: (a) l’abondance de thon estimée par suivis aériens, (b) un modèle bioénergétique estimant des taux d’ingestion par le thon (suite à la calibration d’un modèle énergétique dynamique, DEB), (c) des analyses de contenus
stomacaux pour définir le régime alimentaire de ce prédateur et (d) l’abondance de la population de chaque espèce de petit pélagique estimée par une longue étude de terrain.

Pour le calcul de l’intensité de prédation, nous avons combiné les taux d’ingestion (Kj/jour) disponibles pour chaque classe de poids dans la population de thon (modèle dynamique de budget énergétique) avec la distribution des poids et l’abondance de la population, et ce, afin d’obtenir le besoin énergétique journalier de la population de thon. Nous avons ensuite multiplié ce chiffre par le temps de résidence du thon (estimé à six mois) dans la zone d’étude (le Golfe du Lion). Ce besoin énergétique total de la population a ensuite pu être distribué et converti en nombre d’individus par espèce consommée en s’aidant de la composition des proies dans le régime alimentaire du thon (analyse des contenus stomacaux) et de la densité énergétique (J/g) de chaque espèce de proie. Pour prendre en compte l’incertitude sur les estimations d’abondance du thon et les densités énergétiques des proies, nous avons réalisé un bootstrap des calculs en utilisant une distribution uniforme des deux variables (avec un pourcentage de confiance de 95% et les valeurs minimales et maximales trouvées, respectivement). Le nombre d’individus par espèce préllevé par le thon a ensuite été comparé à l’abondance de chaque espèce dans l’écosystème (estimé par les campagnes en mer PELMED), afin d’obtenir un pourcentage de consommation par espèce et par année. Parallèlement, nous avons vérifié la sélectivité potentielle du thon en comparant la distribution en taille des proies trouvées dans les estomacs de thon avec celle des espèces proies directement préllevées dans l’écosystème (données des campagnes PELMED à nouveau).

Les thons dont les contenus stomacaux ont été analysés présentaient un poids de 12.5 kg à 51.2 kg. A l’exception d’un estomac vide, en moyenne, 44 individus par estomac ont été trouvés. Les sardines et les anchois étaient toujours les proies les plus importantes en termes d’abondance, de poids et de fréquence (tous >79%). Le sprat, au contraire était en général faiblement présent, notamment en 2011 et 2012 (4%), mais présentait une importance plus élevée en 2013 (14%). Les céphalopodes et les maquereaux ne constituaient que 1% à 3% du régime alimentaire (en termes d’abondance et de poids). Ces résultats confirment donc que l’anchois et la sardine sont des proies très importantes pour le thon rouge dans le Golfe du Lion.

Cependant, malgré l’importance de ces deux espèces dans le régime alimentaire du thon, l’influence de la pression de prédation sur l’abondance des sardines et des anchois (ainsi que des sprats) est négligeable (<2% par année et par espèce). De plus, ces calculs ont été réalisés sur les trois dernières années (2011-2013), quand l’abondance du thon était déjà relativement élevée. A titre de comparaison, entre 1995 et 2013, les abondances préllevées par la pêche étaient faibles mais quand même en moyenne au moins six fois plus élevés que la pression top down exercée par le thon.

L’estimation de la pression de prédation a pu être réalisée grâce à un modèle énergétique sophistiqué (le DEB) qui nous a fourni des estimations du taux d’ingestion, autrement indisponibles. Nous avons ainsi trouvé que les thons de 4 kg et 86 kg consomment entre 0.8% et 2.4% de leur poids par jour (soit entre 174 et 1342 kcal). Ces estimations se situent en bas de la fourchette des estimations trouvées dans la littérature scientifique, focalisée cependant sur d’autres espèces de thons, généralement plus petites, exposées à des températures ambiantes différentes, gardées en captivité (probablement soumis à plus de stress) et également vraisemblablement nourris avec des proies d’une densité énergétique plus faible (besoin de consommer un poids plus important de proie pour atteindre un ratio poids consommé/poids de l’individus plus grand). Cependant, même en
considérant un taux d’ingestion maximal (basé sur ces articles scientifiques et donc théoriquement surestimé), les estimations de la pression de prédation restent relativement faibles (toujours <10%).

De plus, le thon ne semble pas avoir changé la proportion des différentes classes de taille des petits pélagiques puisqu’il semble consommer toutes les classes de tailles disponibles, avec aucune préférence consistante pour les petits ou grands poissons. Les petites disparités observées entre les distributions en taille des proies trouvées dans les estomacs et celles de la population sont donc probablement liées aux caractéristiques d’échantillonnage; ou résultent d’une hétérogénéité spatiale des tailles de proies et de la zone de chasse du thon, c’est-à-dire que le thon pourrait chasser dans des zones où les petits pélagiques présentent une taille moyenne spécifique et légèrement différente par rapport à d’autres zones.

En conclusion, ce chapitre fournit un cadre complet et nouveau des analyses proies-prédateur. Nous avons montré que la sardine, l’anchois et le sprat sont des espèces importantes dans le régime alimentaire du thon, sans être pour autant consommées en fonction de leur taille. De plus, le thon ne prélève qu’une très petite proportion en biomasse de la population de ces espèces, et ne peut donc pas être considéré comme une cause majeure de la diminution de leurs abondances et de leurs tailles. Pour toutes ces raisons, nous pouvons également conclure que la gestion du thon et des petits pélagiques peut être réalisée indépendamment.

**Les agents infectieux de la sardine**

Les études qui analysent la dynamique des stocks exploités essaient souvent de relier leurs fluctuations à l’environnement ou la pêche. Mais certains facteurs qui sont généralement peu considérés peuvent aussi avoir un effet, comme les maladies. Par exemple, une infection pathogénique peut limiter la croissance de son hôte et causer sa perte de poids, résultant en une condition corporelle réduite et potentiellement son décès précoce. Des effets masqués et sublétaux des pathogènes peuvent aussi être néfastes, dans le cas où ils diminuent la compétitivité, la capacité reproductrice ou migratrice d’une population. Alternativement, il est également possible qu’un pathogène opportuniste s’impose et aggrave l’état de santé d’un poisson déjà stressé et affaibli. Les changements observés sur les populations de sardines du Golfe du Lion ayant touché principalement les adultes, ce qui est plutôt inhabituel pour des populations de petits pélagiques, nous nous sommes demandés si ces derniers ne subiraient pas une surmortalité à la suite d’une épizootie. En conséquence, cette partie a été dédiée à la description et la quantification de la présence des agents infectieux dans la population des sardines de cette zone.

Toutefois, des analyses concernant l’émergence des maladies sont généralement lancées après l’apparition de symptômes d’alerte (présence de lésions ou de parasites macroscopiquement visibles, mortalité massive des poissons, etc.), inexistantes ici. Néanmoins, aucune étude vétérinaire n’ayant été effectuée sur cette population, il était possible que des symptômes aient pu passer inaperçus. De plus, il est également possible que les poissons infectés aient disparu de la population immédiatement après l’apparition des symptômes, ne permettant pas de détecter ces symptômes d’alerte. Cependant, l’absence de symptômes visuels exclut une piste pour la recherche des classes de pathogènes spécifiques. De ce fait, une étude générale a été nécessaire, avec la capacité de détecter un large éventail d’agents infectieux. Une telle analyse peut aussi fournir des renseignements de base sur la composition et la prévalence des virus, des bactéries et des parasites de la sardine, puisque de telles études sont rarissimes. Le cas le plus étudié est celui de la sardine
Australienne, suite à une mortalité massive causée par l'herpès-virus pilchard en 1995 et 1998. D'autres études sur les pathogènes des sardines adultes sont focalisées soit sur les communautés des parasites pour délimiter des stocks, soit sur un seul agent, principalement à cause de son risque pour la santé humaine.

Utilisant neuf échantillons de 150 sardines chacun et répartis sur une année complète, nous avons examiné la prévalence des agents infectieux au moyen d'une approche vétérinaire traditionnelle aspécifique (nécropsie, histologie, parasitologie, bactériologie et virologie) et d'analyses visant à détecter deux virus spécifiques, l'herpès-virus pilchard et les bétanodavirus. Les bétanodavirus ont une vaste gamme d'hôtes et sont très prévalents dans la région, affectant plusieurs populations de poissons en élevage ou sauvages. Les études pathologiques étant rares et habituellement incomplètes, ce chapitre fournit également une référence pour des études ultérieures.

Curieusement, nous avons trouvé relativement peu d'espèces de bactéries, virus et macro parasites. Néanmoins, des micro parasites ont été trouvés très fréquemment, et deux bactéries ont été détectées sur une courte période: *Tenacibaculum* et *Vibrio*.

Les vibrios n’ont été détectés que dans deux lots de sardines tous deux échantillonnés en Juillet 2015. Néanmoins, la prévalence dans ces lots était assez importante. Dans un quart des hôtes, la bactérie a été identifiée comme *Vibrio alginolyticus*, un pathogène opportuniste et répandu des espèces marines. Cet agent a déjà été décrit comme pouvant infecter la sardine, mais aucune étude ne s’est intéressée à ses effets. En général, sa virulence est très variable, dépendant de la souche et des éléments environnementaux. Cependant, les hôtes semblent habituellement avoir plusieurs symptômes. Dans cette étude, aucune lésion ou indication de dommages liée aux vibrios n’a été trouvée. De plus, les vibrios n’étant pas présents dans des sardines d’une taille ou condition particulières, ils n’ont pas pu causer un changement dans la structure en taille ou la condition de ces populations. Les vibrios sont souvent associés avec des individus soumis au stress, et peuvent ainsi être un indicateur de situations défavorables. Néanmoins, il est aussi possible que les vibrios détectés soient simplement opportunistes, ou résultent d’une contamination post mortem.

La fréquence d’occurrence de *Tenacibaculum* a été relativement faible pendant les deux événements où ils ont été observés. Mais ces deux échantillons étant temporellement dispersés, cette bactérie a pu être présente dans la population entre Juillet et Décembre 2014. *Tenacibaculum* est apparu significativement plus présente dans les poissons relativement grands, et certaines espèces du genre sont réputées pour leur impact sur les poissons. En théorie, cette bactérie pourrait donc bien expliquer les changements observés dans la population des sardines. Mais comme pour les vibrios, le quasi absence de lésions ou d’autres formes de dégradation indique que cet agent n’a pas la capacité de changer profondément l’état corporel de son hôte. Bien que le séquençage ADN de la souche n’a donné aucun résultat positif et ne nous a pas permis de déterminer l’espèce. Il est donc possible que les *Tenacibaculum* détectés soient de caractère opportuniste.

Enfin, des microparasites ont été trouvés à chaque échantillonnage, et toujours dans une grande proportion des sardines. Néanmoins, les mêmes conclusions que précédemment peuvent être mises en avant. En effet ils n’ont été ni associés avec des individus d’un certaine taille ou condition, ni été liés à des anomalies tissulaires.

Malgré l’impossibilité de rechercher tous les agents infectieux, un grand éventail a été testé et ce pratiquement tout au long de l’année. Bien que nous ne puissions pas conclure définitivement sur l’existence d’une maladie capable de restructurer la population de sardines dans le Golfe du Lion, la probabilité qu’un agent suffisamment nocif soit actuellement présent est faible. Ceci est supporté surtout par le fait que pratiquement aucun signe de dommages tissulaires n’a été observé lors des nécropsies et des analyses histologiques. Le rôle potentiel de pathogènes éventuellement inaperçus semble par conséquent aussi peu probable. De plus, si des pathogènes sont le facteur clé pour la diminution en taille et en condition corporelle des sardines, nous pouvons nous attendre à ce que les poissons grands soient principalement affectés. Mais seul *Tenacibaculum* semble être une bactérie associée aux poissons relativement plus grands, et ce sur seulement 2 des 9 échantillons. Cependant, la prévalence de certains agents ne nous permet pas de les exclure comme des facteurs ayant possiblement un effet relativement bas mais agissant en synergie. La détection fréquente des accumulations des MMC a été d’un intérêt supplémentaire. Ceux-ci peuvent indiquer que les sardines sont exposées à un certain niveau de stress. La pollution ou la malnutrition pourraient donc peut-être mieux expliquer la chute récente dans l’état de santé des sardines.

**Discussion et conclusion**

L’objectif de cette thèse a été d’étudier des changements de caractéristiques biologiques dans les populations pélagiques du Golfe du Lion ayant donné lieu à une diminution des captures (crise pêcherie). Dans la discussion générale, un résumé fournit tous les changements observés de 2008 à 2014 ainsi que tous les résultats d’études réalisées dans le cadre du projet EcoPelGol dans lequel se situe cette thèse. Depuis 2007/2008, une diminution de la condition corporelle, de la taille, de l’âge, de la croissance, de la taille à maturité et de la fécondité a été observée chez la sardine et parfois chez l’anchois. Par la suite, tous les facteurs qui ont potentiellement joué un rôle dans ces changements ont été discutés.

Premièrement, la pêche n’est pas le facteur majeur expliquant ces changements, cependant nous ne pouvons totalement exclure son effet synergique. Cette conclusion est basée sur plusieurs constats. L’exploitation ne cible pas clairement les individus les plus grands et le taux d’exploitation est resté faible, au moins sur les 20 dernières années. De plus, la condition corporelle des trois espèces de poissons pélagiques (anchois, sardines, sprats) a diminué en parallèle malgré des pressions de pêche très différentes. Aussi, la condition corporelle des poissons n’est en général pas affectée par la pression de pêche. Cependant, la pêche est connue pour son pouvoir d’agir en synergie avec d’autres facteurs. Aucune étude sur l’impact de la pêche n’a été réalisée à ce jour, par conséquent cette hypothèse ne peut être écartée.
Une deuxième hypothèse était la prédation. D'après nos résultats, le thon n'est pas responsable des changements des caractéristiques biologiques ni des fluctuations de la biomasse des petits pélagiques étudiés. D'autres prédateurs tels que les cétacés, certains poissons ou les oiseaux marins peuvent être présents mais exercent probablement un impact mineur sur les sardines, les anchois et les sprats. En général, la biomasse de la population de ces prédateurs est relativement faible, leur influence est limitée dans le temps ou l'espace, et les petits pélagiques représentent pour eux des proies secondaires. En effet, des études scientifiques ont montré que les dauphins ne sont pas aussi abondants que les thons, et que les petits pélagiques ne sont pas leurs proies principales. Bien que l'effet "prédateur" puisse être additif, leur effet total devrait être six fois plus élevé que l'effet individuel du thon pour seulement égaler la pression exercée par la pêche. De plus, la plupart des populations de prédateurs est stable ou en baisse à l'exception des thons. Donc, si leur effet antérieur a été plus fort ou au moins identique, leur effet aujourd'hui n'a pas pu causer des changements aussi profonds.

Une troisième hypothèse est la migration hors de la zone de campagne scientifique, c'est à dire vers l'extérieur du Golfe du Lion ou vers les zones côtière et les zones situées en dehors du plateau continental (après les sondes de 200m). Suite à une comparaison entre les tailles des sardines et des anchois débarqués en France et en Espagne (zone de migration la plus probable à l'extérieur du Golfe), nous avons observé d'une part que les plus grands poissons ne se déplaçaient pas vers l'Espagne et d'autre part que la taille des poissons avaient également diminué dans cette zone. De plus, aucune indication ne montre qu'une migration des grands poissons s'est faite au-delà du plateau continental ou vers des eaux peu profondes.

Par ailleurs, une épizootie a été considérée pour la sardine mais les pathogènes trouvés n'étaient que peu prévalents et surtout aucune lésion associée n'a été observée. Cette hypothèse ne peut donc pas être validée. Par contre, il a été indiqué que les sardines pouvaient être stressées par la pollution ou la malnutrition, mais cette constatation nécessite d'être vérifiée. Ainsi, les analyses maladie soutiennent surtout ces deux autres hypothèses. Il est à noter que les analyses n'ont pas été faites pour l'anchois, puisque la surmortalité adulte a été observée sur la sardine. Néanmoins, il pourrait être intéressant de vérifier cette hypothèse pour cette espèce.

Deux autres hypothèses ont également été discutées. Premièrement, la pollution a aussi pu affecter les facteurs biologiques des petits pélagiques. Ceci est particulièrement souligné par le fait que le Golfe du Lion est une zone polluée, notamment suite à la décharge du Rhône. Spécifiquement, la pollution peut agir directement sur la physiologie des poissons, ou indirectement en ayant par exemple un effet sur le zooplancton. Deuxièmement, la compétition intra- ou interspécifique pourrait être un autre facteur non négligeable. En effet, la compétition interspécifique agirait comme un stabilisateur de la situation, une fois les ressources réduites. Cette théorie est étayée par des études qui ont montré que les poissons petits pélagiques ont des points communs dans leur alimentation et leur utilisation d'espace. Pour le sprat, la compétition intra-spécifique pourrait bien être la cause de sa condition sous optimale pendant sa période de grande abondance.

La dernière hypothèse repose donc sur un changement environnemental. L'environnement joue généralement un rôle crucial sur ces espèces dans la plupart des écosystèmes. En effet, cette théorie pourrait expliquer les changements de biomasses et des conditions corporelles ainsi que la réduction de taille et de croissance chez la sardine et l'anchois. Malheureusement, les séries temporelles
d’abondance et de biomasse étaient trop courtes pour pouvoir mettre en évidence des relations explicites avec les variables environnementales. Cependant, une autre étude du projet a montré l’influence du WeMO, du mesozooplankton, de la température de surface, de la concentration des diatomées et du débit du Rhône sur la condition corporelle de la sardine ou l’anchois. De plus, nous avons également observé une relation entre les débarquements et l’indice AMO pour l’anchois et la sardine avec le WeMO pour l’anchois.

Pour l’hypothèse finale, nous estimons que la pièce clé du puzzle est donc liée à une baisse de la quantité et/ou de la qualité du zooplancton. La réduction de la qualité pourrait être expliquée par un changement défavorable de la composition ou du spectre de tailles des espèces planktoniques. Un tel changement pourrait être le résultat d’une diminution (probablement hivernale) du mélange vertical des masses d’eau. En effet, la plupart des facteurs environnementaux sont actuellement dans une phase favorisant la stratification. Certains de ces facteurs, comme le WeMO, ont aussi été reliés directement aux dynamiques des populations pélagiques. Un changement planktonique causé par l’environnement pourrait entraîner un important déficit énergétique pour la sardine et l’anchois, qui ont une stratégie et un appareil d’alimentation qui n’est probablement pas adapté à ces modifications. De plus, ceci pourrait expliquer la diminution de la croissance et de la condition corporelle des deux poissons. Cet état pourrait avoir comme conséquences des tailles maximales non atteintes, et un décès précoce des individus. C’est pourquoi, il est aujourd’hui difficile d’observer des individus âgés et de grandes tailles. Le sprat, étant un généraliste trophique et ayant des compétiteurs affaiblis (sardine, et anchois), aurait pu profiter de la situation, expliquant sa multiplication rapide. Cependant, l’état du sprat n’était pas optimal, ce qui peut s’expliquer par une importance élevée de la compétition intra-spécifique. D’autre part, la compétition interspécifique pourrait avoir contribué au maintien de cette situation. De plus, la pêche et la pollution pourraient avoir amplifié les effets. Dans la discussion générale de ce travail, nous avons renforcé chaque élément de cette hypothèse en fournissant des argumentations élaborées et en s’appuyant sur des exemples venant d’autres écosystèmes.

Pour finir, des perspectives sont aussi données. Après plusieurs analyses détaillées, certaines questions restent non ou peu élucidées. Par exemple, toutes nos hypothèses n’ont pas été étudiées en détails. L’effet de la pollution n’est guère connu et l’interaction (ou la compétition) entre les poissons petits pélagiques pourrait par exemple être considérée avec un modèle de dynamique des populations. De plus, nous n’avons pas regardé la présence des pathogènes chez l’anchois. Le projet EcoPelGol dans lequel s’inscrit ce travail continue à planifier des études. Par exemple, des expérimentations avec des poissons en captivité seront réalisées, ainsi que des analyses sur des données satellitaires afin de vérifier la présence de changements de productivité.
General introduction

Understanding the processes involved in population fluctuations is a key objective in ecology. Principally, such knowledge is an absolute prerequisite for the improvement of management strategies, benefiting both the economy and the ecosystem. With a better understanding, for example the appropriate measures can be selected, their effectiveness can be evaluated, and recovery of the population can be enabled. But besides the obvious interest for management, the topic is also interesting from an ecological point of view. For instance, one needs to understand why one component of the ecosystem varies, such as a population, to grasp the idea of an ecosystem’s functioning.

Population dynamics

Population dynamics result from a balance between gains (immigration, birth or growth) and losses (emigration or death, whether natural or not; Russell 1931). So to understand how populations fluctuate, knowledge on these processes and the drivers affecting them is required.

Processes

The biological processes that might alter gains and losses are referred to as life history traits (LHTs, i.e., biological state variables such as growth, fecundity, mortality rate and migration). Depending on the species, some LHTs have however a more important role in the dynamics of a population than others. For example, for species that are prone to high predation pressure exerted mostly during early life stages, rapid and early growth might be more imperative for survival (and thus population dynamics) than for other species. This discrepancy in the relative importance of LHTs to the population dynamics is caused by the fact that energy is limited, so that not all LHTs can be developed to boost fitness (Darwinian demon hypothesis, Law 1979). Thus, animals have to face trade-off between the major life functions, in particular growth, reproduction and survival (Williams 1966). As a consequence, animals have evolved different strategies to maximise their fitness. That is, each individual or population distributes its energy among the LHTs that are most adequate to assure its survival and gene transmission. Because of natural selection, the LHTs that are able to provide a high number of viable offspring are favoured. Life history theory has as main goal to unravel the combinations of traits organisms may develop under specific conditions (Stearns 1976).

Life history strategies can in general be ranged along a slow-fast-continuum (Saether, Ringsby & Roskaft 1996; Saether & Bakke 2000), taking into account differences among taxonomic groups (Jeschke & Kokko 2008), such as reproductive mode (viviparous, oviparous, etc.). Species with a fast life history are typically small, fast-growing, early-mature and have a short generation time, life-span, high natural mortality and maximal fecundity, whereas the opposite is valid for species with a slow life history. A fast life history strategy is usually advantageous in situations that are unpredictable (Schaffer 1974). Much energy is invested in early, frequent and high reproduction, so reproductive success is ascertained. This also brings forth that fast-living species have to grow quickly to attain age-at-first maturity rapidly. However, there are trade-offs linked to the high cost of all of this, meaning that investment in survival or future progeny becomes naturally restricted (Williams 1966). Life history traits thus also define mortality patterns (Read & Harvey 1989). This responsiveness of
fast species might consequently lead to a higher population turn-over and therefore highly unstable population dynamics, again in contrast to species with a slow life history (Goodwin et al. 2006).

Specifically, within taxonomic groups the recruitment of short-lived marine species is relatively more variable than for their longer living counterparts (Goodwin et al. 2006). Long-living species have a more restricted and steadier number of offspring with a relatively high probability of survival to the adult stage (and thus a rather stable recruitment). In contrast, fecundity of short-lived species is high and variable, and during the early life phase mortality rates can be extremely elevated as well (e.g. Jenkins 2005). Consequently, variations in the supply of larvae to the adult population can have a major influence on the population dynamics (Roughgarden, Gaines & Possingham 1988; Caley et al. 1996; Jenkins 2005). Furthermore, when deciding on LHTs that are most important for the rate of population growth of fast-living species, often (but not always, e.g. Gaillard et al. 1989) fecundity and age at maturity are indicated (Oli & Dobson 2003, 2005; Stahl & Oli 2006).

Thus, for fast-living species predicting for example recruitment is of major concern in population dynamics, as this factor is highly variable and contributes greatly to the addition of biomass (in contrast to long-living species, for which e.g. growth is relatively more important, see Pauly 1985). The importance of considering processes during the larval stage to fish population dynamics was already for the first time emphasised by Hjort (1914), who suggested the “Critical Period Hypothesis”. In this theory, recruitment would depend on the first feeding of larvae. Recognizing the importance of investigating the early life stages, a series of other hypothesis followed, most of which were aimed at pelagic stocks (Lasker; Cushing 1975; Parrish, Nelson & Bakun 1981; Iles & Sinclair 1982; Cury & Roy 1989; Bakun 1996). Nowadays, studies still focus on recruitment variability, e.g. by showing the weak relationship with spawning stock biomass, and conclude that Hjort’s theory remains standing (Cury et al. 2014).

Drivers
Processes affecting LHTs, and thus the population gains and losses or dynamics, are plentiful, the most relevant generally being food, temperature, refugia, competitors and predators (Stearns 1976). Usually, they can affect fish 1) directly through physiology (including metabolic and reproductive traits), 2) indirectly through changes in their environment (habitat, food supply, predation pressure, competition) or 3) through the integrated effects of conditions experienced earlier in life on later fitness (Ottersen et al. 2001; Stenseth, Ottersen & Hurrell 2005). For example, this occurs when a change in fish LHTs results from repeated or modulated environmental effects (Ottersen et al. 2001), such as fishing pressure (Heino & Godo 2002). These pathways are not mutually exclusive, and one factor can act in multiple ways.

In general, indirect effects can be categorised as controlling “bottom-up” or “top-down”. Although the exact definition slightly changed over time (see Power 1992), the terms are now widely used to indicate if a population or system is controlled through its resources (such as nutrients, space or light, of which the quantity and quality thus affect a higher trophic level; bottom-up control), or by top-level consumers (which influence lower trophic forms; top-down control). A classic example of top-down control is from Alaskan islands where a food chain is formed by sea otters, sea urchins and kelps (Estes & Palmisano 1974; Estes, Smith & Palmisano 1978; Estes & Duggins 1995). Islands with abundant kelp had few sea urchins, as they were controlled by the sea otter population. In contrast, islands with no sea otters had low kelp abundance, as they were grazed by the uncontrolled sea-
urchins. This example could be extended to demonstrate bottom-up control, which appeared to be of importance to the benthic community of the same ecosystem. When planting mussels and barnacles on both islands, they grew faster on the islands rich in kelp (Duggins, Simenstad & Estes 1989). This resulted from higher kelp-derived detritus levels, which benefited the sessile filter-feeders. Thus, nutrient availability (which was however top-down controlled) had a bottom-up control on the barnacles and mussels. It could also be that a species positions a central position in the food web, which would make them an important energy linkage between both the upper and lower trophic levels. Such centrally places species might not only be controlled by trophic levels between which they are sandwiched, they might also to a certain extent control them (wasp-waist control, Rice 1995; Cury et al. 2000).

Several theories were also developed on how these controlling factors operate. For example, bottom-up control can sometimes be explained by the match/mismatch hypothesis (Cushing 1974, 1975), an extension of Hjort’s “Critical Period Hypothesis“ (Hjort 1914) that also focuses on timing of first feeding. This theory proposes that variations in the year class strength of a population are related to the timing of spawning relative to the timing of plankton increase. When both events are matched, recruitment will be strong. But if the peak in productivity happens late or prematurely, recruitment will be poor. That is, when a mismatch occurs feeding is hampered and consequently fish grow more slowly, remain in a poor state throughout succeeding life stages and are more vulnerable to predators (Cushing & Harris 1973; Jones 1973; Shepherd & Cushing 1980; Anderson 1988; Cushing 1990; Cushing & Hornwood 1994). Climate variability is well-known to be capable of altering plankton phenology (the timing of recurrent life cycle events), so that a mismatch is created if plankton feeders do not adapt their phenology (e.g. Edwards & Richardson 2004). The mechanism behind top-down control is usually observed through direct consumption. Nonetheless, for example predation-avoidance might also reduce food accessibility, potentially causing underdevelopment of life history traits (Lima & Dill 1990).

In fish biology, typical top-down controlling factors are fisheries and predation, and bottom-up is usually attributed to resource changes related to environmental variability. However, the relative importance of each is still debated. Bottom-up control was claimed to be the conventional trophic flow of most marine ecosystems (Cury, Shannon & Shin 2003), although both types of control are generally known to work in concert (Hunter, Varley & Gradwell 1997) and vary geographically (e.g. Oksanen 1988) and over time (e.g. Meserve et al. 1999). Also, although some strong bottom-up controlling factors were pointed out (e.g. food availability), multiple findings also stress the importance of top-down control. So did predator removal profoundly restructure communities and foodwebs (Frank et al. 2005) and can predation be highly important for early life stages (Houde 2008). Additionally, not all population drivers fall strictly into these two categories. Scarcely considered “lateral controlling” factors (e.g. Fuiman et al. 2015) that have a direct, indirect or integrated effect on fish might also be of note. For example, disease might greatly disturb populations (e.g. Whittington et al. 2008), as well as pollution (e.g. Schaaf et al. 1987; Spromberg & Meador 2006). They can act on the species itself (directly or with an integrated effect), or through modification of its prey or predators abundance or composition (indirectly). Consequently, although the bottom-up/top-down concept has been widely used, other studies now even argue that drivers should be classified based on other criteria (e.g. as either “trophic/biological” or “physical/environmental”, Conversi et al. 2015).
Small pelagic population dynamics

One species group that is particularly known for its population fluctuations are the small pelagic fish. On a decadal scale landings of e.g. sardine and anchovy in a given region can drop dramatically from thousands or millions of tons to very low levels (e.g. Lluch-Belda et al. 1989). Even the extensive 1700 year long time series of Southern Californian sardine and anchovy fish scale deposition rates indicate that large fluctuations in abundance are an inherent characteristic of the species (Baumgartner, Soutar & Ferreira-Bartrina 1992). Here, we will not go further into detail about the exact characteristics and underlying processes of the sardine and anchovy fluctuations, as they are highly area-specific and literature is too profuse. However, we will make a summary in a first chapter. Especially their very extensive distribution contributes to this necessity.

Generally, their strong population dynamics principally result from their fast life history and high biomasses at mid-trophic levels (wasp-waist species, Rice 1995; Cury et al. 2000). First, given their fast life history their population dynamics are, as mentioned before, highly unstable and determined by recruitment strength. This strength is determined by both biological (e.g. fish fecundity and abundance, Rickman et al. 2000) and environmental factors (e.g. predation and food availability, Cushing 1990; Chambers & Trippel 2012). Indeed, many studies pointed out the importance of recruitment and these biological and environmental factors for the small pelagic fish fluctuations (Checkley et al. 2009). Second, their central position in the food web exposes them to several bottom-up, top-down or laterally controlling mechanisms. Such a large set of influencers also magnifies their dynamics. Additionally, small pelagic fish are in general commercially very important. For example, in 2009 22% of the world’s landed species were small pelagics (FAO 2014). Therefore, fishing might amplify the small pelagic fish population fluctuations (Berkeley et al. 2004b; Anderson et al. 2008), as was shown in some cases (e.g. the Benguela, Roux et al. 2013).

The dynamics of the small pelagics of the Gulf of Lions

This study focuses on the small pelagic community of the Gulf of Lions (GOL, Fig. 1), a shelf area in the north-western Mediterranean known for its upwelling, which is mostly created by strong and transient winds (Millot 1990). This upwelling together with the Rhône discharge make it one of the most productive areas of the Mediterranean (Palomera et al. 2007). But around 2007, the prevailing small pelagic species, i.e. sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus), have exposed a lasting decrease in size, as well as a decline in the ratio of population biomass to abundance. Although biomass and abundance individually fluctuated considerably over the last decade (Fig. 2, note that we added data for 2012-2014 which was not available when we started this study), neither of these two parameters truly dropped, as was seen in other ecosystems, such as the boundary currents (Checkley et al. 2009). This loss of large individuals in the GOL made sardine and anchovy far less profitable and thus exploitable (GFCM 2007, 2012). Most pelagic trawls that targeted sardine and anchovy turned towards other more valued species, or halted their activity. So did lamparo’s (Fig. 2C), fishing vessels that use light to attract fish. Consequently,
in this Mediterranean area landings of both species, but especially sardine, dropped to insignificant levels during the last years (Fig. 2). Such a crisis however usually occurs after the biomass of a stock collapsed, and not necessarily its size. When fish size of a commercial stock did considerably decrease, this usually went together with evident changes in biomass (e.g. Jarre et al. 2015), and this usually happened only for either sardine or anchovy. In addition, the sprat (Sprattus sprattus) population which had been scantly present for the last two decades, showed a remarkable upsurge (GFCM 2007). Because sprat is of no commercial interest in this region due to its small size, this recent shift resulted in a fishery crisis. But despite the enormous economic stakes for fisheries, the mechanisms responsible for these fluctuations were unknown.

As pointed out, when looking at the factors controlling small pelagic population fluctuations, two common causes are considered. First, recruitment might have failed. Changes in recruitment caused sardine and anchovy populations to change drastically worldwide (e.g., Jacobson & MacCall 1995; Watanabe, Zenitani & Kimura 1995; Santos, Borges & Groom 2001; Borja et al. 2008). But in this case, recruitment remained surprisingly high (Fig. 2D). This is also confirmed by the relatively high abundance of sardine and anchovy during the last years, which could not have sustained if recruitment was low. As this finding is particularly unusual, it gives further rise to a situation that is very intriguing from a scientific point of view. Second, overfishing is often, whether or not collaboratively, responsible for the decline of a small pelagic fish populations (Radovich 1982; Csirke et al. 1996; Gucu 2002; Klanjšček & Legović 2007; Roux et al. 2013). But fishing as well was not considered to be the main driver of the observed changes (GFCM 2007), mainly because of the relatively low exploitation rate. And although its potential synergetic effect cannot simply be neglected, as overexploitation often interacts with environmental changes (Anderson et al. 2008; Planque et al. 2010), other factors need to be considered. Given the distinctiveness of the changes and the absence of classic mechanisms to explain most of them, some out-of-the-box studies might be needed to explore the population dynamics of the Gulf of Lions.

This might also be particularly desired as drivers explaining the small pelagic population dynamics in this area (environmental factors, predation, etc.) were barely considered, despite for instance the importance of the environment on the GOL anchovy population (Pethybridge et al. 2013). Most studies are rather descriptive and report on the more general biology of the species (spawning area, growth, etc.; Lee 1961; Lee & Juge 1965; Aldebert & Tournier 1967, 1971; Lee et al. 1967; Campillo 1992), whereas others focused on e.g. aspects such as their diet (Plounevez & Champalbert 2000; Costalago et al. 2012; Pethybridge et al. 2014). Therefore, the EcoPelGol (écosystème pélagique du golfe du Lion) project was created, a study of the pelagic ecosystem dynamics in the Gulf of Lions. This work is a part of this project, aiming at a better understanding of the population changes in this area, and at assessing the factors which are controlling them.
Fig. 2 A) Trend in total abundance (number) and B) biomass (tonnes) of anchovy, sardine and sprat in the Gulf of Lions estimated from a July acoustic survey (see chapter 2). C) Annual landings (tonnes) of sardine and anchovy for the region (sprat is not targeted). Two pictures are given to illustrate the two main local fishing techniques used to target the small pelagic fish (upper picture: lamparo, lower picture: pelagic trawl), although no distinction in their landed quantity was made. Landings data for 2014 are not yet available. D) Annual recruitment of sardine and anchovy, calculated as the abundance of the species (facet A of this figure) multiplied by the percentage of age 0 (sardine) or age 1 (anchovy) individuals in the population (see chapter 2). The difference in selected age classes to represent recruitment is related to the timing of spawning of both species (sardine in winter and anchovy in spring/summer) relative to the timing of the scientific survey (July). The sum of all series per species is indicated in grey.
Project outline

This study was developed into 5 parts (Fig. 1):

We started with a literature study on how and why small pelagic populations fluctuate in different ecosystems around the world. We discriminated between the large boundary systems and smaller less productive areas, which might be more similar to the Gulf of Lions. Such a summary can be used throughout this work, as often reoccurring important mechanisms might be key for the Gulf of Lions pelagic ecosystem as well.

In the second part of this work (chapter 2) the temporal changes of the “health” of the stocks were investigated using barely exploited biological information of the scientific survey on small pelagic fish in the area. Looking deeper into fluctuations in growth, condition and age and size structure could give more information on the current state of the populations. Additionally, it could indicate hypotheses concerning the major drivers. For example, a change in fish condition is more likely to be caused by a bottom-up control than a top-down one. This second chapter could thus be seen as the foundation of this work, outlining the current situation and paving the way for succeeding analyses on the possible drivers. That is, chapters 3, 4 and 5 each give a more in-depth look on specific factors that might potentially have led to the current economically unfavourable ecosystem state. Specifically, three hypotheses were put forwards: environmental changes, an increase in predation pressure and disease.

We looked at environmental factors first (chapter 3). Therefore, exceptionally long time-series of landings were compiled, and the effect of SST (Sea Surface Temperature), river runoff (Rhône) and climate indices such as the NAO (North Atlantic Oscillation), WeMO (Western Mediterranean Oscillation) and AMO (Atlantic Multidecadal Oscillation) were considered. Although the effect of fisheries could not be assessed directly, the use of historical landing data provided a baseline scenario and thereby helped in understanding the influence of fishing.

Fourthly, the role of predation (top-down control) was considered. Although this pressure was estimated to be of limited importance, it might still have a secondary effect. Especially the tripling of the main predator in the area – tuna – simultaneously with the decrease in sardine and anchovy size (and briefly sardine biomass) led to the decision to perform a detailed analysis on this predator.

In chapter 5, sardine were analysed for the presence of pathogens, which could also greatly alter the populations’ biomass, abundance and biological characteristics as observed. As no alerting indications of an epizootic disease had been observed (e.g. marked lesions, mass mortality, etc.), a more general study was performed (chapter 5), using multiple techniques directed towards the detection of different pathological vectors (bacteria, viruses or parasites).

Finally, I described the current state of the small pelagic populations, discussed on the possible drivers responsible for the observed changes and gave perspectives to pursue this work.
Fig. 1 Conceptual framework of this PhD.

References


Chapter 1: The status and dynamics of small pelagics in the world

To understand how the pelagics in the Gulf of Lions might fluctuate, it is important to consider how these populations act in other ecosystems of the world. Sardine and anchovy have a very wide distribution. They are especially known for their prevalence in the five boundary current systems (Fig. 1), i.e. the Humboldt (South American west coast), California (North American west coast), Kuroshio-Oyashio (around Japan), Benguela (Namibia and South-Africa) and Canary (between Guinea and Morocco) currents. However, their landings are also important in the Northeast Atlantic (around the Iberian Peninsula and Bay of Biscay), south-west Australia and the Mediterranean and Black Sea. Given that in the five major boundary currents stocks are remarkably large, they are also by far the best described. For example, the Peruvian anchovy (*Engraulis ringens*) was the world most landed marine fish species of at least the last decade (FAO 2014). Checkley *et al.* (2009) give in their book already a very extensive review of the fluctuations of small pelagics in these five zones. Not only the trends in landings and biomass are discussed, but also the moments when turning points occurred and the factors thought to be of importance. But other smaller stocks exist in less productive zones (the NW Atlantic and the oligotrophic Mediterranean), so one might wonder if the factors controlling the populations in these areas are similar to those of the boundary currents. Also, the small pelagic fish populations of these less productive zones might display dynamics more comparable to those of the populations of the Gulf of Lions. Therefore, we provided an up-to-date summary of how and why sardine, anchovy and sprat fluctuate in different regions of the world, focusing especially on the non-productive zones and stressing similarities with the observed changes in the GOL small pelagic fish populations. As the main aim of this section is to summarise the already identified main factors important for small pelagic population fluctuations, we do not give an exhaustive list of all associated literature (such as for e.g. the Black Sea, for which literature on the anchovy population is copious). Also, most trends are based on landings data (fishery dependent), as usually no long-term information about biomass is available.

[Fig. 1 World map with indication of the zones discussed in this chapter. (adapted from Checkley *et al.* 2009)]
Boundary currents
Along the eastern boundaries of the oceans, trade winds blow in parallel to the coast in the direction of the equator. The Ekman effect causes the wind driven surface layer to turn away from the coastline (90° to the right of the wind direction in the northern hemisphere, and to the left in the southern), thereby creating upwelling of colder waters from the deeper layers and resulting in high productivity. This process is especially important for the western coasts of South and North America, as well as along north-west and south-west Africa (Russell & Yonge 1976). More specifically, it creates the Humboldt, Benguela, California and Canary upwelling zones (Fig. 1). A fifth zone of high upwelling is the Kuroshio-Oyashio extension, although the hydrodynamics are somewhat different.

Benguela (Namibia and South-Africa)
The Benguela ecosystem is characterised by moderate to high mesozooplankton concentrations (Checkley et al. 2009) and is separated in two subecosystems; one north and one south of the Lüderitz upwelling cell (Namibia). Both systems have an independent sardine and anchovy stock. In the north, sardine landings (peak: 1400 Mt) collapsed around 1969-1970, remained low from 1970 to 1977 and subsequently dropped even further. Particularly interesting in light of the GOL situation, during this drop a decrease in fish size and length at first maturity was noted (Jarre et al. 2015). Also, a condition factor fluctuated differently, as before the turnover it was lower than afterwards, perhaps caused by a density-dependent response (Checkley et al. 2009).

Thus, in contrast to the GOL where sardine size and condition decreased simultaneously (see chapter 2), in the Benguela both parameters changed oppositely. Anchovy landings (peak: 376 Mt) surpassed those of sardine in 1978 and dropped again in 1984. In addition to these biomass changes, significant changes in the spatial distribution of both species occurred (van der Lingen, Coetze & Hutchings 2002; van der Lingen et al. 2005). Currently, both species have a low biomass and appeared to have been replaced by other pelagic species. However, this replacement happened by multiple species, such as horse mackerel (Trachurus capensis) and bearded goby (sufflogobius bibarbatus)(Boyer & Hampton 2001), that have a different trophic level than sardine and anchovy and might have a relatively dissimilar ecological role. The upsurge (rather than replacement) of sprat in the Gulf of Lions might therefore be very different in nature. For example, inter-specific competition might be of much higher importance in the GOL than in the Benguela when trying to explain the mechanism behind the shift. In the south, sardine landings increased from the 1950 onwards, peaked in 1962.

Fig. 2 Landings of sardine, anchovy and sprat for all five major boundary currents and the Black Sea. Values were scaled per species and per ecosystem, so that maximum landings correspond to 1. Official time series of the California and Kuroshio-Oyashio Current start before 1950, but were not available from the Sea Around Us project (Pauly and Zeller, 2015), from where data was downloaded for these Large Marine Ecosystems.
(410 Mt) and collapsed between 1963 and 1966 in part the result of a poor recruitment (Cury & Shannon 2004). A strong 1961 year-class allowed the anchovy population to increase after 1964 (Cury & Shannon 2004). Landings peaked around 1987 (5967 Mt) and decreased thereafter.

No clear underlying mechanism has been described for any of the two subsystems, which in contrast to most other major upwelling systems did not show a clear opposition in the landings of the two species during the last decades. However, multiple studies reviewed the causes and consequences (Cury & Shannon 2004; van der Lingen et al. 2006; Checkley et al. 2009; Jarre et al. 2015; Blamey et al. 2015). In a nutshell, the most frequently indicated drivers are, parent stock overfishing (Boyer & Hampton 2001; Coetzee et al. 2008), low oxygen events (Boyer & Hampton 2001), environmental effects such as cooling or heating of the surface waters (thereby changing food quantity and composition, e.g. Verheye & Richardson 1998; Verheye 2000) and to some extent jellyfish (Cury & Shannon 2004) and intra-guild predation on the eggs of the small pelagic fish (Valdés et al. 1987; Valdés 1991).

Concerning the latter, up to 62% of anchovy egg mortality was estimated to be caused by mostly sardine predation, but also cannibalism (Valdés 1991). Some of the mentioned factors are also linked. For example, overfishing of small pelagics in the Northern Benguela is thought to have promoted a jellyfish proliferation, which in turn could have increased predation on the fish eggs or competition for zooplanktonic prey (Roux et al. 2013).

This was also the first ecosystem for which it was shown that anchovy and sardine are trophodynamically distinct, and that this distinction might lead to feeding environments that are more beneficial for one of the species (van der Lingen, Hutchings & Field 2006). That is, anchovy feed most efficiently on large zooplankton whereas sardine are able to feed on phytoplankton but derive the bulk of their required energy from smaller zooplankton. Physical forcing is assumed to be on the basis of changes between food regimes (Fig. 3). This essential difference between the adults of both species was subsequently confirmed for several ecosystems (Nikolioudakis, Isari & Somarakis 2014). But it was also reported that anchovy and sardine can still prey on similar food items (the key is in the extent in which they consume each, Louw, van der Lingen & Gibbons 1998) and that the extent of the trophical difference between both species can vary slightly between areas (Costalago, Garrido & Palomera 2015). As will become clear throughout this summary, this finding formed the backbone of many hypotheses aimed at explaining sardine and anchovy alterations (e.g. Ayón et al. 2011).
Humboldt (South American west coast)

The Humboldt ecosystem is characterised by intense coastal upwelling (created by a northward boundary surface current) along Chilli, Peru and Ecuador. It is known for its high productivity, which varies however considerably with ENSO events and on a multidecadal basis (Checkley et al. 2009). Sardine and anchovy of the Humboldt compose multiple stocks, that all seem to fluctuate more or less in parallel. During the last decades, two important turning points took place. The first critical moment was in 1969-1971, when the anchovy stock collapsed and changes in the fish and zooplankton community were observed (Fig. 2). Around the same time, recruitment of anchovy also collapsed (1971, Csirke et al. 1996). Subsequently, sardine became the dominant small pelagic fish. Nevertheless, in 1985-1988 the system turned back to the anchovy regime when their recruitment started to improve dramatically and sardine landings declined (Csirke et al. 1996). Simultaneously, changes in fish and phytoplankton were noted (Alheit & Niquen 2004).

The general mechanism is believed to work as follows. Regime shifts appear to be linked to lasting periods of either cold or warm water anomalies (Alheit & Bernal 1993; Alheit & Niquen 2004; Chavez, Messié & Pennington 2011). When Cold Coastal Water (CCW) is dominant, SST lowers (Montecinos, Purca & Pizarro 2003) and the thermocline shallows (Pizarro & Montecinos 2004). This production stimulation state is associated with a high mesozooplankton biomass (Chavez, Messié & Pennington 2011), which reduces the oxygen concentration and results in the oxycline becoming shallower (Bertrand et al. 2011). Given that anchovy tolerate low oxygen conditions (Bertrand et al. 2008; Bertrand, Ballón & Chaigneau 2010) and feed on larger zooplankton (Pauly et al. 1989), the perfect conditions for them to thrive are created (Alheit & Niquen 2004) (Fig. 4).

On the other hand, when Surface Subtropical Water (SSW) intrudes, SST warms and the thermocline deepens. The main food source of anchovy, i.e. large calanoid copepods, then decreases, whereas predation pressure intensifies. For example, a temperature rise causes an increase in spatial overlap with predators such as mackerel and horse mackerel, but also anchovy egg consuming sardine (Alheit & Niquen 2004). Sardine appear to benefit from this environment as their population biomass becomes higher when the oxygen concentration increases, and as they feed mostly on phytoplankton and especially small zooplankton. Thus, dynamics of both small pelagics are highly dependent on long-term decadal-scale physical processes. Additionally, intermediate scale-
processes such as ENSO (El Niño Southern Oscillation) might cause short-term perturbations (Alheit & Niquen 2004), and overfishing might have had an aggravating effect (accelerating decline or retarding recovery), especially during the 1970 anchovy collapse (e.g. Csirke et al. 1996; Bertrand et al. 2004).

**California (North American west coast)**

Sardine and anchovy of the north-western American coast both had one major period during which they were amply landed. First, sardine landings were high from the 1920s until the early 1950s (peak: 1936, 700 000t). Second, anchovy landings intensified in the late 1960s and became again negligible around 1990 (Fig. 2). For sardine, a moratorium was established from 1966 until 1985, when landings started to increase again, albeit gradually (Lluch-Belda et al. 1989; Schwartzlose et al. 1999; Checkley et al. 2009; Barange et al. 2009). Sardine in the area is also known for its seasonal migration, of which the intensity is variable (Zwolinski & Demer 2012). Anchovy on the other hand can even shift its distribution over multiple years (McFarlane & Beamish 2001; Demer et al. 2012). Furthermore, the Californian coast is known for its exceptionally long series of anchovy and sardine scale deposition rates, obtained from anaerobic sediment cores (Soutar 1967; Soutar, John & Isaacs 1974; Baumgartner, Soutar & Ferreira-Bartrina 1992). This proxy for abundance indicated for example that historically, Californian anchovy and sardine fluctuations were very weakly but positively related, in contrast to the opposite fluctuations of both species observed in several ecosystems during the last decades (Baumgartner, Soutar & Ferreira-Bartrina 1992).

Information on the possible drivers was reviewed by Checkley et al. (2009) and Zwolinski (2012), who concluded that despite the long history of fisheries research in the area, no clear general mechanism was found that could explain the alterations. A plethora of studies however linked the small pelagic population fluctuations again to climatic changes, quantified as regional indices (e.g. ENSO), temperature, currents and upwelling, as well as occasionally to plankton biomass (Jacobson & Maccall 1995; Lluch-Belda et al. 2001; Lynn 2003; Reiss, Checkley & Bograd 2008; Song et al. 2012; Sugihara et al. 2012; Lindegren & Checkley 2013; Deyle et al. 2013; Lindegren et al. 2013). Upwelling, dependent on whether it is caused by coastal alongshore wind-stress or wind-stress curl, influences water temperature, alters plankton productivity and in turn changes small pelagic fish production (Rykaczewski & Checkley 2008). But although productivity (i.e., plankton quantity and composition) appears to be important for the sardine and/or anchovy success, this is clearly not the only factor. On the one hand, there is no clear relationship with a long-term zooplankton series, perhaps masked by the sampling methodology and the imprecision of the landings as a proxy of actual biomass (Checkley et al. 2009). On the other hand, recruitment strength can be stronger when temperature is high and productivity low (Agostini, Bakun & Francis 2007; Galindo-Cortes et al. 2010). Such an inverse relationship was suggested to be caused by for example increased predation on larvae and egg during years of high zooplankton biomass, exerted by elevated numbers of planktonic invertebrates and the attracted nektonic zooplanktivores (e.g. Pacific mackerel Agostini, Bakun & Francis 2007). Also, the PDO (Pacific Decadal Oscillation), representing spatial variability in SST, appeared to vary similarly to the ecosystem, but no correlation was found with paleoclimatic and modern sardine and anchovy biomass series (McClatchie 2012). Other mechanisms that were shown to be of importance were density-dependence and fisheries (Lindegren et al. 2013). The latter induced demographic changes (mean age at spawning) that might have resulted in an increased variability of the stock. Furthermore, the 1947 collapse of the sardine fishery off British Columbia was initially labelled as a
typical case of over-fishing (Hilborn & Walters 2003). Although the explanation was reconsidered, so that the effect of ocean conditions on distributions and survival was also suggested to be of importance, an effect of fishing might still have been present (McFarlane & Beamish 1999). At last, during some periods the dominant pelagic species was neither sardine nor anchovy, but mackerel (Zwolinski & Demer 2012), showing again that another species might temporarily dominate in waters were usually anchovy and sardine prevail.

**Canary (between Guinea and Morocco)**

The most recent review of changes in the fish community of the Canary current as well as the characteristics of the area is given by Arístegui (2009). Given that hardly any new studies appeared on the matter since its publication, this part will only be discussed limitedly, with a wink to the GOL situation.

The Canary current, as the Kuroshio-Oyashio system, is reasonably different from the other eastern boundary upwelling systems, i.e., the Humboldt, Benguela and California zone. Differences are caused by multiple factors. First, its hydrodynamics are fairly unalike and heterogeneous, related to the presence of the Canary archipelago, a relatively variable shelf width, major capes and Mediterranean and river outflow (Arístegui et al. 2009). Discrepancies are also seen in the biological communities. Anchovy are generally present in low abundance, and sardine usually dominate, whether or not together with other species (such as *Sardinella aurita* and *S. maderensis*). Also, the population dynamics of anchovy and sardine appear to be mainly characterised by huge geographic expansions, retractions and migrations (Holzlohner 1975; Belvèze & Erzini 1983; Gulland & Garcia 1984; Kifani 1998; Bakun 2005), rather than by the upsurges and crashes noticed in the other upwelling systems (Humboldt, Benguela and California). Thus, besides often observed seasonal migrations (e.g. sardine in the California current, Zwolinski & Demer 2012), both sardine and anchovy can displace their habitat over a multi-annual period (for anchovy this also happened in California, (McFarlane & Beamish 2001; Demer et al. 2012). Next, outbursts of other species were also identified. For example snipefish (*Macrorhamphosus* spp.), triggerfish (*Balistes carolinensis*) and octopus thrived shortly in certain parts of the area (Brêthes 1979; Caverivière 1991; Caddy & Rodhouse 1998). Depending on the species this was presumably caused by a decrease in river discharge or predator release (Gulland & Garcia 1984; Caverivière 1991; Caddy & Rodhouse 1998). Despite the substantial differences between the Canary Current and the GOL, this shows at least that outbursts of other species can occur. However, here such outbursts appeared limited in time. This is in contrast to for example the Benguela, where a true species replacement took place (Boyer & Hampton 2001). As very little is published on the Canary current, the important drivers remain to be identified. However, it was suggested that, as in most ecosystems discussed so far, a change in upwelling and the coupled SST might be essential (Holzlohner 1975; Sedykh 1978; Belvèze & Erzini 1983; Binet 1988; Machu et al. 2009). This might be produced by the intensification of the trade winds (Binet 1988) or a spatial dislocation of the upwelling core (Estrade 2006). Such changes might have caused for example also the migration stop to feeding areas (Kifani 1998; Bakun 2005).

**Kuroshio-Oyashio (Japan)**

This zone differs from the above discussed in that it is not an “eastern” boundary current. But even although this zone is situated on the western side of the Pacific and is therefore not a classical upwelling system, sardine and anchovy are landed in high quantities and show similar large
amplitude fluctuations. Sardine landings of Japan showed a first relatively small peak around 1936 (1.6 million t) and a second much larger one in 1988 (4.5 million t), that was quickly followed by a decline resulting from recruitment failures over four consecutive years (Watanabe, Zenitani & Kimura 1995). This failure was induced by a high mortality during the early life stages, rather than a reduced productivity. In between the two peaks (so during the 1950s and 1960s), sardine landings were extremely low (Fig. 2). Anchovy landings increased somewhat in the end of the 1940s, but their most important rise took place in the end of the 1980s. Two regime shifts were defined: in the late-1960s and the mid-1980s (Checkley et al. 2009).

Although the details of the mechanism are again not yet fully understood, since the review given in Chekley et al. (2009) a general concept has more clearly emerged. In (2011), Nishikawa and Yasuda indicated that the velocity of the Kuroshio Current determines the period over which surface water can cool down during winter. When the jet accelerates, SST is thus warmer and deepening of the mixed layer is restricted. Both SST and Mixed Layer Depth (MLD) were clearly shown to be important for e.g. recruitment, juvenile mortality or the number of recruits per spawning stock biomass, for one or both species (Noto & Yasuda 1999, 2003; Nishikawa & Yasuda 2008; Itoh et al. 2009; Watanabe 2009; Nishikawa, Yasuda & Itoh 2011). This is likely because the MLD is related to the production of phytoplankton, in at least a part of the zone (Nishikawa et al. 2013). During years when the MLD deepened, sardine was dominant (Yasuda et al. 2000). These were also the years during which a decline in zooplankton was observed (Odate 1994; Chiba et al. 2006). Therefore, the sardine and anchovy populations seem to depend on a basin-scale circulation, whereby sardine thrive during warm, shallow MLD years with a reduced meso-zooplankton biomass (Odate 1994; Nakata & Hidaka 2003; Chiba et al. 2006), whereas the opposite is valid for anchovy. Interestingly, in contrast to the previously discussed heavy upwelling regions, the chief characteristic of the regional hydrodynamics (in function of small pelagic fish dynamics) appears thus to be current speed, rather than upwelling intensity.

South Australia
In Southern Australia, there is no clear dominance of two small pelagic species, as in most other discussed ecosystems. Additionally, sprat also occurs (Hobday, Ward & Griffiths 2012). For sardine, several stocks are defined (Fig. 5), of which those inside the Great Australian Bight are the largest (Izzo, Gillanders & Ward 2012). This is thought to be related to the higher productivity in this area caused by the northern boundary current (Ward et al. 2006). In contrast, along for example the neighbouring south-western coast of Australia the Leeuwin current is not associated with upwelling (Muhling et al. 2008). What sets the Australian sardine fisheries also apart is their rather late establishment (Schwartzlose et al. 1999; Ward et al. 2001b). Also, catch limits were imposed before the fisheries was fully developed (Schwartzlose et al. 1999; Ward et al. 2001b). In Southern Australia, an extreme increase was observed from around 2001 onwards (Ward, Burch & Ivey 2012). But even after such an increase, catches are far below those of the 5 previously discussed regions (around 30 000 tonnes), and are rather in the same order of sardine landings from Mediterranean countries. Since 1995, the spawning stock biomass of sardine in a certain part of the Great Australian Bight has also been estimated, but no conspicuous trend is visible yet (Ward, Burch & Ivey 2012).
Interestingly, the fluctuations of the sardine populations were twice related to mass mortality events (Jones et al. 1997; Ward et al. 2001b; Whittington et al. 2008). These took place in 1995 and 1998-99, affected the whole sardine range and were at that moment considered to be the largest single-species fish kill reported (Jones et al. 1997). Specifically, during both occasions over 70% of the population was estimated to have died. Jones et al. (1997) also suggested that the exotic virus responsible for the kills (herpes virus) could have been introduced with clupeids imported to feed sea-caged tuna. Such a high reduction in biomass was reflected in the landings (Ward, Burch & Ivey 2012). But after the first epizootic, sardine biomass rebuild very quickly given that juveniles did not strand. The second time, a considerable abundance of juveniles was also affected, so recovery might have been slower (Ward et al. 2001b). Also, when sardine abundance temporarily diminished, the distribution and abundance of anchovy enlarged (Ward et al. 2001a). From this observation, it was concluded that competitive interactions between the two species might also be of importance to explain their dynamics. Furthermore, despite the general low level of exploitation, sardine abundance declines in the South-Western part of Australia have still been related in part to fisheries (Hobday, Ward & Griffiths 2012). At last, both sardine and anchovy biomass and distribution are thought to be connected to upwelling and productivity (Ward et al. 2003; Lynn 2003; Muhling et al. 2008; Ward, Burch & Ivey 2012), although no clear mechanism has been proposed.

**NE Atlantic**

I focus on the French part of the Bay of Biscay, as this zone has a relatively large small pelagic population in comparison to other NW Atlantic waters, related to its relatively high temperature and hydrodynamic characteristics (Uriarte, Pouzet & Villamor 1996). Additionally, an annual scientific campaign is well-established in the area and other surveys take place as well, so information is - although limited in comparison to the upwelling zones - still substantial for this part of the ocean. However, most research fixated on anchovy, to which by consequence this discussion will be limited.

Anchovy landings increased greatly from the 1980s onwards, to a peak of approximately 20 000 tonnes (Fig. 6). Around 2000, landings decreased sharply, so that in 2005 the stock collapsed and the fisheries remained closed from then until 2010 (Uriarte, Pouzet & Villamor 1996; ICES 2010).

Two interesting facts were pointed out. First, during some years most juvenile anchovy were located off the shelf (Boyra et al. 2005), despite that spawning does essentially not occur after the edge (Motos, Uriarte & Valencia 1996). Such a recurrent phenomenon still resulted in good recruitment and fish growth (Cotano et al. 2008; Irigoien et al. 2008) and the mechanism behind this was suggested to be the avoidance of predation (Irigoin et al. 2007). This discovery as well is rather remarkable, given that usually anchovy and sardine are constrained to the shelf and predation was so
It is also important to note that these results indicate that off-shelf waters can be important, whereas in several other areas (including the GOL) they are neglected (see further). Second, Bachiller et al. (2015) recently called attention to the intensity of intraguild predation between the small pelagic fish. Specifically, up to 33% of anchovy eggs can be removed by sardine and an additional 4% by themselves, mackerel or sprat. Again, this strongly reinforces the idea that a multitude of drivers should be looked at to obtain an improved understanding of the small pelagic fish dynamics.

Potential environmental influencers of anchovy are abundant, but no general description emerges. Recruitment was not only positively correlated to spring coastal upwelling produced by north-easterly winds of low to medium intensity (Borja et al. 1996, 1998), but also negatively to summer water-column stratification breakdown caused by strong winds (Allain, Petitgas & Lazure 2001). The latter was however unsuccessful in predicting recruitment during some of the following years (ICES 2010). In contrast, the importance of wind speed and direction was also shown for the growth and survival of anchovy larvae, based on a hydrodynamic model (Allain, Petitgas & Lazure 2007). The significance of wind was attributed to transport related processes (conveyance of larvae and river discharge), rather than a turbulence increase. Hence, little evidence surfaced for the common prominence of upwelling to anchovy dynamics, mainly through the alteration of food concentration and composition. But the Bay of Biscay is not a real upwelling zone (Irigoin et al. 2008) and the primary production in this area is highly determined by river discharge, which is spread by winds (Irigoin et al. 2007) and already known to be important for anchovy spawning (Bellier, Planque & Petitgas 2007; Bergeron, Delmas & Koueta 2010). So the relatively weak upwelling present might be comparatively more important for larval dispersal than food provision (Cotano et al. 2008; Irigoien et al. 2009). This was suggested after finding that anchovy growth rate and survival were not linked to food concentration (Cotano et al. 2008), and anchovy recruitment and biomass was respectively negatively or non-correlated with mesozooplankton biomass (Irigoin et al. 2009). Albeit the warnings of the last authors about the shortcomings of their analyses, they could still conclude that persistent low recruitment could not have been caused by a decrease in mesozooplankton biomass.

**Mediterranean and Black Sea**

In the Mediterranean, three small pelagic fish represent round 45% of the total 2013 landings (FAO 2015); the European anchovy (*Engraulis encrasicolus* L.), sardine (*Sardina pilchardus* Walb.) and sprat (*Sprattus sprattus*). Anchovy and sardine are widely distributed along the Mediterranean coasts, but with irregular hotspots so they appear as a set of independent stock units (Garcia et al. 1994; Tugores et al. 2011; Giannoulaki et al. 2013). Some of these are also truly genetically distinct (e.g. the Adriatic and Aegean Sea populations), whereas others are not (e.g. most of the Western Mediterranean stocks, see Viñas et al. 2013 and references therein). In general, sardine and anchovy stocks are slightly overexploited in the Mediterranean, although age selectivity is sustainable (Vasilakopoulos, Maravelias & Tserpes 2014). However, exploitation rates differ per region, so fishing...
pressure is for example lower on the sardine stock of the Gulf of Lions than on the one of the neighbouring Spanish waters (GFCM 2014a). Vasilakopoulos et al. (2014) also indicated a decrease in the overall spawning stock biomass (SSB) of Mediterranean anchovy and sardine. Nonetheless, the influence of fisheries on both fish stocks was only rarely detailed. But the absence of information does not imply the absence of effect. In the Mediterranean, the mechanisms behind the small population fish population fluctuations are generally not yet completely understood, although more so in some regions than in others.

Fig. 7 Discussed Mediterranean and black Sea areas, with indication of the main rivers and hydrography. (redrawn from Artegiani et al., 1997, 1997; Millot, 1990; Oguz et al., 1993; Patti et al., 2004;Somarakis et al., 2002 and based on Tugores et al., 2011)

Mediterranean stocks of anchovies and sardines are annually assessed by the WGSASP (Working Group on Stock Assessment of Small Pelagic species), a working group of the GFCM (General Fisheries Council for the Mediterranean) of the FAO (Food and Agriculture Organisation), while the European part is assessed as well by the STECF (Scientific, Technical and Economic Committee for Fisheries) of the EU. Assessment is usually based on fisheries data, sometimes tuned by acoustic and trawl small pelagic surveys, which follow the MEDiterranean International Acoustic Survey (MEDIAS) protocol. While such surveys start to become implemented in several countries, only five of them have taken place on a regular basis for at least a decade. These regular surveys were only installed along Northern Mediterranean coastlines; the Iberian coast, the Gulf of Lions, The Adriatic Sea and Slovenia, the Sicilian channel and Malta and the Aegean Sea (Fig. 5). By consequence, we only discuss those ecosystems that have a relatively large pelagic biomass and for which an adequate amount of information is available (i.e., we excluded for example the Levantine sea, the Tyrrhenian Sea, the Gulf of Gabes and the Nile delta).

Catalan coast

Given the geographical proximity of the Catalan coast to the Gulf of Lions, sardine and anchovy population dynamics in both zones might show some correspondence. For example, migration between the areas could occur and meteorological circumstances might be comparable. Along the Catalan coast, landings of sardine and anchovy fluctuated considerably during the last 4 decades (Fig. 8), but did so rather synchronously (Martín et al. 2012). From the middle 1990s, landings of both species started to decline, although not for the first time (Palomera et al. 2007; Martín et al. 2012;
GFCM 2014a). Also, sardine and anchovy biomass declined around the same year (Palomera et al. 2007; GFCM 2014b).

So far, population fluctuations were mainly linked to the environment, using landings data standardised or not for the changes in effort. During multiple studies, river outflow from the French Rhône river (discharging in the Gulf of Lions) or the Spanish Ebro almost always popped out as an important driver for anchovy fluctuations at the Southern Spanish coast (sometimes including a part of the Gulf of Lions), with a lagged effect of 12 to 18 months (Lloret et al. 2001, 2004; Martín et al. 2008). Also, for anchovy surface chlorophyll concentration was found to be of importance (Martín et al. 2008), as well as the WeMO index (Western Mediterranean oscillation, Martín et al. 2012). The latter appeared as a good proxy for regional environmental conditions, as for the period 1974-2009 this index was positively correlated with the local sea surface temperature (SST) and river run-off. As this index was calculated as the sea level pressure difference between the North of Italy and Southwest Spain, it is likely to be a good proxy for the climate of the lying-in-between GOL as well. Additionally, this index was also a significant factor explaining variations in the sardine population. But unlike for anchovy, so far no evidence was found linking most of the sardine population fluctuations to Rhône runoff in the Catalan Sea. Besides the WeMO index, only changes in wind mixing seemed to be of relevance to this population (Lloret et al. 2004). However, only the most straightforward drivers known to be important in the region have so far been considered (e.g. temperature, chlorophyll concentration, wind mixing and the NAO index).

**Strait of Sicily**

Landings from the Sicily channel are essentially recorded in Sciacca (Fig. 7), the main fishing port for small pelagic species in the area. During the last years (1998-2012), landings of both sardine and anchovy showed large inter-annual fluctuations, with only a very general decrease (GFCM 2014a; UNEP-MAP-RAC/SPA 2014). Landings of both species fluctuate generally in parallel with their biomass (Patti et al. 2004; Bonanno et al. 2005). The fishing harvest rate of sardine is around 10% (similar to the GOL), whereas for anchovy this circles around 40% (GFCM 2014a), much higher than in the GOL. Despite high fisheries-caused mortality of anchovy, stock fluctuations of the small pelagic fish appear to be highly environmentally driven.
The biomass fluctuations of sardine and especially anchovy in Southern Sicily are relatively well understood. The surface circulation is characterised by the amply described Atlantic-Ionian Stream (AIS; Robinson et al. 1991, 1999), which enters the channel from the western Mediterranean, describes a large meander so it touches the South Sicilian coast halfway and moves further off-shore again to exit the strait into the eastern basin (Fig. 9). Associated with it are vortexes and fronts that create upwelling and thus colder and nutrient rich waters. Anchovy larvae are known to be transported with the AIS, to a cyclonic gyre that aids their retention (Lafuente et al. 2002; Cuttitta et al. 2003), although this might not be the area with the highest primary production or column stability (Cuttitta et al. 2006). Yearly variations in AIS strength or pattern (causing changes in upwelling, SST and nutrient concentration, see Lafuente et al. 2005) determine the anchovy recruitment success (Lafuente et al. 2002) and its spawning activity (Cuttitta et al. 2003). For example, most years during which egg abundance was low were warmer years with a lower primary productivity (Basilone et al. 2013). The significance of elevated productivity (or lower temperatures as proxy) was also shown by Basilone et al., who indicated that both factors were important for anchovy condition (Basilone et al. 2004) and spawning intensity or seasonality (Basilone et al. 2006). Importantly, a direct negative connection was found between sardine and anchovy biomass and the mean SST of the months corresponding to larval and juvenile growth of the preceding year (Patti et al. 2004). Thus, in the case of the Strait of Sicily, it appears that enrichment processes determine spawning dynamics, recruitment success, survival and finally the population biomass of the small pelagic species. As river discharge is negligible (in contrast to e.g. in the Gulf of Lions or Adriatic Sea), enrichment is determined by the hydrodynamics of the area, or the AIS in particular (Patti et al. 2004).

Adriatic Sea

The Eastern Adriatic sardine landings (Fig. 10) increased greatly from the 1960s onwards (around the same period as landings increased in the GOL, Bailey et al. 2010) reached a maximum in 1981 and started to decrease subsequently (Grbec, Dulcic & Morovic 2002). Although landings differed between the Adriatic countries, all showed approximately the same trend (Morello & Arneri 2009). Anchovy did not fluctuate in parallel to sardine, although the general trend was roughly similar (Fig. 10). In general, during 1960-1985 anchovy landings were usually very high, whereas between 1986 and 1993 the population crashed and landings did no recover directly (Grbec, Dulcic & Morovic 2002). Sprat landings in the area resemble those of anchovy in terms of pattern and biomass, hence both are positively correlated (Grbec, Dulcic & Morovic 2002). For both sardine and anchovy, the biomass trend estimated using several methods was roughly similar to the pattern in landings, although more so for anchovy (Cingolani, Giannetti & Arneri 1996; Regner 1996; Azzali et al. 2002; Sinovčić 2003; Santojanni et al. 2003). The most up-to-date series of sardine and anchovy biomass can be found in the GFCM report (2014a).

Sardine landings are influenced by Mediterranean inflow into the Adriatic, such as the Levantine Intermediate Water (LIW, Zupanovic 1968; Grbec, Dulcic & Morovic 2002). A strong inflow increases salinity (for which a direct connexion was also established, Grbec, Dulcic & Morovic 2002) and thus vertical mixing. Years of intensified inflow consequently showed a rise in primary and secondary production (Pucher-Petković & Zore-Armanda 1973). Sardine CPUE indeed increased when primary production increased and SST decreased (which might however also be related to a change in catchability, see Sinovcic & AlegriaHernandez 1997 and cited studies). Thus, despite the hydrodynamic differences with the previously discussed Strait of Sicily, it appears that the general
mechanism might be comparable, i.e., the arrival of cold water on the surface creates a more productive zone that supports a higher sardine biomass.

Fig. 10 Interannual catch series of sardine (a) mackerel, anchovy and sprat (b) from the Eastern Adriatic. (from Grbec, Dulcic & Morovic 2002)

This is also valid for anchovy, as high production also favours its abundance. For example, Regner (1974) linked annual egg quantity directly to primary production. Later, Regner (1996) confirmed this correlation by indicating that egg production and larval abundance were indeed correlated with one year lagged primary production and zooplankton quantity, as well as temperature and salinity. Therefore, similarly to the role of the Sicilian AIS, the Mediterranean inflow was considered important (Vucetic 1971). Nutrient input was also stressed by the significance of upper layer salinity, indicating the influence of river runoff (Coombs et al. 2003). Hence, this is another Mediterranean area (in addition to the Catalan coast) where river discharge is important for anchovy, although it has not yet been indicated for sardine. However, not all parameters that have the potential to increase or restructure the plankton levels are found to be significant. For example, anchovy larvae can successfully adapt for changes in wind-mixing (Conway, Coombs & Smith 1998) and both anchovy fertility and larval mortality are independent of this index as well (Coombs et al. 2003; Zorica et al. 2013). Besides from enrichment processes (Mediterranean and inflow), overfishing also had an important role in the anchovy dynamics (Klanjšček & Legović 2007), as it is being held partially responsible for the 1986 anchovy collapse, combined with e.g. an environmentally induced recruitment decline and massive summer blooms (Regner 1996; Santojanni et al. 2003). Although Santojanni et al. (2003) believe recruitment failure to be the chief cause, more recent evidence points towards the inevitability of the collapse at the prevailing fishing effort (Klanjšček & Legović 2007). Specifically, both for the mature and the immature fish were considered overfished during four non-consecutive years preceding the collapse (Klanjšček & Legović 2007). In any case, as for example in the Humboldt, a collapse was caused rather by a combination of factors than by a single variable. Additionally, the role of sardine predation on the anchovy dynamics was also already mentioned as a contributing factor (Barba 2013).

Aegean Sea

In the Aegean Sea, anchovy landings reached a maximum in 1987 and subsequently showed a general decline. Sardine landings only dropped by the end of the 1990s, after multiple decades of relatively stable levels (Papaconstantinou et al. 2007). For both species, landings are highest in the northern part of the Aegean, caused by an eutrophication and river runoff gradient and the extent of the continental shelf (Stergiou 1997; Papaconstantinou et al. 2007). But in this zone, recent landings do not necessarily reflect population biomass (Papaconstantinou et al. 2007; Antonakakis et al. 2011; Giannoulaki et al. 2014), in contrast to the Strait of Sicily and the Adriatic.
Interestingly, two parameters (that were equally stressed for the previously discussed zones) continually reoccur in studies considering the small pelagics in the Aegean; depth and productivity. Specifically, sardine are found in warm shallow waters often in proximity to river mouths whereas anchovy are residing in depths shallower than 140 m, and both are associated with anticyclonic systems (Giannoulaki et al. 2005, 2008, 2013; Tsagarakis et al. 2008; Bonanno et al. 2014). Food is more accessible in these gyres, as they are plankton retention areas characterised by high concentrations of mesozooplankton (Somarakis 1999). The interaction between bottom depth and chlorophyll also explained most of the variance related to spawning habitats (Schismenou et al. 2008) and increased productivity is beneficial for sardine and anchovy egg production (Somarakis 2005; Ganias 2009). Additionally, catches of the two species were linked to large scale atmospheric patterns (West African Summer Monsoon, East Atlantic Jet and Pacific-North American pattern), as well as SST and at local scale wind and mesoscale circulation (Katara et al. 2011). So although care should be taken when interpreting this result (landings were taken instead of relatively lowly related biomass) and until now mainly local drivers were found to be important, the examination of large scale patterns might also provide welcome results.

**Black Sea**

The small pelagic community of the Black Sea is characterised by anchovy and sprat (instead of sardine), which are both landed in much higher quantities than in any of the Mediterranean areas. Anchovy are the predominant pelagic species in terms of landings and commercial value (GFCM 2012). Although the Black Sea anchovy might be considered as subspecies (*E. encrasicolus ponticus* and *E. encrasicolus maeoticus*), no distinction is made in the landings data and during most analyses (Prodanov et al. 1997). Importantly, there is a seasonal migration between the north-western productive shelf and the warmer south-eastern Turkish waters, which anchovy populates from October-November until March in dense wintering concentrations (Chashchin 1996; GFCM 2012). This is when they get caught by Turkish vessels, which make up 97% of the total Black Sea anchovy catch. Landings increased until 1988 to more than 400,000 tons (Fig. 2), to subsequently drop abruptly. During the years that stock biomass remained very low, individuals were also small and immature (Shlyakhov & Daskalov 2008). Between 1995 and 2010 landings fluctuated considerably between again relatively high levels (315,000 – 400,000 tons, (GFCM 2012). In contrast to anchovy, sprat are represented by a unique stock (*Sprattus sprattus*) and does not migrate on a basin scale. Its landings fluctuated considerably before crashing around 1989 (Fig. 2), similarly to anchovy. As in 2007 Turkish interest in sprat was boosted, levels almost attained again those of before the collapse (GFCM 2012; FAO 2015). Biomass estimates of both species are generally done through modelling (e.g. Prodanov et al. 1997; Prodanov & Stoyanova 2001; STECF 2011), especially as acoustics were only used recently or on a limited geographic extent (e.g. Panayotova et al. 2014).

The evolution of the Black Sea food web thus showed clear fluctuations with great economic consequences, of which the pattern and underlying mechanisms were by consequence often characterised and investigated (see Akoglu et al. 2014 and references therein) (Fig. 11). Multiple factors caused those changes, working synergistically or interchangeably. In summary, eutrophication and reduced top-down control (e.g. caused by overfishing of predators such as bonito, bluefin tuna, mackerel, bluefish and dolphins) caused an increase in the small pelagic fish abundance. Around 1989, both the anchovy and sardine collapsed spectacularly, which was attributed to low recruitment caused by an outburst of an invasive non-native jellyfish, *Mnemiopsis leidyi*, together with
overfishing (Kideys 1994; Daskalov 2002; Gucu 2002; Bilio & Niermann 2004; Knowler 2005, 2007; Oguz, Salihoglu & Fach 2008; Akoglu et al. 2014). Specifically, *M. leidyi* feeds directly on the eggs of the small pelagic fish and is also a competitor for zooplankton (Bilio & Niermann 2004). The collapse might also have been expedited by the large hydrological and meteorological changes that occurred, which could have caused subsequent alterations in the phyto- and mesozooplankton communities (Bilio & Niermann 2004). Eventually, small pelagic fish stocks recovered because of reduced fishing pressure and a retreating biomass of the comb jellyfish, in turn caused by the increased predation pressure exerted by another jellyfish (Akoglu et al. 2014). But besides these major restructuring mechanisms, other drivers work synergistically. For example, the importance of environmental variables such as SST, wind stress and river runoff on the recruitment of anchovy and sprat has been shown (Daskalov 1999; Guraslan, Fach & Oguz 2014). Furthermore did the body condition of sprat gradually decrease over approximately the last two decades, caused by the warming of the Black Sea and a subsequent decrease in their main food item, i.e., cold-water copepods (Nikolsky et al. 2012). Another factor that might be important is the top-down control of bonitos (2004-2006), through either predation or the prevention of anchovy to freely forage in feeding areas (Sahin et al. 2008). Therefore, the Black Sea might be an example of how various drivers dictate the small pelagic population fluctuations. It is thus not inconceivable that in most Mediterranean ecosystems, the multitude of actors is underestimated. But as the Black Sea is a closed basin and much larger than the regions we discussed, its functioning might be highly different. This is already clear by for example the dominance of sprat over sardine, the superior landings (and hence the effect of eutrophication) and the migration of anchovy.

**Fig. 11** Schematic illustration of the four periods in the Black Sea. (from Akoglu et al. 2014)
Discussion

Before making more general conclusions on the different drivers of the anchovy and sardine fluctuations, the major differences between the ecosystems should be pointed out. Large differences between ecosystems that have similar drivers might for example point towards more general mechanisms. On the other hand, when a driver is only important for certain areas (generally in combination with other factors), this might provide information on the circumstances during which the influence of this driver peaks. At first sight, the population dynamics of sardine and anchovy in the boundary current zones appear rather different from the GOL and Mediterranean. Generally, in the boundary currents regime shifts take place, whereby the populations of several species are altered and sardine and anchovy biomass changes dramatically. In the Mediterranean areas, regime shifts seem to be the exception rather than the rule. For example, although in the GOL the pelagic ecosystem changed, no evidence is present of other species being affected too. Hence, no actual regime shift took place. Also, the large fluctuations of anchovy and sardine biomass and abundance in the Mediterranean appear generally not as drastically as in the boundary systems (i.e., the amplitude appears smaller and crashes are less common). Additionally, both species also do usually not oscillate in alternation and widespread seasonal migration is not salient or documented.

Consequently, the relative importance and mechanism behind most of the drivers can change substantially between the areas. But despite these differences, there are some highly recurrent factors, which might very likely be of importance to the GOL as well (Table 1). Most importantly, productivity alterations appear to be of chief importance in almost every discussed region. This is not unexpected given that the importance of nutrients was already indicated decades ago (Atkins 1923, 1925a; b) and theories are often based on this observation. For example, recruitment variation is summarised by Bakun’s (1993) triad of retention, production and concentration. In other words, recruitment is high when the early life stages of a species are dispersed limitedly and growth rate is high because of expanded production and food concentration (see the general introduction for the link with fish life history traits). Indeed, the habitat distribution of sardine and anchovy in the Mediterranean already appeared to be associated to productive areas over the shelf (Tugores et al. 2011; Giannoulaki et al. 2013; Bonanno et al. 2014). Productivity might be especially important in the Mediterranean, as this is an oligotrophic sea (and is thus in sharp contrast with the large upwelling systems). For example, differences in anchovy growth between the Mediterranean areas and the more nutrient rich North-Western Atlantic is mainly explained by differences in chlorophyll concentration, and to a lesser extent SST (Basilone et al. 2004). Additionally, a mass-balance model for the Catalan Sea also indicated that this ecosystem might be limited by productivity, as both primary production and detritus are intensively reused (Coll et al. 2006). Associated with productivity is river discharge. Indeed, river outflow and thus nutrient enrichment was important in almost all regions where large streams were present (e.g. the Spanish Ebro, the French Rhône, the Italian Po and the Romanian Danube, see also Agostini & Bakun 2002). Factors such as SST, wind and current characteristics (Table 1) were very recurrent as well, often because they are associated to productivity, although they can also have a disjoint effect (e.g. through larval advection).

But many other factors were also pointed out, such as top-down control by predation. Density-dependent mechanisms also play a role, as well as factors such as fisheries and disease (see the Australian sardine population; Jones 1973; Whittington et al. 2008). Another important point is the tolerance level of both species to environmental conditions. Some environmental variable (e.g. SST, salinity and oxygen) might surpass or border this level, thereby drastically altering its distribution...
and/or abundance. For example, low salinity water is unfavourable to sardine (Twatwa et al. 2005), as are low oxygen concentrations (Bertrand et al. 2011) and relatively deep shelf waters in the Mediterranean (e.g. Giannoulaki et al. 2005).

So it did become clear (especially for the Black Sea) that multiple drivers can be important, each of them working on their own temporal and spatial scale and acting rarely alone. But some of the mentioned factors received only little attention (e.g. predation), relative to the number of studies considering changes in productivity or SST. This might be because these factors are estimated to be inconsequential (and truly are), because studies directed to them are difficult to perform (e.g. essential data is unavailable or relationships are methodologically harder to establish) or their importance is underestimated. To avoid especially the latter, a maximum of potential drivers should be investigated. Also, it is often very unclear of what the actual driver is, because there is a large interplay between multiple ecosystem state variables. For example, reduced fish growth might co-occur with a decrease in temperature. But in such case, is the effect direct or is it the result from the interplay with upwelling, and is this the actual driver? To fully understand the changes, both should ideally be considered.

All of this shows that there is a need to consider the ecosystem as comprehensively as possible. Thus, although bottom-up controlling mechanisms appeared to be of global and high importance and should definitely be given thought, it remains also indispensable to look at other mechanisms that might work in synergy. Therefore, during this work an adequate set of possible drivers of the GOL’s small pelagic fish populations was investigated. In doing so, this study might also represent an illustration for studying population dynamics elsewhere.

Table 1 Summary per ecosystem of main factors that were clearly shown to drive the fluctuations of the sardine (S), anchovy (A) or both (X) population. This list is rather illustrative and not exhaustive. Factors are also simplified (fishing, river outflow, hydrodynamics which include e.g. upwelling and current speed, wind, productivity which was assessed in terms of e.g. chlorophyll concentration or zooplankton quantity, Sea Surface Temperature, other climate indices independent if they were local or regional, and predation pressure). Some factors (e.g. density-dependence, salinity, thermocline or mixed layer depth) were not included because they were often associated with the other included drivers or because they were only rarely shown to be of chief importance (potentially because of lack of information). References and further information are provided in the text.

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Chapter 2: Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean

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Abstract
Since 2007 the ecosystem of the Gulf of Lions has shifted to a different regime, characterised by a low anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) biomass and a remarkably high sprat (*Sprattus sprattus*) biomass. Surprisingly, the abundance and recruitment of anchovy and sardine remained high. To understand which processes (bottom-up or top-down control, etc.) could have caused this shift, we studied the changes in body condition, growth and size and age of anchovy, sardine and sprat over 1984-1985 and 1992-2012, using data from scientific surveys. The annual age structure of anchovy and sardine was estimated using Bayesian mixture models based on size frequency data with priors on the age-length relationship derived from independent otolith readings. The results indicated periods during which anchovy and sardine were in an average (1992-2004), good (2005-2007) or poor (2008-2012) overall state of condition. For sardine, the shift towards smaller fish observed during these past 4 years was explained by a combination of slower growth and the disappearance of older individuals (ages 2+). Despite the increase in biomass of sprat since 2008, indications were found that sprat was also smaller than in the past. As growth and condition decreased and overexploitation has not been documented or suspected for those three species in this area, we propose that the current decline in sardine and anchovy biomass could be due to qualitative and/or quantitative modifications in the planktonic production (i.e. a bottom-up control) or mass mortalities of adults due to an epidemic disease.

**Keywords**: population fluctuations, anchovy, sardine, sprat, mixture models, ageing, Gulf of Lions
Introduction
Small pelagic fish are a key component of pelagic ecosystems owing to their high overall biomass at a mid-trophic level, which provides an important energy linkage between upper and lower trophic levels, i.e. wasp-waist control (Rice 1995; Cury et al. 2000). Their population dynamics are known to be strongly affected by environmental fluctuations and predator abundance/human induced changes (bottom-up and top-down effects), causing populations to commonly face conspicuous variations in abundance (Checkley et al. 2009). Those fluctuations can have great consequences for both fisheries and the ecosystem structure and functioning (Cury et al. 2000; Shannon, Cury & Jarre 2000; Daskalov 2002).

Recently, an important shift in the small pelagic fish community of the north-western Mediterranean Sea has been observed. The dominant species, i.e. sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus), declined in biomass while sprat (Sprattus sprattus) which has been rare for the last two decades increased tremendously in most recent years (Palomera et al. 2007; GFCM 2011; Fig. 1). Surprisingly, the abundance (total number of fish) of both anchovy and sardine has remained relatively high (GFCM 2011; 2012) and their mean size has dramatically diminished, making these two species less exploitable (GFCM 2011; 2012). Whereas sprat is of no commercial interest in this region due to its small size, adult anchovy and sardine have a high economic value. When biomass decreased, commercial landings did as well. Between 1992 and 2004 on average 7094 t of anchovy and 11467 t of sardine were landed per year in this area, while only 2084 t and 7967 t were on average landed per year over 2005-2010 (Demaneche et al. 2009; GFCM 2012; FAO 2015), generating important socio-economic consequences.

The major drivers for these changes are yet unknown. The yearly ratio of landings to biomass (i.e. a proxy for the exploitation status) of anchovy and sardine is generally lower than 0.2, with the exception of 1993, 2003, 2004 and 2007 for anchovy and 1997, 2000 and 2001 for sardine. For anchovy, this ratio was thus maximal after their biomass decreased, while for sardine this was before a biomass increase took place. Therefore, fisheries alone is an improbable cause of the observed changes (the General Fisheries Commission for the Mediterranean Sea, GFCM, indeed did not document or suspect overexploitation for those two species in this region). However, overexploitation often interacts with environmental changes, possibly promoting an accelerated population decline and hence becoming an important driver (Planque et al. 2010). Also, large fluctuations in small pelagic fish biomass have often been related to environmentally driven changes in recruitment success (Checkley et al. 2009). Intriguingly, based on size at first maturity, high levels of sardine recruitment have been observed in this area during the decline in biomass of those populations, making the recruitment failure hypothesis rather unlikely.

So why does biomass decrease while abundance increases? And which parameters could be used to help identify the possible drivers (alone or combined)? Several hypotheses may explain the alteration in the population ratio of biomass to abundance, whereby one does not necessarily exclude the other. Firstly, fish might grow up more slowly, so that on average they dwindle in size and accordingly reach a lower weight. Secondly, big old fish may to a certain extent have disappeared from the population (through emigration and/or death). Thirdly, a decrease in condition could lead to fish that have a lower weight for a given size. Depending on which hypotheses are valid, alternative processes driving the population changes (e.g. survival vs. reproduction) could be
identified as they might for example be pointing towards bottom-up or top-down control of the pelagic ecosystem, or the occurrence of an epidemic disease.

**Fig. 1** Trend in total abundance (number) and biomass (tonnes) of anchovy, sardine and sprat in the Gulf of Lions. Data are from acoustic surveys (July).

To resolve the posed hypotheses, body condition, growth and size and age structure were investigated. These parameters are frequently considered for fisheries research, but are rarely reported simultaneously over a long-term period for multiple species. According to the Marine Strategy Framework Directive (MFSD), a “healthy” stock is considered to be a population within safe biological limits, exhibiting a population age and size distribution that is indicative of a healthy stock (European Commission 2008). So far no description could be provided as how a healthy age and size structure should be like and for management purposes other parameters have been suggested (Brunel & Piet 2013). However, knowledge on the age and size structure still contributes to the comprehension of how populations fluctuate and the awareness of their condition. In addition to these two variables, we also studied two commonly used population features: condition and growth. Condition factors (such as Fulton’s index; Ricker 1975 and Le Cren’s relative condition index; Le Cren 1951) are commonly considered to be closely related to fitness, determining the survival and reproductive capacity of individuals (Jakob, Marshall & Uetz 1996). They are calculated on length-weight relationships and are convenient to compare the physiological status of fish, assuming that this depends on their relative weight (Froese 2006). On-going research on anchovy and sardine in the Gulf of Lions already confirmed that the relative condition index is correlated to the fat content (P.
Brosset pers. comm.). Although body condition and growth are both based on the length of individuals, they provide different information and do not always fluctuate in parallel (Sinovčić, Keč & Zorica 2008).

In this study, we investigated the changes in these key biological population parameters to see if a decrease in biomass co-occurred with a decrease in fish condition or size, which might be the result of slower growing or younger individuals. To do so, we examined acoustic and scientific trawl data from the Gulf of Lions over a period of 21 consecutive years (1992 – 2012) and two earlier exploratory years (1984 and 1985), and used innovative Bayesian mixture models to get accurate age compositions. By characterising condition, growth and age and size structure, the state of the population can be investigated, after which the importance of possible mechanisms explaining the observed shift (e.g. environmental factors, competition, disease) can be discussed.

Materials and methods

Data collection

The Gulf of Lions is a continental margin in the north-western Mediterranean Sea, covering about 20400 km². In this area, yearly standardised acoustic and trawl surveys of small pelagic fish (PELMED, “PELagiques MEDiterranée”) were carried out in 1984 and 1985 and continuously since 1992 on board the research vessels N/O Thalassa (1984-1985) and l’Europe (1992-present). Sampling was generally done in July, except in 1984-1985 and 1995, when individuals were caught in August. Data were systematically collected along 9 parallel transects perpendicular to the coastline, 12 nautical miles apart (22 km). The vessel navigated at depths between approximately 20 m to 200 m (the border of the continental shelf, where the abundance of most small pelagic fish drops critically). When the echosounder detected sufficiently long fish traces (≥2 nm) or a change in the echotrace characteristics, a pelagic trawl was deployed to assess the species composition. The content was sorted and the total weight of every species caught was measured. Anchovy, sardine and sprat were then classified in 0.5 cm size classes (with their length rounded down), of which the total weight and the fish count were afterwards determined. When the total catch was too large, a random subsample was taken. Over the whole period, the number of trawls made per survey (≥30 min at 4 nm/h) varied between 15 and 54 (with the exception of 1984 when only 10 trawls were taken). The protocol of acoustic and trawl surveys to assess pelagic fish stocks was described by Doray (2010) and further details on the sampling methodology can also be found in Plounezvez and Champalbert (2000) and Brehmer et al. (2006).

To estimate age from length, otoliths of anchovy and sardine were collected during the period 2002-2012 (as well as in 1993, 1998 and 1999 for anchovy). During the PELMED and June MEDITS surveys (MEDITS working group 2012) individuals were selected for otoliths reading so that the entire size range was covered. Throughout certain years, fishermen were asked to randomly select anchovy (2006, 2009-2012) and sardine (2005, 2006, 2009-2011) caught in the Gulf of Lions from June to September, doubling the amount of length-age records for each species. The total length of each individual was measured (to the inferior 0.5 cm) before the otoliths (sagittae) were extracted and read.
Data analysis

**Length-weight relationship and body condition**

The condition of the three species was compared between years, using weight-length relationships and a relative condition factor (Le Cren 1951). Both analyses are reported in this study because they differ in results and utility. An analysis of covariance (ANCOVA; Zar 1999) was performed so a difference in the year-to-year slopes of the fitted linear relationships \( \log(W) = \log(a) + b \log(L) \) could be detected (were \( W \) is the mean weight of individuals of length \( L \)). Because we wanted to test for a year-to-year difference, the interaction between the categorical predictor variable (year) and the covariate was included in the full model. This model was superior based on AIC selection and ANOVA tests compared to more parsimonious models with only an additive effect of year and size or with size alone. A Tukey test was then used to investigate the pairwise relationship between all years.

Because length distributions changed on a yearly basis and \( b \) was not always equal to 3 (Froese 2006), a relative condition factor (measuring the anomaly in weight of a fish of a given length) was calculated per year and per trawl for each size class:

\[
K_{rel} = \frac{W}{al^b}
\]

where \( a \) and \( b \) are the regression parameters of the length-weight relationship computed over all data pooled together. These length-weight relationships were highly significant for all three species (\( R^2 > 0.95, \ p < 0.001 \)), with the following allometric formulas:

\[
W = 3.86 \times 10^{-3} L^{3.20}, \quad W = 5.90 \times 10^{-3} L^{3.10} \quad \text{and} \quad W = 3.21 \times 10^{-3} L^{3.37},
\]

for anchovy, sardine and sprat, respectively. A Kruskal-Wallis test was used to check for statistical differences in body condition index between years, followed by a multiple comparison post hoc test. Furthermore, the use of the relative condition factor allowed for a comparison between age groups by attributing an age to each length class, based on the output of the age structure analysis.

**Size distribution**

We plotted a size frequency distribution per year per species in order to describe the temporal variations in length structure of the three populations. The number of measured fish (\( n \)) and the number of trawls from which they originated (\( N \)) ranged between 811-6229 (\( N=5-40 \)), 564-5060 (\( N=9-42 \)) and 0-5004 (\( N=0-30 \)), for anchovy, sardine and sprat, respectively. For sprat, no or very few individuals (<6) were found in 1993, 1998, 1999 and 2001. When only a subsample had been measured, the total frequency of individuals per length class was obtained by weighing the measured frequency of individuals per length class of a trawl by the total species weight in the trawl divided by the subsample weight. Anchovy smaller than 8 cm were removed from all analyses because they were generally not caught or targeted (except during 1995).

**Size at age and growth**

Growth was only considered for anchovy and sardine since no otolith readings were available for sprat. Age-length data from fish caught between June and September were selected, so all factors investigated reflected the status of the populations during summer. To measure growth rates of anchovy and sardine and to construct the age-length priors for the mixture models, 3313 and 2974 otolith readings acquired during the summers of 13 and 11 years were used for anchovy and sardine,
respectively. Both species displayed year-to-year variations in length-age relationships that were similar to what was observed for the condition index and median size. Therefore, these data were split up into periods, which we retained for age structure analyses. For sardine, nonlinear least square regression was used to fit a Von Bertalanffy model for each period, using the nls function of R (R core team 2013):

\[ L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \]

where \( L_t \) is the expected length at age \( t \), \( L_\infty \) is the asymptotic maximum length, \( K \) is the von Bertalanffy growth constant, and \( t_0 \) is the theoretical age at length zero. For sardine, too few otolith readings were available per age class per year to fit annual models, especially for the early period. For anchovy, length at age 0 was removed since data were originating from a small number of individuals found during few years. As a result, not enough age classes were present for anchovy to accurately fit a growth model. For sardine, we also calculated the overall growth performance (Pauly and Munro 1984):

\[ \phi' = \log_{10} K + 2 \log_{10} L_\infty \]

This enabled us to reduce the number of parameters of the Von Bertalanffy growth model to one, as to compare growth more easily between periods and with previous studies.

**Age distribution**

Bayesian mixture models were used to estimate the age structure from both length frequency data and age-length keys. In doing so, a framework was developed that is more powerful than traditional mixture models that are based on only one of these information sources. As the age-length keys used as priors were based on otolith readings, this analysis could only be performed for anchovy and sardine. Priors were constructed based on the extracted summary statistics (mean length, standard deviation, number of data points) of a normal distribution fitted to the length frequency plots of each age class, per species and per period. To do so, size frequency per age class was first weighted by the total frequency of that age to compensate for potential biases in the sampling. The choice for a prior per period (instead of one general prior) allowed us to obtain a more accurate estimation of the age structure. For the years where no data derived from otoliths were available (mostly before 2002), the prior from the period after was used. Since the priors were constructed based on data from more recent years, we considered them to be unreliable for the use of age structure analysis of 1984 and 1985.

The finite mixture model was fitted on the weighted size distributions using Rstan, an R package for Bayesian modelling that uses a variant of the Markov Chain Monte Carlo sampling technique (Stan Development Team 2013). The model had the following output parameters (per mixture component): \( \mu_{age} \) (mean length at age), \( \sigma^2_{age} \) (standard deviation of \( \mu \)) and \( \theta_{age} \) (mixing proportion). The mixing proportion is an estimate of the relative abundance of each age category in relation to the total population. The prior for \( \mu_{age} \) was a normal distribution where \( \mu \) and \( \sigma^2 \) were replaced with values from the age-length prior. Age classes were forced to be ascending. Therefore, we truncated the upper limit for \( \mu_{age} \) by the value for \( \mu_{age+1} \) reduced with the minimal distance between two mixture components. This value was calculated as the minimal difference in mean length found between 2 successive age classes from 2 successive years (so a cohort was followed) from individuals used for otolith analysis. For our data, this improved the results significantly as label switching (when
within or between chains labels switch between peaks) was avoided, allowing the model to converge (Stephens 2000; Jasra, Holmes & Stephens 2005). Furthermore, on the uniform prior for sigma, a constraint on the lower and upper limit was set (0.2-2) to avoid extreme values that were highly unlikely from a biological point of view. The starting values for the parameters $\mu_{age}$ and $\sigma^2_{age}$ were based on the prior, and $\theta_{age}$ was initiated at 1/M (with M being the number of mixture components).

Since a finite mixture model was used, it was necessary to find the optimal number of components (M) to fit. We decided to select M manually, since M was impossible to be determined from the data alone (Hunt & Jorgensen 1999; Laslett, Eveson & Polacheck 2004). Given that the prior indicated the expected mean length and standard deviation of each age class, the estimation of the number of components likely to be present was mostly straightforward. Still, each time the model was run for at least 2 different values of M. For each year and species, the model outputs were compared by superimposing them on the observed histogram. Together with convergence assessment, this allowed us to select the optimal M value and to confirm that the results were biologically plausible.

Relationship with abundance and biomass

Principal component analyses were used to summarise into a few dimensions (i.e. the principal axes) the variability of the different population parameters (the descriptors) over time (the objects), so that we could comprehensively consider the state of the population during certain periods. Estimates of the total abundance and biomass of anchovy, sardine and sprat in the Gulf of Lions were deduced from acoustic information, except for 1992 and 1994. We considered the relationship (with and without lag) between abundance and biomass (both log transformed) and the average fish size, body condition (Le Cren’s relative condition index) and age (calculated as the sum of all ages multiplied by their relative abundance in the population, i.e. $\theta_{age}$ from the mixture models). Growth was excluded since data is limited to certain years. Since age information was not available for sprat, we only conducted this analysis on anchovy and sardine.

Results

Length-weight relationship and body condition

The ANCOVA established that yearly length-weight relationships differed significantly (anchovy: $F=14.79$, $p<0.001$, sardine: $F=32.34$, $p<0.001$, sprat: $F=6.31$, $p<0.001$; Fig. S1). However, a post hoc test revealed no apparent grouping of certain years for sardine and sprat. For anchovy, the 3 last years were significantly different from almost all other years as individuals had a lower allometric coefficient (“b”). Although not significant, the graphs for the other two species indicated likewise a lower b during these last years. The highest condition was demonstrated to be around 2005-2007 for anchovy and sardine, but again the result was not significant. Regarding these last two points, we cannot conclude if the lack of significance is due to limited information for some years and/or a real absence of contrast between years.

A significant difference between all years was also established for the three species in the condition factor $K_{rel}$ (Kruskal-Wallis test, $p<0.05$), which ranged from 0.96 to 1.05 for anchovy, from 0.92 to 1.08 for sardine and from 0.96 to 1.22 for sprat (Fig. 2). Because of the few data available for sprat, the standard deviation is relatively high in most years. In contrast to the results from length-weight relationships, the use of Le Cren’s $K_{rel}$ index led to the grouping of some years, i.e. both anchovy and sardine exhibited a higher $K_{rel}$-value in 2005 and 2006 than in other years, while they were in lower
condition in 2003 and in 2009-2012. For sprat, those two periods were also visible, but they were not significantly different from the earlier years since they were characterised by large fluctuations and standard deviations. Although we only had few data in 1999 and 2000 for sprat, it is of interest to note that the condition factor was high in those years. For anchovy and sardine we found no pronounced discrepancy between the changes in body condition of different age classes, although in 2011 a slight increase in condition of 2-year-old sardines was visible (Fig. S2).

**Fig. 2** Evolution of the mean relative condition index per year for anchovy, sardine and sprat with the standard deviation. N is the number of data points used (i.e. the number of size classes of a given year for which weight data was available, over all trawls) and n, the number of fish measured.

### Size distribution

The maximum total length of anchovy observed was 18.5 cm and 95% of all individuals had a length between 10.0 cm and 15.5 cm (median = 12.5 cm, Fig. S3). The modes of the mostly unimodal size distributions remained fairly constant until 2005, whereupon a sudden shift towards larger individuals was detected (Fig. 3). During the following years, a size decline took place, whereby after 4 years the size range reached the same state as before 2005. The continuation of this decrease caused the median fish size of the anchovy populations of the last 4 years (2009-2012) to be smaller
than in all preceding years (median = 11 cm). The size distribution of 1984 and 1985 did not noticeably differ from the early invariable period (1992-2004).

Sardine had a median length of 14.5 cm, with 95% of all fish having a size between 8.5 cm and 17.5 cm (min = 5.5 cm, max = 22 cm, Fig. S3). In contrast to anchovy, two distinct modes were discernible for most years, of which the second (containing the larger individuals) seemed to diminish gradually from 2009 onwards (Fig. 3). When looking at absolute values, it becomes clear that this tendency is not only caused by a decrease in the proportion of larger fish (possibly caused by e.g. an increase in younger fish), but also by their disappearance, as for instance fish larger than 17 cm were not caught in 2012, whereas before 2009 this always happened in considerable abundances. From 1992 to 2008 there were some fluctuations in the proportion of individuals belonging to each peak and the mean size of both modes, but no clear trends. During 1984 and 1985, individuals were on average larger than in most other years. These 2 years were the only ones in which sardines bigger than 21 cm were found.

The size range of measured sprat was between 5 and 14.5 cm (median = 9.5 cm and $Q_{2.5-97.5} = 8-12.5$). Although in the last years more individuals were sampled, the maximum size observed was still smaller than during previous years in which, however, only few sprat was found (Fig. 3). This period (2008-2012) was mainly characterised by one single peak (except for 2011), while in other years two modes were clearly visible (1984-1985, 1996, 2004-2006). Because of the lack of data for some years, it is difficult to detect any clear trend. A comparison between species showed that sprat and sardine displayed larger year-to-year variations in size distribution than anchovy (Fig. 3).

![Fig. 3 Half-violin plots showing the change in size distribution of all three species over the studied period (years with less than 10 individuals measured were removed).](image-url)
Size at age and growth

For anchovy and sardine, otoliths of age categories 0-4 and 0-8 were found, with very few individuals belonging to the oldest age classes. Periods with a dissimilar age length relationship were observable; hence, the data were split based on visual inspection into years with relatively slower, intermediate or faster growing individuals (Table 1; Fig. 4). For anchovy, such a pattern was less visible because of the few age classes. Notably, the years 2006 and 2007 were characterised by the presence and large size of age 4 anchovy. For sardine, a fast growth rate was distinctive throughout 2006-2008 and a clear decrease was visible during the last 4 years (2009-2012). The asymptotic length found for sardine during the slow growing period is particularly high, as a result of the lack of older individuals and the more linear appearance of the Von Bertalanffy growth curve.

### Table 1 Estimation of the Von Bertalanffy growth curve parameters and the phi-index for sardine during the following periods: 2009-2012 (slow), 2002-2005 (intermediate), 2006-2008 (fast). All parameters are significant (p<0.001).

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>$L_\infty$</th>
<th>$K$</th>
<th>$t_0$</th>
<th>$\phi'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sardine</td>
<td>Slow</td>
<td>33.57</td>
<td>0.09</td>
<td>-4.1</td>
<td>2.01</td>
</tr>
<tr>
<td></td>
<td>Inter.</td>
<td>18.38</td>
<td>0.45</td>
<td>-1.73</td>
<td>2.18</td>
</tr>
<tr>
<td></td>
<td>Fast</td>
<td>18.88</td>
<td>0.56</td>
<td>-1.64</td>
<td>2.30</td>
</tr>
</tbody>
</table>

Fig. 4 Growth of anchovy and sardine per year obtained from otolith readings. Periods with a different growth rate are used as priors for the mixture models and are indicated with a different colour family. Because these periods differ for anchovy and sardine, years are not always indicated with the same colour for both species. Points indicate outliers (values more than 1.5 times the length of the box away from the box quantiles). Boxplots for age 0 anchovy were removed because of doubtful values, as well as boxplots based on less than five samples.

Age distribution

For most years there was a number of cohorts (M) for which the model gave biologically sound results and all parameters converged. The model did not converge only 3 times out of 46, i.e. for the 2003, 2008 and 2011 size distributions of anchovy that were normally distributed and that could thus not be split into multiple components. All results are summarised in Fig. 5.
For anchovy, the total number of age classes estimated with the Bayesian mixture model varied between 2 and 3. Most years (12 out of 18) were typified by only ages 1 and 2, while other years consisted out of a mixture of ages 0 to 3. During 2009, 2010 and 2012 individuals had in general a lower length at age 1 and 2 (except age 2 anchovy in 2010) and during 2010 and 2012 age 1 was dominant. Age 3 anchovy were only consecutively present between 2005 and 2007, during which age classes 1 (when included) and 2 had a higher mean length (although the standard deviation is relatively high). In 1998 and 2000, age class 3 was incorporated as well but had a lower average size than during the 3-year period. The contribution of each age to the annual population did not follow any clear temporal pattern, so that strong or weak cohorts could hardly be followed (Fig. 5 and S3).

Sardine exhibited an estimated age structure made up of a combination of ages 0 to 3, with age 4 present only in 1996, 1997, 2001 and 2002 (Fig. 5). All age categories showed large temporal variations, but older age classes fluctuated relatively less. From 2006 to 2008, the average length of almost all age classes (0-3) was visibly higher than during all other years. After this period, an overall downwards trend was visible in mean size, together with a decrease in the proportion of older fish and their progressive loss. That is, from 2009 onwards age 3 became unobservable, followed by age 2 in 2011 (while this age class had previously always been present). We found that in the bimodal size structure of sardine, the first mod is always shaped by age-0 fish, sporadically supplemented by a smaller proportion of age 1.

**Fig. 5** Evolution of the mean length per age (upper row) and the percentage of the population belonging to each age category (lower row) resulting from the mixture models.

### Relationship with abundance and biomass

The PCA analysis allowed us to objectively define the state of health of the populations during the different years, with years situated in similar situations clustered together. The first and second axis of the PCA encompassed together 82% (anchovy) and 78% (sardine) of the total variance. The first
axes of both PCAs, which alone summarised respectively 49% and 59% of the total variance for anchovy and sardine, opposed condition, age and size to abundance (Fig. 6). The first parameters are more or less bundled together and have similar heavy loadings for axis 1. Biomass and abundance are slightly related as well, although this is less noticeable for sardine. Axis 1 separated years with larger and older fish in a better condition, such as 2005 and 2006 for anchovy or 2006 for sardine from years of reduced size, age and condition, such as 1999, 2010 and 2011 for anchovy or 2008, 2009, 2010 and 2012 for sardine (Fig. 6). Axis 2, which was predominantly explained by biomass, mostly differentiated years of high biomass (2001 for anchovy and 2004 and 2005 for sardine) against years of low biomass (2007, 2010 and 2011 for anchovy or 1997, 2009, 2010 and 2011 for sardine). Note that years of low biomass did not always imply years of low abundance (such as the years 2009, 2010 and 2011 for sardine). So in this study, three periods emerged, with the last period (2008-2012) converging to a low biomass and non-optimal biological population indicators. The other two situations could be interpreted as optimal (2005-2007; best state of all parameters) and the baseline scenario (1992-2004).

Fig. 6 PCA (without time lag) for anchovy and sardine showing the relative importance of five variables to explain the year-to-year variance, with the variance explained by each axis between brackets. No abundance data was available for the years 1992, 1994 and 2012, so they were excluded from the analyses.

Discussion
This study allowed us to (i) assess the amplitude of inter-annual changes and outline the state of the populations, (ii) develop an advanced method to obtain age structures from length data, (iii) document new biological information on anchovy, sardine and sprat in the Gulf of Lions and (iv) make an hypothesis about the possible drivers of the regime shift. For this, different biological parameters were used that are scarcely reported in parallel and simultaneously for multiple species despite their importance. In our study, these parameters fluctuated during the whole period almost independently from biomass and abundance data, only for sardine we found a weak inverse relation of abundance. Even more, sardine abundance was not highly correlated with sardine biomass, indicating that high numbers of individuals in the ecosystem do not always equal a high biomass (and vice versa). This study illustrates how looking at changes in biomass alone can be misleading as they
might reflect various types of changes in the health of a population. The use of the biological parameters allowed us to define periods in which species were in a relatively good or poor state, which could not have been done with abundance and biomass data alone.

State of the populations

Body condition, growth and size and age structure varied mostly in parallel for sardine and anchovy (except for condition in 1996). Before 2005, most of the parameters showed little variations, apart from body condition for anchovy in the early 1990s. The years 1984 and 1985 were a bit different in terms of mean length for sardine (larger individuals), but only the size structure and the body condition were considered. For anchovy, there was a sudden shift in the size distribution between 2004 and 2005, which went concurrently with a shift towards older and faster growing individuals with a better body condition. The two subsequent years (2006 and 2007) displayed the same features, but with a diminishing tendency. In contrast to anchovy, the period 2005 to 2007 was for sardine less eye-catching since the size distribution did not show such a clear shift and an increased growth and a change in age structure was observed only from 2006 onwards. For both species, this shift was followed by an inversion of the pattern from 2009 onwards, with fish becoming smaller, slower growing and having a relatively weaker body condition. Note that body condition started to decrease before the other parameters (i.e. since 2007) for both sardine and anchovy. Additionally, old sardines disappeared, leading to a multiannual low-grade situation that was not observed before. During the latest years (2008-2012), sprats were also smaller and had an average (but not a good) body condition, despite their increase in abundance and biomass. To evaluate the uniqueness of the observed changes and the utility of the selected parameters, we discuss these separately.

Biological parameters

Length-weight relationship and body condition

Several length-weight relationships have been given for anchovy, sardine and sprat in the Mediterranean, but in the Gulf of Lions this relationship was as far as we know only published for anchovy by Campillo (1992) and calculable for sardine based on the data given by Lee (1961, \[ W = 33.70 \times 10^{-3} \cdot L^{2.46} \]). Essentially, the established length-weight-relationships were useful for obtaining the relative condition factor (as was previously done for these species; see Millán 1999; Sinovčić et al. 2008; Pešić et al. 2010), which in this study proved to be giving more clear-cut results and allowed straightforward inter-species and inter-annual comparisons. That is, distinct periods during which species were in a relatively good (e.g. 2005-2006 for all three species), average (most years preceding 2005) or poor condition (2010-2012 for anchovy and sardine) were most easily defined. Data from Lee (1961) also allowed us to obtain the relative condition factor for sardine in 1959 (1.015). Thus, their condition was probably only slightly higher than average and in the range found for 1984 and 1985.

Size distribution

Size structures had not been documented for pelagic species in the Gulf of Lions, with the exception of landing-based surveys for sardine in 1959 (Lee 1961) and sprat in February and April 1945 (Furnestin 1948). In spite of fisheries selectivity causing a difference between landing-based and scientific trawl surveys and hence bringing forth unimodal size distributions in these two previous studies, the second mode (with the largest individuals) can still be compared. In July 1959, the largest
proportions of sardine (>95%) ranged between 15 and 17 cm, which is similar to the size of the second mode of several years we investigated (1984, 1985, 2006 and 2007). While comparison of the first mode of small sardines is prevented, it highlights once more the anomaly of the gradual disappearance of this second mode since 2009. Similarly, in 1945, mostly sprat of 11cm was caught in the Gulf of Lions, which only happened occasionally from 2009 onwards (Furnestin 1948). Sprat in the Baltic Sea is known to have a bimodal structure similar to our findings for 1984 and 1985, i.e. a first mode (comprising the small individuals) and a second much larger peak (Cardinale et al. 2003). This study revealed that although the sprat biomass has considerably increased, the absence of the second mode in most recent years and a body condition factor close to 1 suggest that sprat is probably not in its best “state of health”, in contrast to what could have been expected. For anchovy, the unimodal size distribution observed corresponds to what was previously seen in other regions (Barange, Coetzee & Twatwa 2005).

**Size at age and growth**

Growth values for sardine showed no remarkable deviation from other regions, except for the last 4 years which exhibited slower growth rates (Morales-Nin & Perttierra 1990; Voulgaridou & Stergiou 2003; Kada et al. 2010). Growth parameters given for the Gulf of Lions (when sampling was done during the spring, summer or autumn of 7 years; Alemany and Álvarez 1993) matched those of the fast growing period. This indicates that this fast growing period is probably not exceptional and that similar fluctuations might have occurred just before the period of our study. Nonetheless, in Alemany and Álvarez (1993), the actual age of individuals was calculated as the age read plus the year fraction between the survey date and a theoretical birthdate, as to correct for the different sampling periods. Since sardine has a prolonged spawning period, their birthdate is not fixed, possibly leading to different age estimates. For anchovy, length at age in the area was previously given by Campillo (1992), who found values of length at age 1 and 2 most similar to what we found for the slow growing period.

**Age distribution**

To test the hypothesis that fish were smaller because they were younger, age structure information was needed. We are to our knowledge the first to combine multimodal decomposition of fish population size structures with otolith readings (age-length priors) within a Bayesian framework. Multiple programmes and packages built on mixture models have been developed which can be used for (or are created exclusively for) detecting age classes (e.g. NORMSEP, Tomlinson 1971; mixdist, Macdonald and Du 2012; mclust, Fraley et al. 2013; flexmix, Grün and Leisch 2013). However, they are usually likelihood-based and do not include systematic prior information, which makes them less efficient at distinguishing the age composition in length-frequency data that does not display clear modes. Software with a Bayesian perspective on mixture modelling (such as bayesf for MATLAB, Frühwirth-Schnatter 2008) is less available and is not always appropriate for the envisioned analyses (e.g. developed for another research field, limited flexibility, etc.).

The mixture model that we used provided consistent results, despite the absence of several observable peaks in the size frequency data. Only in the few cases where the size distribution resembled a nearly perfect normal distribution did the model not converge. Fish for otolith readings were not randomly sampled but an effort was made during the PELMED surveys to include the largest and smallest individuals, thus enlarging the probability of selecting the oldest and youngest fish. Therefore, older individuals were found in the otolith dataset than were included in the mixture
model (age 4+ for anchovy and ages 5+ for sardine). These age categories were present in certain years, but were too low in proportion (< 0.5% and 0.1% for anchovy and sardine, respectively) to be included in the mixture analyses. Furthermore, age 0 was not detected in multiple anchovy size distributions, but this does not imply the absence of this age category at that moment. These youngest individuals were most likely too small to be caught in sufficient numbers by the trawl. In contrast, age 0 sardine were caught in considerable quantities. This discrepancy was probably caused by different spawning seasons (autumn/winter vs. spring/summer for sardine and anchovy, respectively, Palomera et al. 2007; Tugores et al. 2010), making age 0 sardine more prone to PELMED surveys in July.

The life span of anchovy (age 0-4 with age 4 only occurring in extremely small percentages) corresponds to what was found in several other parts of the Mediterranean (Morales-Nin & Pertierra 1990; Bacha & Amara 2012) and earlier in the Gulf of Lions (Campillo 1992). Other studies reported a life expectancy of 3 (Basilone et al. 2004) to 5 years in the Atlantic (Uriarte, Pouzet & Villamor 1996), but all concluded that only a minor fraction belongs to these oldest age classes. Correspondingly, age 4 was completely lacking from the age distribution of anchovy, which was clearly dominated by ages 1 and 2. The importance in terms of relative abundance of these two age classes was also observed in the strait of Sicily (Basilone et al. 2004) and the western coast of Algeria (Bacha & Amara 2012). The authors also noted the potential quantitative underestimation of age 0 anchovy. In the Mediterranean, sardine was aged up to 8 years (in agreement with the otolith readings in this paper), but age distributions were not reported afterwards (Pertierra & Morales-Nin 1989; Morales-Nin & Pertierra 1990; Alemany & Álvarez 1993; Kada et al. 2010). In contrast to anchovy, we found a high proportion of age 0 for sardine, and generally a somewhat lower proportion of age 1 fish, but age proportions varied vastly between years. For both species, we were unable to follow cohorts over time, indicating that there might be a certain degree of emigration/immigration or age-specific selectivity of the fishing gear (GFCM 2007).

Implications

The four biological parameters (body condition, size distribution, growth and age distribution) gave additional information on the population fluctuations and general “state of health” of the three stocks investigated that could not have been obtained when investigating these factors and stocks separately. For example, by comparing trends in three species, we were able to infer the scale at which the changes took place. The similarity between the patterns allows us to conclude that the main drivers are unlikely to be species specific. This information could not have been inferred from biomass or abundance data, which fluctuated differently from the studied parameters. The complex relationship between both types of parameters (quantitative vs. biological) delivers an additional stimulus to implement indices of population structure and dynamics when assessing a population’s status. Overall, our results confirm that the decline in the anchovy and sardine biomass is most likely not related to recruitment but could be due to the combined effects of poor condition, slower growth and the disappearance of older and larger individuals. This is especially surprising for short-lived species, of which biomass fluctuations are known to be mainly influenced by reproductive success rather than adult survival (see for instance Oli and Dobson 2003; Stahl and Oli 2006). During the studied period, the last years were the only period during which a simultaneous decrease in all four parameters was observed. Moreover, previous research that focussed on small pelagic species
of the Gulf of Lions indicated that this simultaneous decline in condition may be a unique occurrence during the last decades (Lee 1961; Lee & Juge 1965).

Possible mechanisms causing such an anomaly can be related to human pressure (fishing) or environmental changes (Sinclair and Iles 1989; Agostini and Bakun 2002; Bakun 2010). Because of the preceding exploitation levels (ratio landings/biomass) of the three main species (maximal when their biomass was already low or started to increase) and the nature of the observed changes (e.g. almost parallel for anchovy, sardine and sprat; the latter being not exploited), overexploitation is unlikely to be the prime force of this pelagic ecosystem shift. Furthermore, during the last years the size structure of the landings is also skewed towards small individuals. Thus, the removal of large individuals by fisheries is only occurring to a very minor extent. This does however not exclude fisheries as a possible agent of change, as fishing and other factors can have a joint effect. Since growth and condition are affected, we suggest bottom-up processes (e.g. prey availability and composition) as the main hypothesis. For example, environmental factors might influence the productivity and the quality of the plankton community, possibly favouring sprats, which are known to have a more diversified diet than anchovy and sardine (Banaru pers. comm.). Such environmentally driven changes in small pelagics habitats have already been observed in various ecosystems (e.g. Barange et al. 2009). However, we do not rule out the possibility of an epidemic disease, which could also alter the age and size structure of small pelagics fish, as observed in this study. The risk of infection is estimated to be increased worldwide (Harvell et al. 1999) and previous examples of disease outbreaks drastically affecting small pelagic fish populations exist (e.g. Sardinops sagax in Australia, Jones et al. 1997). Future studies investigating the influence of environmental factors or density dependence on population fluctuations and the presence of pathogens in adult fish should help distinguishing among these 2 main hypotheses.

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References


Chapter 2: Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean


Chapter 2: Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean | 79


Supplementary material

Figure S1

Fig. S1 Length-weight relationships of anchovy, sardine and sprat over the studied period.
Figure S2

Fig. S2 Mean relative condition per year and per age (0-4) for anchovy and sardine. Each data point corresponds to 1 trawl and boxplots consisting of less than 5 trawls were removed. The total number of data points is marked in the upper left corner.
Figure S3

Fig. S3 Superimposition of the output of the mixture models and the sum of its components on the yearly size and age structure of anchovy (left), sardine (middle) and sprat (right) with indication of the number of individuals measured (n) and the number of trawls from which they originate (N).
Chapter 3: The fisheries history of small pelagics in the Northern Mediterranean

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Preface

In the previous chapter, which was also the first executed part of my PhD, we concluded that bottom-up control was the most likely chief controlling mechanism responsible for the observed changes. But as bottom-up control is a general principle, the next obvious step was to verify the effect of more specific drivers that fall into this category. Chapter 1 showed that food is generally important, but data on plankton is extremely limited for this area (see the general discussion). Hence, data on other potentially important drivers needed to be collected, such as sea surface temperature, chlorophyll concentration, river discharge, climate indices, wind speed or direction, sea level anomaly, etc. We tried linking the mentioned variables to the previously used readily available time series of biomass, abundance, size or condition. Models such as GLMS (General linear Models) and GAMs (General Additive Models) were used, predicting for either sardine or anchovy its fluctuations in function of the potentially important environmental factors. Moreover, a factor for competition (although not a bottom-up controlling mechanism) could be included, as total abundance or biomass estimates of six other pelagic species in the ecosystem (Scomber colias, S. scombrus, Trachurus trachurus, etc.) are also available (data from the pelagic scientific survey).

Additionally, using again the biomass or abundance data of all small pelagics, it was for example even tested if some species reacted similarly to changes in the environment as others using multivariate statistics. One might wonder why such results are not included in this work. Details on the analyses will not be given for the simple reason that the discussed data is generally only available for one month a year, and merely so for about 20 years. This proved to be too short to obtain any sound conclusion. Therefore, longer time series were needed. France has a long history of collecting landing statistics, information that was until now almost completely neglected. These records were used for the following chapter, that aimed at a better understanding of the fisheries history and the environmental factors that influence the small pelagic fish population dynamics.
Abstract
Since 2007, the biomass of sardine and anchovy in the NW Mediterranean has remained persistently low while the sprat population that has no commercial value exploded. Also, simultaneous adverse deviations in the condition and size and age structure of these populations were observed. Altogether this resulted in a drop of the landings of small pelagics. To understand the cause and amplitude of these events and to provide a baseline scenario against which current changes can be compared, we compiled exceptionally long landings series (1865-2013) of sardine, anchovy and mackerel (another important pelagic species) for different maritime quarters of the southern French coast. We characterised the fluctuations of these landings and linked those to environmental drivers (Sea Surface Temperature, Rhône river discharge, North Atlantic Oscillation, Western Mediterranean Oscillation and Atlantic Multidecadal Oscillation), using different time series analyses. A spectacular effort-related increase in landings was observed around 1962 for all three species, and current sardine landings dropped below levels observed before this period. Sardine and anchovy were respectively positively and negatively related to the AMO index and anchovy was also connected to the WeMO. We presented our findings in light of the current ecosystem changes and discussed why none of the environmental variables or fisheries is likely to be the chief agent, and suggested other potential drivers.

Key words: sardine, anchovy, mackerel, Gulf of Lions, fish landings, historical time series
Introduction

Small pelagic fish stocks are known to fluctuate substantially worldwide. These fluctuations are often attributed to climate variability, and sometimes to predator abundance (Checkley et al. 2009). Additionally, these effects can be contingent on or amplified by fishing pressure (Deyle et al. 2013). Here, we focus on the fluctuations of the small pelagic fish stocks of the Gulf of Lions, a bay spanning a substantial part of the French Mediterranean coast. In this area, a recent change in the pelagic ecosystem has been observed, as the biomass of sardine and anchovy has remained persistently low while the sprat population has increased considerably since 2007. Van Beveren et al. (2014) documented changes in length and age structure of the populations as well as a decline in fish condition and postulated a bottom-up control as one of the possible main drivers of such changes. According to the last GFCM reports (GFCM 2014), those populations were not overfished, but we still ignore if such low levels in catches of sardine and anchovy have been already observed in the past and could thus be related to natural and recurrent fluctuations.

As major environmentally driven population fluctuations can occur with an extended periodicity (e.g. Ravier & Fromentin 2001), processes can be slow and the effects of fisheries can be long-lasting (possibly creating a “shifting baseline syndrome”, Pauly 1995), relatively short time series might not be enough to depict substantial changes in the populations biomass, abundance or their landings. Therefore, there is a need to consider the largest time span possible when looking at population dynamics (Jackson et al. 2001). Unfortunately, no sufficiently long time series of population biomass and/or abundance exist for the small pelagic stocks from the NW Mediterranean. However, an extraordinary long series of historical landings was compiled from French national statistics over the period 1865-2013 (SPM, http://archimer.ifremer.fr/statistique-peches-maritimes.htm; statam, Le Corre, 1971; France Agrimer, www.franceagrimer.fr).

Before 1940, the pelagic fisheries of the Gulf of Lions only used traditional techniques (albeit increasing motorization after World War I). After the beginning of the Second World War, several improvements allowed the fishery to develop, such as the expansion and innovation of the train network, the use of freezing and the modification of fishing techniques. Importantly, in 1941 “lamparo’s”, i.e. fishing vessels that use light to attract pelagic species, were introduced (Doumenge 1952). However, they were banned quickly in some areas and were only legalised in 1960-1961 (Bailly & Le Grel 1996). Almost simultaneously, the Algerian independence (1962) led to the repatriation of several fishing units. In addition, ultrasound sonars were implemented concurrently, larger nets were employed, fishing power increased significantly and gas was replaced by butane or propane for lamparo lamps. All of this coincided with a sudden increase in landings (Maurin 1965; Bailly & Le Grel 1996). Modern trawls were only employed from around 1975 onwards, as a reaction to a foregoing decrease in pelagic landings. Successively, trawling methods diversified and the number of lamparo’s diminished. However, in 1977 regulations were already set to limit their numbers, fishing zone and timing (Pichot & Dremière 1978). Anchovy landings increased after 1986 when Spain became a member of the European Union, causing an upsurge in the demand. Around 2007, the biomass of sardine and anchovy dropped, leading to a current low level of exploitation (GFCM 2014; Van Beveren et al. 2014). However, sardine landings already showed a decrease from 1980 onwards (Farrugio & Marin 1999).

Although such basic prior knowledge is available, neither all the causes for the fluctuations of landings are known, nor is their extent. Specifically, these potential sources of variations are mostly
qualitative and reported landings are punctual or of very limited extent. Therefore, a baseline scenario to which the current situation could be compared is unavailable and the ecosystem conditions cannot be reproduced. Here, we compiled the longest possible landings series from the French Mediterranean fisheries for three species (sardine, anchovy and mackerel). They were first characterised in terms of patterns, variability, cyclicity and breakpoints. Then, we tested the relation between landings and SST (Sea Surface Temperature), river runoff (Rhône) and climate indices such as the NAO (North Atlantic Oscillation), WeMO (Western Mediterranean Oscillation) and AMO (Atlantic Multidecadal Oscillation), as these parameters had previously been shown to have an influence on small pelagic biomasses and/or landings (Grbec, Dulcic & Morovic 2002; Lloret et al. 2004; Martin et al. 2008, 2012; Checkley et al. 2009; Alheit et al. 2014). Therefore, we compared the environmental patterns, cycles and breakpoints with the landing ones and assessed potential relationships using Generalised Additive Models (GAMs). Although the use of landings instead of abundance or biomass can be misleading (Pauly, Hilborn & Branch 2013), it is the only long-term information available and we can interpret results with care, given for example the available qualitative knowledge on effort. To conclude, we discussed the results in view of the current pelagic ecosystem situation.

Material and methods

Data

Landings

For sardine, anchovy and mackerel, annual landings from the French Mediterranean fisheries in terms of total weight and market value (if available) were obtained from three principal sources: 1. the « Statistique des pêches maritimes » (SPM, http://archimer.ifremer.fr/statistique-peches-maritimes.htm), 2. statam (Le Corre 1971) and 3. France Agrimer (www.franceagrimer.fr). Although some records were also available for sprat and horse mackerel, these species were not included in this study as they were generally not targeted by fishermen, potentially totally disconnecting landings from population fluctuations. Data were aggregated into different areas (which will be referred to as maritime quarters) in correspondence with current administrative units (such as Port-Vendres, Sète and Marseille) or according to historical grouping of several administrative units (such as Martigues, Nice and Toulon that were pooled together, see Fig. 1). Landing series from the different chief data sources were verified against each other (as there were periods of overlap) and against literature and other data sources, such as Pêche sardinière en Méditerranée (Marine marchande 1964), La pêcherie des petits pelagiquestes (Bailly & Le Grel 1996), Monographie des pêches maritimes (Gouvernement français 1975), Statistique des régions de pêches (l’Institut Scientifique et Technique des Pêches Maritimes 1924), Système d’Informations Halieutiques (SIH, http://sih.ifremer.fr) and IFREMER files. For the overlapping periods, we selected only the most consistent data (showing maximal correlation with other information sources). Therefore, the final landing series were composed out of data from different origins: 1865-1970 (SPM), 1971-1993 (statam) and 1994-2013 (France Agrimer). Over the recent period (1950 until recent), the sum of the landings of all quarters is consistent with FAO data (Fig. S1).

From these series, small pelagic fish that were caught outside the Gulf of Lions were excluded. Also, we did not include catches taken inside the Gulf but landed by foreign vessels (Spanish or Italian) because of a lack of data. Given the local scale of this fisheries and the prevailing restrictions (both
practical and lawful), this biomass is however limited (e.g. less than 5% for sardine during recent years, STECF 2013).

![Fig. 1 France’s Southern coast, subdivided into the maritime quarters applied in this study, named after their chief port. Borders are indicated by pale lines.](image_url)

Together with these landings, we tried to build time series of fishing effort. However, data on total capacity and boat numbers was only available for the whole quarters. That is, these variables included numerous but unknown numbers of vessels directed towards benthic and cultured species (mostly oysters and mussels). Because the landings of these other species were only incompletely present (gaps, grouped data, unconvertible units, etc.) and the relative effort directed to each of them is unknown and changes over time, it was impossible to assess the capacity of vessels targeting the small pelagics. Therefore, the following analyses were computed on catch time series and not catch-per-unit-effort series, which has been done in many past studies (see e.g. Ravier & Fromentin 2001, 2004; Grbec, Dulcic & Morovic 2002; Alheit et al. 2014), but implies careful interpretation.

**Environment**

Environmental time series were collected from online databases (Sea Surface Temperature; SST, North Atlantic Oscillation; NAO, Western Mediterranean Oscillation; WeMO, Atlantic Multidecadal Oscillation; AMO) or communicated by specialised companies (Rhône river flow). They all spanned the period of the landings (1865-2013), except for the Rhône river flow that only started in 1920. We used three global indices (NAO, WeMO and AMO) and only two local climate variables (river discharge and SST), as on such a long-term basis, local variables were only sporadically available. Also, these holistic indices might be more strongly related to biological effects than any single variable and can provide at least an initial robust and integrated idea of the ecological effect of climate variability (Stenseth et al. 2003). The description of the environmental series can be found in Appendix S1.

**Statistical analyses**

**Landings**

As some selected statistical analyses require contiguity and our series were plagued by some missing values, these were estimated using additional information present for those years or time-series modelling. Sardine landings between 1874 and 1890 were recorded in numbers, which were converted in biomass with the help of the earliest data available; the mean size of sardine caught in
Marseille, Port-Vendres and Sète during 1972-1977 and the weight-length relationship calculated from Lee (1961). Since landings and total market value were always highly correlated for all three species between 1874-1890 and 1894-1914 (p<0.01 and R² between 0.92-0.97), we estimated missing values for the periods 1865-1873 and 1891-1893 from market values using a linear regression. Only data up to 1914 was used for this, because afterwards the linear relation changes because of a war associated price increase. Also, data was lost for 1894 and incomplete between 1994 and 1996 (and 1997 to a lesser extent) because of a change in the administrative data system. These years were filled per species and per maritime quarter with an ARIMA (autoregressive integrated moving average) model based on the preceding series, i.e. respectively 1865-1893 and 1970-1993 (so the 1960s increase was excluded). Furthermore, no data was available during the Second World War (WWII). This five year gap was deleted or filled up depending on the analysis (see further). When filled, this was done by taking the mean of the two adjacent values. Also, from 1994 onwards no data was available for Marseille. Because this gap was fairly large and significant changes in exploitation took place between 1994 and 2013, we considered two types of total landing time series for the following analyses: 1. the sum of the landings of all the quarters from 1865 to 1993 and 2. the sum of the landings from 1865 to 2013 of the quarters without Marseille.

The population variability (PV, Heath 2006) of all 12 time series (3 species x 4 quarters) was calculated to examine the difference between species and quarters in terms of temporal variations. PV is a more recent metric than the more commonly used coefficient of variation (CV) and is less seriously influenced by rare events and zeros. Also, PV measures variability on a proportional scale, and should therefore be especially appropriate to compare populations experiencing different dynamics. Namely, it quantifies the average percentage of the absolute differences between all combinations of the time series:

\[
P_{(z)} = \frac{\sum_{x=1}^{C} D_{(z)}}{C} = \frac{\sum_{x=1}^{C} D_{(z)}}{C}
\]

Where C is the number of all possible combinations of landing values at two given time steps (z₁ and z₂) of the time series of length n. PV fluctuates between 0 and 1, with 0 being complete stability.

**Patterns, periodicity and breakpoints**

The environmental and landings series were analysed together so that the main characteristics of the time series could be identified, as well as compared. Correspondence in terms of patterns, periodicity or breakpoints could indicate if the environment could influence small pelagic landings. Excluding potential resonant effects for small pelagics (see Bjørnstad, Nisbet & Fromentin 2004), the forcing and the response variable might be quasi-linearly related, in which case the patterns of both tracks might be similar. However, a small time-lag and/or a strongly non-linear relationship might conceal such an interaction, but not the patterns of cyclicity that should remain analogous in such case (on the condition that exploitation does not change the cyclic dynamics over time). Also, a discontinuity in the landings might be caused by an abrupt change (regime shift) in the environment and/or fishing effort. Hence, verifying the occurrence of such discontinuities is of interest and was done through a breakpoint analysis (see below). For all analyses (except the link with the environment and the breakpoint analysis), annual landings (without Marseille) were log-transformed (natural logarithm) to stabilize the variance (Sen & Srivastava 1990), whereby 1 was added due to the occurrence of zeros.
To estimate the general trend of each time series, data were analysed with Eigen Vector Filtering (EVF, Colebrook 1978), as this technique has the advantage that the importance of the calculated trend is quantified (%) and the smoothed series is not shortened. For each time-series, an autocovariance matrix is constructed by shifting the series between one and 5 years (this lag allows for retention only of medium- to long-term fluctuations, i.e. >15-20 years, Ravier & Fromentin 2001). The series’ trend is then given by the first axe of a PCA (Principal Component Analysis) performed on this matrix. Because the percentage of variance explained can be calculated, this enables us to quantify the importance of the main trend (Ravier & Fromentin 2001). EVF was done for all environmental series and the overall landings per species (without Marseille) and with the WWII period filled.

Given that non-stationary was most often the rule in our series (e.g. because of the known drop in landings during the last years) and that the removal of the main pattern would discard part of the information, we used wavelet (Daubechies 1992) rather than Fourier analyses to inspect the periodicity of the landings (without Marseille) and environmental series. This methodology has the intrinsic property to not only decompose the variance of a time series over frequencies, but also over time domains (hence tolerating non-stationary data). The wavelet transform (W) is done by decomposing a signal over functions called ‘mother wavelets’ $\Psi(t)$, which can be dilated (related to the frequency, $a$) and translated (related to the time position, $\tau$):

$$W_x(a, \tau) = \frac{1}{\sqrt{a}} \int_{-\infty}^{\infty} x(t) \Psi^* \left( \frac{t - \tau}{a} \right) dt$$

where the asterisk indicates the complex conjugate form and $x(t)$ the signal. In this study, we selected the Morlet mother wavelet, a continuous and complex wavelet with a simple link to frequencies and adapted to wave-like signals (Mallat, Papanicolaou & Zhang 1998). Also, we used beta-surrogates to test for significance, as they take both low and high frequencies into account and proved to be well-suited for ecological time-series (Rouyer et al. 2008; Cazelles, Cazelles & Chavez 2014). Beta was calculated as the slope of the spectrum in log-coordinates. The final wavelet power spectrum is presented as a time/frequency plot, with the intensity of the match between the time series and the wavelet represented on a colour scale range (blue=low variance and grey=high variance). Further details on the methodology can be found in Rouyer et al. (2008). When considering periodicity, continuous time series need to be used, so we filled the gap of the Second World War for this analysis.

For the environmental and all 12 landing series, a breakpoint analysis (R package strucchange, (Zeileis et al. 2013) was performed to compare the periods of major changes between time series. This method performs an ordinary least squares (OLS) for every segment of the time series, and puts the resulting residual sum of squares (RSS) in a matrix, with rows being the starting point of the OLS and columns being the end points. Then, the optimal combination of segments is found by minimizing the residual RSS. This method has the advantage that the number of breakpoints is automatically determined and a confidence interval can be given. The period of the WWII was deleted for this analysis.

**Relationship with the environment**

We modelled the effect of multiple environmental factors (SST, NAO, WeMO, AMO and river outflow) on the landings of each species separately, using GAMs (Generalized Additive Models). This
technique extends the linear models by handling multiple error types (i.e. not only Gaussian) and by allowing the effect of the predictor(s) to be non-linear, as it can be estimated as a smooth function (Hastie & Tibshirani 1990). Here, a smoother (cubic spline) was only applied on the year effect (except for mackerel) to capture the nonlinear trend in landings that is likely mostly due to changes in fishing effort (see below). As this approach did not remove all autocorrelation, landings at t-1 were also added as explanatory variable (note that different intervals were tried, but a one year delay proved to be optimal). We repeated each model for two types of time series, i.e. including (1865-1993) or excluding (1865-2013) Marseille. Similarly, data for the Rhône was only available from 1920 onwards. Hence, the models were run first including this factor, but for a shorter period. Only when river flow was shown insignificant, the models were run for the complete period. The WWII period was deleted from all the time series. The correlation between all environmental variables (Table S1) was, although sometimes significant (p<0.05), never strong (r<0.45). For most variables, this linear relationship has already been discussed, albeit for a shorter time series (Martín et al. 2012). The mgcv R package (Wood 2014) was used, and a gamma distribution with log link was selected, as the estimates of this model performed best.

Results

Landings description

The three most important small pelagic species in terms of landings were, by decreasing order, sardine, anchovy and mackerel (Fig. 2). Maximal reported landings in the total region were 22090t for sardine (1970), 9593t for anchovy (1988) and 1693t for mackerel (2007). Over the studied period (1865-2013), sardine was the most landed species in every maritime quarter. Anchovy was especially more important than mackerel during the last two decades, whereas before their relative importance depended on the quarter.

Generally, sardine and anchovy landings increased sharply in the early 1960s, but strongly declined during the most recent years, eventually reaching a level similar as 60 years earlier. This pattern however differed for the grouped quarters (Nice, Toulon and Martigues, NI/TL/MT), for which a sharp rise only took place around 1986, succeeding a more gradual intensification. Also, the timing of the last main decrease in landings was irregular as this already occurred sooner for eastern quarters (Marseille and NI/TL/MT). For anchovy, the 1960s increase in landings was not as abrupt as for sardine. The most prominent rise in the anchovy time series actually took place around 1987. Furthermore, when compared to the earliest years (1865-1914), total anchovy landings were relatively low between the First World War and the 1960s rise.

We also noticed that anchovy landings fluctuated on average more heavily than sardine and mackerel landings (PVanchovy between 0.67-0.75, PVsardine between 0.52-0.68 and PVmackerel between 0.51-0.64 depending on the quarters). Species landings in NI/TL/MT were usually the most stable (except for anchovy, PVNI/TL/MT for sardine, anchovy and mackerel respectively 0.52, 0.67 and 0.51), followed by the quarter of Marseille (also except anchovy, PVMarseille respectively 0.55, 0.74 and 0.54) and then by Port-Vendres and Sète (PVPort-Vendres respectively 0.60, 0.75 and 0.65; PVsète respectively 0.69, 0.72 and 0.61). For these 2 last quarters, landings in Port-Vendres were always fluctuating most, except for sardine, for which landings were more variable in Sète.
Fig. 2 Landings of anchovy, mackerel and sardine per quarter. No data was available for the Second World War (1939-1944) and from 1994 onwards for Marseille. The total series (sum of the other four series) thus underestimates landings slightly during this period (see text). The upper facet indicates several events that impact fisheries effort.

Patterns, periodicity and breakpoints

Environmental factors and landings fluctuated differently in terms of pattern and periodicity (Fig.3). Log transformed total landings (without Marseille) showed a clear long-term pattern. Sardine was characterised by the 1960s increase and smaller heights around the beginning of the time series and between the two World Wars. This trend explained 90% of the variance of the series. Anchovy landings were intermediate before 1914, low between the wars and elevated after them (explained variance by the trend: 87%, Fig. 3). Mackerel showed an uneven gradual increase, but this trend is not as important as for sardine and anchovy (explained variance: 61%). The landings also showed a generally red-shifted spectrum (i.e. dominated by periods > 10 yr). Periodicities were however still moderately different for the three species. Sardine only had low frequency oscillations (around 35 years) during the whole period, whereas mackerel had beside those also intermediate periodicities (around 16 years) before 1910. Anchovy had significant patterns around 11 years (during the 1920s)
and 30 years (±1945-2000). This corresponds with the PV values per species, as one could expect a higher PV when high frequencies are relatively more important.

SST and AMO showed a clear pseudo-cyclic long-term trend together with year-to-year fluctuations (Fig. 3). SST displayed three periods of higher values (around 1860s, 1950s and 2000s) and two periods of lower values (around the 1910-1920s and the 1970s). The AMO had maximal values around 1884, 1948 and 2008 and minimal ones around 1915 and 1980 (i.e. quite similar to those of the SST). Both series had significant low-frequency patterns (period>40 years) and the trends explained 46% and 68% of the variance of the SST and AMO time series, respectively. Additionally, SST had also had some high power values at higher frequencies (Fig.3). Consequently, no common pattern emerged with the landing time series.

The Rhône debit and the NAO and WeMO indices mostly displayed year-to-year fluctuations without any clear trend, although the WeMO index decreased slightly during the most recent years (Fig. 3). Therefore, the percentage of variance explained by the EVF-trend was rather low for each of these three time series (respectively 24%, 21% and 28%). All three series were characterised by mainly high to intermediate frequencies (periods up to 10 years for NAO and up to about 20 for the Rhône debit). Only the WeMO had also high power values for low frequencies during certain periods, which mainly fell out of the cone marking the influence of the edge effect. A 40 years oscillation pattern around 1910 and 1980 was also observed in sardine, but despite this small similarity, these three series also differ from the landings’ ones in both the frequency (wavelet) and the time (EVF) domain (Fig. 3).

For each of the 12 landings series, the breakpoint analyses detected several discontinuities (Fig. 4, top). A breakpoint was identified for most of the series (8 out of 12) around 1962 because of the steep increase in the landings (except for all species in the quarter of NI/TL/MT and in Marseille for mackerel). Two periods around which breakpoints were also common (although to a lesser extent) were near the beginning of the First World War (5/12) and 1985-1992 (5/12), caused by upsurges in Sète and NI/TL/MT. Also, breakpoints appeared to be more similar between quarters than between species. Breakpoints were not always detected for each environmental time series (Fig. 4, bottom). The NAO index and the Rhône debit did not display any discontinuity, while the WeMO index showed only one breakpoint (1988). Although the AMO index and SST displayed several breakpoints, it is interesting to note that most breakpoints from environmental series had a large uncertainty and did not clearly co-occur with most breakpoints of landings series. In general, the breakpoint analysis was quite consistent with the EVF: time series displaying significant long-term fluctuations also displayed several breakpoints, while time series without long-term fluctuations had no or little breakpoints.

Relationship with the environment

As EVF and wavelet analyses showed that long-term trends as well as periodicity were different between landings and environmental series, we included a smoother on the year effect in the GAM models (except for mackerel) to account for the long-term trend that should be related to another external factor (probably to fishing effort, as indicated by the co-occurrence of the breakpoints in the early 1960s in the landings series and expert knowledge, see also the Discussion). Adding the landings at t-1 in the explanatory variables (with a linear effect) allowed us to successfully remove any autocorrelation in the residuals of each model.
Fig. 3 Wavelet and EVF analyses for each of the normalised landings and environmental time-series. The main panels are the wavelet power spectrum. Power values range from blue (low) to grey (high). The black striped line forming a cone delimits the region not influenced by edge effects. Continuous black lines show 5% significant areas. The top panel represents the standardised data time series (in red) as well as the EVF analysis of this series (in black). The right panel is the global spectrum. The percentage on the top right represents the percentage of deviance explained by the EVF. All series begin in 1865, except the Rhône (1920).
Environmental explanatory variables were included as linear effects. The outputs of the GAM analyses with (1865-1993) or without (1865-2013) Marseille were always highly similar and led to the same conclusion (Table 1). Finally, the Rhône river runoff (1920-2013) was never significant, so the model could be run on the complete datasets. Residuals were always normally distributed and no outliers were present when plotting the predicted versus the fitted values. The deviance explained (respectively for models with and without Marseille) was highest for sardine (93.3% and 88.8%), followed by anchovy (79.6% and 79.0%) and mackerel (43.1% and 46.2%). This was mainly due to the high deviance explained by the smoothed predictor (year), which was, in general, very similar as the trends extracted by the EVF analyses (Fig. S2). Therefore, the actual environmental factors (i.e. leaving out this year effect and the landings at t-1)

![Graph showing landings series and environmental factors](image)

**Fig. 4** Breakpoint analyses of the 12 landings series (per quarter and per species, top) and the 5 environmental factors (bottom). Horizontal lines indicate the confidence interval around the detected breakpoint.

explained respectively only 5.80 and 1.60% of the deviance for sardine, and 12.2% and 2.4% for anchovy. For sardine, the AMO was the only significant (positively related) environmental variable (p<0.05). Anchovy landings were significantly and positively influenced by the WeMO index and the
AMO was exerting a negative effect. Mackerel on the other hand did not show any significant relationship with an environmental factor.

Table 1 Results of the GAM models, per species and for two series (with and without Marseille). For every retained linear term, the estimate (mean) is given with its standard error (s.e.) and the corresponding t- and p-value. For the smoothed (s) year effect, the effective degrees of freedom (edf), the estimated smoothing parameter (λ), the F-statistic and the p-value are shown. P-values were categorised into high (p<0.001,***) intermediate (0.01<p<0.001,**) or low significance (0.05<p<0.01,*).

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<th>Species</th>
<th>With Marseille</th>
<th>Without Marseille</th>
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Discussion

In this study we investigated the characteristics and causes of fluctuations in the landings of sardine, anchovy and mackerel from the French part of the Mediterranean Sea. Therefore, we compiled exceptionally long time-series. Such series are hard to obtain, as long-term data are often inexistent or (partially) lost, fragmented, hardly accessible, geographically scattered, not digitized, etc. Here, we managed to obtain 12 sound extended time series, allowing us to not only consider a multispecies fishery, but also to account in part for its geographical aspect. Such data is extremely rare for most species in the Mediterranean (except for bluefin tuna, Ravier & Fromentin 2001), and especially pelagics, as for example a single long-term series for sardine was only known from the Adriatic (Grbec, Dulcic & Morovic 2002). Even globally, long-term small pelagic landings series are uncommon, the longest being from Japan, California and the Canary Current, starting between around 1890 and 1915 (Lluch-Belda et al. 1989; Schwartzlose et al. 1999).

In this study, the two most striking events were the rapid and considerable (i.e. at least five-fold) increase in the landings of sardine and anchovy around 1962 and their recently observed decrease. Sardine is now landed even less than before 1960, as landings were never as low as during 2010-2013. Even during the 1800s, at least twice as much sardine was fished. This stresses the exceptionality of the current situation. Present anchovy landings still remain at rather high levels, but
landings were extremely low before the 1960s, in contrast to sardine. Mackerel landings did not show as prominent fluctuations as sardine and anchovy (beside a relatively small increase around the 1960s). This might be because mackerel is less targeted.

Landings of sardine and anchovy elsewhere in the Mediterranean fluctuate since 1950 mostly different (Fig. 5). However, in most locations landings of small pelagics generally increase in the 1960s or 1970s, probably related to technological developments. For example, in the Eastern Adriatic landings started rising around 1960 too, also claimed to be caused by the installation of echo-sounders (Grbec, Dulcic & Morovic 2002). However, these increases are usually more gradual. Particularly the concurrent addition of multiple Algerian vessels triggered by the Algerian independence is likely to have caused a steeper increase in the French landings. But not all major variations in landings could be explained by changes in effort or market demand (Grbec, Dulcic & Morovic 2002). Hence, these fluctuations might be related to a changed availability of sardine (resulting from a higher biomass or capturability caused by e.g. more near-shore located or denser schools). Furthermore, changes in fishing effort do not always result in a visible change in catch. This was the case for e.g. the adoption of more developed Italian fishing techniques, motorization and freezing, that did not translate in higher landings even some years after they were implemented. In the present study, the smoothed year effect of the GAM analyses roughly matches the trend in total vessel capacity (tonnage) for all species (incl. benthic ones, etc.) and follows the general qualitatively known trends in effort in the area (see upper panel Fig. 2 and introduction). Therefore, it is very likely that the major changes in those landings time series (which translate mostly into long-term trends) were due to major shifts in fishing effort.

However, variations in landings are not only driven by changes in the fisheries and market demand, but can also be environmentally-driven (Cushing 1995). From all the environmental factors considered, the AMO appeared to be the most important, for both anchovy and sardine (but with opposite effects). In some cases, its positive phase is known to be associated with a population increase (reviewed by Nye et al. 2014), through intensified recruitment and growth resulting from an increased temperature. This hypothesis would fit the positive effect of the AMO on sardine landings that we found in this study. However, other mechanisms might be important for anchovy landings in the NW Mediterranean, that are negatively related to the AMO (as was already noted by Alheit et al. (2014) and by Friedland et al. (2014) for other species elsewhere). For our study, one possible explanation could be based on different trophic niches. Anchovy generally feed on larger zooplankton than do sardine. The AMO, having the capacity to indirectly affect plankton communities (Edwards et al. 2013; Harris, Edwards & Olhede 2014) can thereby alternatively favour sardine or anchovy. A positive AMO phase can have a negative effect on large copepods (Harris, Edwards & Olhede 2014), resulting in an equally negative effect on anchovy. Also, anchovy was positively related to the WeMO index, which supports Martin (2012) who postulated that the regional WeMO index can provide a more accurate representation of the environmental conditions affecting anchovy biomass in the NW Mediterranean than the NAO.

Additionally, the effects of river discharge, the NAO and SST on sardine and anchovy landings might have been too small to be detected or work at different time scales. For example, a relation between small pelagic population size (LPUE or CPUE) and the Rhône outflow was already established twice for the NW Mediterranean (Lloret et al. 2001; Martín et al. 2008). However, these studies used relatively shorter time series and more importantly, monthly data. When for example both landings
and an environmental factor have a strong seasonal cycle, a relationship between them could be unambiguous, but might be undetectable on a yearly basis. Furthermore, the functional response of the populations to the environment might change over time (Schmidt et al. 2014), so that looking at small and long time-series might produce different results.

Fig. 5 Mediterranean landings of European sardine, European anchovy and Atlantic mackerel by country (only the 9 most important were considered, that had the highest landings and a complete time series). Data are from the FAO (FAO-FIGIS, 2015), even for France. Black dots indicate FAO-estimated values. Former Yugoslavia is the sum of the landings from Croatia, Slovenia, Montenegro, Serbia and Montenegro (1992-2013) and Yugoslavia SFR (1950-1991).

Overfishing was so far not considered to be the chief origin of the recent changes (GFCM 2014). This idea was mainly based on the magnitude and timing of maximal exploitation levels, as well as the nature of the observed changes (Van Beveren et al. 2014). However, these two components were only considered for the last two decades. Our analyses clearly show that the bulk of the variance in landings time series is due to long-term trends that are very likely related to abrupt changes in fishing effort in the early 1960s. Therefore, fishing-induced mortality on small pelagic fish in the Gulf of Lions had to increase greatly since the 1960s, its effect perhaps echoing in what we observe today. But although the presence of it is undeniable, the resulting effect should be put into perspective. Specifically, the biomass of sardine and anchovy in the ecosystem during the most recent years (1993-2015) attained levels ten times higher than the earlier historical peak of landings. This shows that both populations can still attain relatively important biomasses in regard to the preceding fishing pressure. Therefore, this study supports the previously stated idea that overfishing alone is an improbable cause of the recent changes (GFCM 2014; Van Beveren et al. 2014).
To conclude, the compilation and investigation of historical landings of sardine, anchovy and mackerel in the French part of the Mediterranean Sea 1) shed light on environmental population drivers, although not being conclusive about the causes of the recent changes and 2) also put into perspective the history of the fisheries. This could both benefit to the understanding of the pelagic ecosystem and the management of the stocks.

Acknowledgments

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Supplementary material

Appendix S1 Description of the environmental time series.

The time series of the winter (December-March) North Atlantic Oscillation (NAO) index was downloaded from the NCAR (climatedataguide.ucar.edu). This annual station-based index is based on the difference of normalized sea level pressure between Lisbon (Portugal) and Reykjavík (Iceland), whereby the positive phase corresponds to a wetter and milder weather over Western Europe. The NAO in winter controls the Northern Hemisphere climate stronger and exhibits a more intense interdecadal variability than in summer. The more regional Western Mediterranean Oscillation (WeMO) was obtained from the Group of Climatology from the University of Barcelona (www.ub.edu/gc/English/wemo.htm). This index is defined as the standardized sea level pressure difference between the North of Italy and the Southwest of Spain (Martin-Vide & Lopez-Bustins 2006). When negative, humid easterly winds cause heavy rainfall on the eastern coast of the Iberian Peninsula. When positive, dry winds are blowing from the West. Monthly values were averaged only for the winter months (December to March to match with the NAO index) to obtain the winter WeMO index, which should for example reflect more pronouncedly the Mediterranean rainfall than the annual index. The WeMO could also reflect local conditions in the NW Mediterranean (SST, salinity, etc.) better than the NAO index (Martin-Vide & Lopez-Bustins 2006; Martín et al. 2012).

A third index is the AMO (Atlantic Multidecadal Oscillation), which is the detrended weighted average of the SST over the North Atlantic (0-70°N). It exhibits positive (warm) and negative (cool) phases, with a difference around 0.5°C (Alexander et al., 2014). We extracted the data from the Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/data/timeseries/AMO/). For SST, multiple long-term datasets are available, that are based on the ICOADS (International Comprehensive Ocean-Atmosphere Data Set) v2.5 data set (HADISST, HADSST3 and ERSST.v3b). We selected ERSST.v3b, as complete data was present for the region from 1865 onwards on a 2°x2° grid. The Northwest Mediterranean (40-44°N, 1-7°W) was selected rather than the Gulf of Lions, to avoid errors due to the statistical interpolation of the temperature data. The series showed good correspondence with satellite data for the Gulf of Lions available during the last years (R²=0.72, p<0.01). Monthly data was downloaded from NOAA (http://www1.ncdc.noaa.gov/pub/data/cmb/ersst/v3b/netcdf/) and averaged per year. Although multiple rivers discharge into the Gulf of Lions, the Rhône is by far the most important one, as its flow is more than 10 times higher than the one of the other foremost rivers together (Aude, Hérault, Orb). Its yearly flow rate was received from the CNR (Compagnie Nationale du Rhône, www.en.cnr.tm.fr). Measurements are from Beaucaire, a station close to the river mouth.


Gouvernement français. (1975) *Monographie des pêches maritimes*.


l’Institut Scientifique et Technique des Pêches Maritimes. (1924) Statistique des régions de pêches.


Marine marchande. (1964) *La pêche sardinière en Méditerranée.*


Fig. S1 Per species comparison of the landings data from FAO and this study (summing all quarters and putting zero for Marseille after 1993). The striped line indicates 1993, after which the data from this study was expected to be slightly underestimated. The Pearson correlation coefficient for the whole series is indicated.
**Figure S2**

*Fig. S2* Effect of year on sardine and anchovy landings, with or without Marseille in a GAM model. The cubic smoother (solid line) is given with its 95% CI (shaded area).
### Table S1

**Table S1** Linear correlation between annual environmental values (1865-2013).

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</table>

*Significant at p < 0.05; **significant at p < 0.01
Chapter 4: Prey predator interactions in the face of effective management strategies: changes in Mediterranean small pelagics are not due to increased tuna predation

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Abstract

1. In recent years, the biomass and size of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) has decreased in the Gulf of Lions (NW Mediterranean), causing an important fishery crisis. Concurrently, the abundance of juvenile Atlantic bluefin tuna (*Thunnus thynnus*), a predator of these species tripled in this area following effective management measures implemented in 2007. Investigating whether the predation of bluefin tuna could have driven the recent decrease in small pelagic fish biomass is critical to determine if these prey and predator species should be managed simultaneously.

2. Combining the observed diet composition of bluefin tuna, their daily energy requirements obtained from a comprehensive bioenergetics model and their population size inferred from a local tuna population census, we estimated the amount of each prey species consumed each year by the bluefin tuna population. These values were then compared to the abundance of prey species in the area estimated from an acoustic scientific survey to examine the proportion of the prey populations that were consumed by bluefin tuna annually (2011-2013). To assess whether tuna could alter the size structure of the three small pelagic populations, the size distributions of the consumed prey species were compared to those of the wild populations. Such a state-of-the-art framework has not yet been used to estimate predation pressure in the marine environment.

3. Sardine and anchovy were consistently the main prey species of juvenile bluefin tuna over the sampled period and area. However, we found that annual consumption of small pelagic fish by bluefin tuna accounted for less than 2% of the abundance of these populations. Size selectivity patterns were not observed.

4. Synthesis and applications. We showed that tuna predation could not have led to the sharp decrease in small pelagic fish biomass or to the disappearance of large individuals, indicating that tuna and small pelagic fish stocks can be managed independently in this area. The novel analytical approach itself to estimate predation pressure could be applied to other predator-prey studies (in both terrestrial and marine ecosystems).

**Key words:** anchovy, Dynamic Energy Budget theory, ecosystem approach, Gulf of Lions, predation pressure, sardine, sprat, stomach contents
Introduction

Understanding predator-prey relationships is crucial for ecosystem-based management. One of the key aspects of these relationships concerns estimates of predation strength, which can be affected by conservation measures (Bailey et al. 2010). Assessing predation pressure is a data intensive issue (Essington, Kitchell & Walters 2001) and direct information at the population scale is difficult to obtain for marine systems due to the practical constraints of observing marine species. Estimates are generally based on the predator population abundance, energy requirements and prey composition, as well as the population abundance and energetic value of the prey. Estimates of food requirements are particularly problematic due to the limitations of the existing methods. We used an integrative and original approach to estimate the predation pressure of Atlantic bluefin tuna (ABFT, *Thunnus thynnus*) on the small pelagic fish populations by combining modern methods with extensive field surveys.

Since 2007, significant changes have been observed in the small pelagic populations of the Gulf of Lions in the north-west Mediterranean Sea. Biomass of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) has significantly decreased resulting in important economic losses for fisheries; while sprat (*Sprattus sprattus*), a species with no commercial value, has shown a remarkable upsurge (GFCM 2011). In addition, the populations of all three species have simultaneously shifted to smaller individuals of poorer body condition (Van Beveren et al. 2014; Brosset et al. 2015). Multiple hypotheses have been suggested as potential drivers for these changes, including predation, a planktonic change and an epizootic disease (e.g. Van Beveren et al. 2014; Brosset et al. 2015). These are not exclusive hypotheses, but potentially multiple factors acting in synergy (Planque et al. 2010). Here, we investigate the potential impacts of top-down control. As fishing is an unlikely driver due to low exploitation rates of this population (Van Beveren et al. 2014), we consider the possible effect of predation.

Atlantic bluefin tuna are a known predator of small pelagic fish (de la Serna et al. 2012). Juveniles of this species reside many months in the Gulf of Lions (Fromentin & Lopuszanski 2014) and represent a potentially important source of predation for sardine, anchovy and sprat in the area. Other predators are also present (e.g. dolphins), but they prey mostly on other species (e.g. David & Di-Méglio 2013) and their biomass is generally concentrated in deeper waters than those inhabited by sardine, anchovy and sprat (Praca & Gannier 2008). Juvenile ABFT abundance in the Gulf of Lions has been much higher in recent years (2009-2012; Bauer et al. 2015) because of a successful recovery plan implemented in 2007 which included fishing season restrictions, quotas and a minimum landing weight of 30 kg. These management measures have considerably decreased the fishing pressure on juvenile ABFT in the NW Mediterranean (Fromentin et al. 2014). The increase in juvenile ABFT abundance thus occurred concomitantly with the biomass and size decrease of sardine and anchovy. This leads to the question: could the increase in tuna abundance, and thus increased predation pressure, have caused the changes in the small pelagic fish populations? Currently, most management approaches focus on a single species, without considering subsequent impacts on other species in the ecosystem. However, if these management measures have repercussions on other species, management strategies should be adapted accordingly.

Thus, we aimed at investigating the predation pressure exerted by ABFT on sardine, anchovy and sprat from 2011 to 2013 in terms of abundance and size distribution. The annual proportion of each small pelagic population consumed by ABFT and its size selectivity was estimated using as key inputs
(a) tuna population abundance estimated from a tuna census, (b) a comprehensive bioenergetics model to estimate consumption rates of ABFT, (c) stomach content analyses to define the predator diet and (d) the population size of each small pelagic species estimated from a small pelagic fish census (Fig. 1). A relatively large predation-associated mortality could completely or partly explain the recently observed changes in the Gulf of Lions ecosystem.

**Fig. 1** Schematic representation of the data and the analyses.

### Material and methods

**Estimating predator abundance: ABFT census**

Annual tuna abundances (2011-2012) were obtained from aerial surveys (Bauer et al. 2015, see Appendix S1: tuna abundance). Tuna schools were counted along strip transects and densities were multiplied by the analysed surface. Annual abundances (mean±sd) of ABFT were found to be of 16242±4415 in 2011 and 12480±3836 in 2012. As variations in tuna abundance were low during the most recent years of the survey (Appendix S1), the missing value for 2013 was set equal to 2012.

The residence time of the tuna population in the area was estimated based on tag data (Fromentin & Lopuszanski 2014). We considered that juveniles reside in the Gulf of Lions a total of six months (consistent with previous assumptions, i.e., Bănaru et al. 2013), from approximately early-March to end-May and from end-July until end-October.

Finally, the mass distribution of tuna population was assessed combining mass values of tunas sampled for stomach contents together with additional measurements from other periods (sampling period: April-May and July-December of 2011-2014, N=310). A gamma distribution (shape=15.21 and rate =0.57) was fitted, which was also used to determine the ABFT weight range (3.8 kg – 85.9 kg).
A Dynamic Energy Budget (DEB) model describes an individual’s energy acquisition (food intake) and use (for e.g. maintenance, growth, reproduction) throughout its life cycle, taking into account external variables, such as temperature and food density (Nisbet et al. 2000; Kooijman 2010). DEB-based modelling is a general and formal approach built on the guiding principle that the mechanisms responsible for running a metabolism apply universally to organisms of all species (Sousa, Domingos & Kooijman 2008; Kooijman 2010; Sousa et al. 2010). We used a DEB model for ABFT by reparameterising a calibrated and validated model for Pacific Bluefin tuna (Jusup et al. 2011; Jusup, Klanjšček & Matsuda 2014) using the covariation method (Lika et al. 2011; Lika, Kearney & Kooijman 2011). For our study, the most important aspect of the model (see Appendix S2 for the basic equations, parameter values and age-length and -body mass curves) is to relate tuna body size to the ingestion rate function (Jusup, Klanjšček & Matsuda 2014):

\[
\text{Ingestion rate} = \frac{p_{Am} \cdot M_1 \cdot L^2}{\kappa_x} \quad f = 0.92 \text{ and } T = 21°C
\]

where \(p_{Am}\) is the maximum surface-area-specific assimilation rate, \(M_1\) is the shape correction function, \(L\) is the structural length, \(\kappa_x\) is the assimilation efficiency, \(f\) is the food availability and \(T\) is the average temperature. The body mass distribution of the juvenile tuna population was the most detailed population information available (age or size structure data are lacking or more limited); thus, we focus on the relationship between ingestion rate (expressed in kJ per unit of time) and body mass.

Individual ingestion rate values were scaled up to the population level. To do this, ingestion rates (kJ\(\cdot\)day\(^{-1}\)) were estimated from the DEB for the full body mass gamma distribution of sampled tuna. Total annual ingestion rates for each body mass class (around 1 g) were then multiplied by their relative frequency in the population (again based on the gamma distribution) and the annual tuna abundance. The sum of those values was multiplied by the residence time of the population.

**Tuna diet from stomach content analyses**

Stomach content analyses of tuna caught in the Gulf of Lions have been carried out annually since 2011. Tuna were captured between late-July and early-December of 2011 (n=42), 2012 (n=39) and 2013 (n=37) by small-scale fisheries using longlines or handlines. Individuals were measured (±1 cm, fork length) and weighed (±0.1 kg). Stomach contents were weighed and completely and partially intact prey identified to the lowest possible taxonomic level. Prey items were measured when possible (using total and/or standard length) and weighed to the nearest millimetre and gram. All otoliths (fish) and beaks (cephalopods) were collected to determine the total number of prey per species. For the three key prey species, otolith lengths were converted to prey item length using linear relationships based on independent readings (see Table S1). Body mass of five key species was obtained by converting indirectly from size (sardine, anchovy and sprat) or directly (mackerel, squid) from otolith length (using again independent readings, Table S1). Longline baits of undigested sardines of sizes >17.5 cm were removed.

The importance of each prey species in the tuna diet was expressed as the percentage of prey composition by number (%N), body mass (%M), and the frequency of occurrence of each item (%F). For some rare species (referred to as the diverse group), no body mass information was available so
they were excluded when calculating %M. All three indices can be combined, so that the index of relative importance (IRI; Pinkas, Oliphant & Iverson 1970) can be calculated to indicate the relative importance of each prey species relative to the others, whereby:

$$ IRI = \left( \%N + \%M \right) \times \%F, $$

which is reported as a percentage,

$$ \%IRI = \frac{100 \times IRI}{\sum_{i=1}^{n} IRI_i}, $$

where $n$ is the total number of prey species.

Feeding selectivity was calculated with Chesson’s index ($\alpha_i$; Chesson 1978):

$$ \alpha_i = \frac{r_i}{\sum_{j=1}^{k} r_j}, $$

where $r_i$ is the proportion of prey species $i$ (among $k$ total prey species) and $p_i$ is the proportion of this prey species in the environment. The index ranges between 0 and 1 (indicating complete avoidance and full selection, respectively), with $1/k$ indicating neutral selection (here: 0.25).

We tested whether prey length (anchovy, sardine and sprat) could be related to sampling date or tuna size, using Spearman’s rank correlation. We also tested whether the prey composition of the eight most frequently occurring species (expressed as %N) could be related to the sampling date or tuna size using a Mantel test to correlate the two dissimilarity matrices. The prey item matrix was created based on the Bray-Curtis method (as percentages are used, see Legendre & Legendre 1998) and Euclidean distances were used for the tuna size and sampling date matrix.

To estimate the energetic importance of sardine, anchovy and sprat in the diet of tuna, it is necessary to also consider other relevant prey species (i.e., squid and mackerel). For example, a tuna whose stomach contents are comprised of 50% fat sardine and 50% small squid will acquire more energy from sardine than from squid. Thus, we must know the energetic density (J/g), body mass distribution and %M of each major prey species consumed in order to estimate their energetic importance. Each body mass class (0.5 g) of a given prey species was multiplied by the energetic density of that species (see Appendix S1: Energetic density) and the relative frequency of that body mass class. These values were summed per species to obtain the energetic value (J) of a standard individual, with which the number of individuals per species consumed by all tuna was found.

**Estimating prey abundance: small pelagic fish census**

Annual standardised acoustic and pelagic trawl surveys (PELagiques MEDiterranée, PELMED) have been carried out continuously since 1993 to estimate biomass and abundance of several small pelagic fish and to collect basic biological parameters. Sampling is performed in July along nine equidistant parallel transects perpendicular to the coastline, ranging between depths of 20 m and 200 m. Here, we used resultant abundance estimates for sardine, anchovy, sprat and mackerel for 2011-2013 and biological data to calculate size distributions and morphometric relationships (e.g. a
length-weight key to obtain prey item body mass) for these species (see Table S1, Fig. S1 and Van Beveren et al. 2014; Saraux et al. 2014).

**Predation pressure on small pelagic fish**

To obtain a percentage of “population consumption” (i.e. the percentage of each prey population consumed by the tuna population), we divided the estimated total number of sardine, anchovy and sprat consumed by tuna by their population abundance in the ecosystem. A uniform distribution was assigned to the prey energetic densities (between minimal and maximal values, Table S1) and the annual tuna abundance (a confidence interval of ±95%) and values were bootstrapped (10000 iterations) in order to account for the uncertainty.

![Fig. 2 Annual results of the stomach analyses (2011-2013): the prey’s relative abundance (%N), mass (%M), importance (%IRI), occurrence (%F) and Chesson’s selectivity index, with the horizontal line indicating neutral selectivity (α = 0.25). The “diverse” class groups all species less abundant than 1%N. The relative mass of this group is unknown and thus not included when calculating %M and %IRI. Chesson’s index is given only for species whose proportion in the ecosystem is known (based on the prey population census) and the percentage of occurrence is given only for the most prevalent species (%F>10), i.e. sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*), sprat (*Sprattus sprattus*), pouting (*Trisopterus luscus*), goby (Family Gobiidae), hake (*Merluccius merluccius*), jack mackerel (*Trachurus spp.*), red bandfish (*Cepola macrophthalmia*), mackerel (*Scomber colias* and *S. scombrus*) and cephalopods (mostly *Illex* spp.).](http://example.com)

Tuna selectivity for certain prey sizes was also investigated by comparing the size distributions of sardine, anchovy and sprat in the tuna stomachs with the size distributions of those obtained from the pelagic survey. As the survey takes place in July and the tuna stomachs were collected from August to November, the theoretical sizes of anchovy and sardine ingested by tuna were back-calculated for comparative purposes, using age-length keys developed from PELMED otolith data (2008-2013, Fig. S1), and accounting for seasonal variability (Somers 1988; García-Berthou et al. 2012). This is important as small pelagic fish mainly grow in summer. For sprat, an annual linear model was used as only data for two age classes were available (Fig. S1). As growth for sprat is also stronger during summer, the back-calculated difference in length was multiplied by 1.5, a factor estimated from the anchovy data. Also, tuna consumed small-sized anchovy that could not be caught...
during the survey because of the limiting mesh size (only 0.5% of all-time survey captures of anchovy were smaller than 9 cm). Therefore, when comparing the diet and population census size classes, ingested individuals smaller than 9 cm were not considered (43%). As data were highly unbalanced, non-normally distributed and obtained from different sources, only the percentage of overlap of the two size distributions was calculated, as well as the differences between the frequencies of each size distributions (so positive values correspond to positive selection).

Results

Tuna diet and selectivity

Length and mass of the tuna analysed for their stomach content ranged between 89 cm and 158 cm and 12.5 kg and 51.2 kg, respectively. Of the 118 stomachs examined, only one was found empty (in 2011). No significant relationships were found between prey composition and the sampling date or tuna length (p>0.05, Mantel test), nor between the prey length and the sampling date or tuna length (p>0.05, Spearman’s correlation), so that interannual differences in prey length and composition could not be attributed to minor changes in these two factors.

Fig. 3 Size distributions per year and per species, i.e. sardine (Sardina pilchardus), anchovy (Engraulis encrasicolus) and sprat (Sprattus sprattus), found in the stomachs of Atlantic bluefin tuna (Thunnus thynnus) (red) and by the small pelagic survey (blue). The black line is the difference between the frequencies of each size class (positive values correspond to positive size selectivity by tuna). The numbers of individuals sampled is indicated (N), as well as the percentage of overlap of the two distributions.
In total, 5099 prey items belonging to 29 prey species or families were identified, resulting in a mean prey abundance of 44 individuals per stomach. Anchovy and sardine were always the most important species in terms of abundance, body mass and frequency of occurrence, although these indices varied considerably between years (Fig. 2). Together they consistently accounted for more than 80% of the juvenile ABFT diet (both in mass and number) and each was present in at least 79% of the stomachs. In contrast, sprat was little present in 2011 and 2012 (4%N), but became relatively more important in 2013 (14%N). Cephalopods and mackerel only constituted between 1% and 3% of the diet (for both mass and number). These results were also reflected in the %IRI (Fig. 2), as anchovy and sardine were always by far the most important prey, particularly anchovy in 2011. During the following two years, the dominance of anchovy declined and became similar to sardine.

According to the Chesson’s index, ABFT generally selected anchovy and mackerel, rather than sardine and sprat (Fig. 2). Tuna always positively selected for anchovy, although this selection almost doubled between years (i.e., 2011 and 2013). Mackerel were both positively and negatively selected, depending on the year. Sardine and sprat were negatively selected (although sardine was preferred to sprat). Anchovy was the only prey species for which the proportion in the stomach fluctuated in parallel with its proportion in the ecosystem found by the pelagic survey.

Larger sardines were found more frequently in the tuna diet than during the pelagic survey (although positive selectivity was also visible on small size classes in 2013, Fig. 3). No consistent or clear size selectivity was present for anchovy, as both the size distributions found had a high level of overlap (67-77%). For sprat, there was a consistent difference between the two distributions over the three years, with a much greater proportion of small individuals in the tuna diet.

**Predation pressure on small pelagics**

The body mass distribution of the juvenile tuna population had a median of 24.55 kg (Fig. 4a). At this median mass, individual tuna ingestion rates given by the DEB (Fig. 4b) were predicted to be between 1.2%-1.3% body mass*d⁻¹ (%Mᵇ, depending on the annual average energetic density of consumed prey), 2435 Kj*day⁻¹ or 99 Kj*kg⁻¹*day⁻¹. For tuna between 4 kg and 86 kg values were ranging between 0.8%Mᵇ and 2.4%Mᵇ, 726 Kj*day⁻¹ and 5617 Kj*day⁻¹ or 65 Kj*kg⁻¹*day⁻¹ and 181 Kj*kg⁻¹*day⁻¹. Thus, given tuna abundance and residence time in the study region, the local juvenile tuna population was estimated to require 6.30x10⁶±1.35x10⁶ MJ on average over all three years.

Anchovy and sardine were the most important species in terms of caloric importance, given their relatively high caloric density (Table S1) and %M (Fig. 2). The importance of sprat, mackerel and especially cephalopods was minor. The annual total abundance of sardine, anchovy and sprat consumed by tuna is given in Table 1. Given the abundance of those species in the area (Table 1, based on pelagic survey data), the consumption by tuna represents a maximum of 1.85%±0.53% of the anchovy, 0.57%±0.16% of the sardine and 0.07%±0.02% of the sprat populations (Table 1). Thus, the predation pressure of juvenile ABFT in the Gulf of Lions on their main prey species is extremely low (< 2% of the prey populations).
Table 1. The annual percentage of population consumption, ecosystem abundance and total number consumed by tuna (Thunnus thynnus) of anchovy (Engraulis encrasicolus), sardine (Sardina pilchardus) and sprat (Sprattus sprattus).

<table>
<thead>
<tr>
<th>Population consumption</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anchovy</td>
<td>1.85±0.53%</td>
<td>0.50±0.18%</td>
<td>0.81±0.29%</td>
</tr>
<tr>
<td>Sardine</td>
<td>0.57±0.16%</td>
<td>0.40±0.14%</td>
<td>0.53±0.19%</td>
</tr>
<tr>
<td>Sprat</td>
<td>0.07±0.02%</td>
<td>0.01±0.00%</td>
<td>0.05±0.02%</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Ecosystem abundance (millions)</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anchovy</td>
<td>3601.59</td>
<td>5142.30</td>
<td>2685.86</td>
</tr>
<tr>
<td>Sardine</td>
<td>5655.76</td>
<td>9370.83</td>
<td>7927.86</td>
</tr>
<tr>
<td>Sprat</td>
<td>5577.21</td>
<td>4649.02</td>
<td>9969.93</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Total abundance consumed by tuna (millions)</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sardine</td>
<td>32.37±9.32</td>
<td>37.84±13.38</td>
<td>42.12±14.95</td>
</tr>
<tr>
<td>Sprat</td>
<td>3.87±1.12</td>
<td>1.55±0.55</td>
<td>5.26±1.87</td>
</tr>
</tbody>
</table>
Discussion

We developed an original approach to assess predation pressure, which could be applied to many prey-predator studies. This should be especially useful for management, as repercussions of measures should ideally be evaluated so the need for ecosystem-based management can be assessed. We examined whether in the Gulf of Lions, the effective management of ABFT could have resulted in the biomass and size decrease of sardine and anchovy.

Effect on the abundance

Despite the fact that sardine and anchovy are the main prey of juvenile ABFT, the influence of their predation pressure on the abundance of these species is negligible (<2%). Moreover, these predation pressure estimates are based on calculations performed for the last three years (2011-2013), when tuna biomass was relatively high and sardine and anchovy biomass was already relatively low (Van Beveren et al. 2014; Bauer et al. 2015). Hence, in previous years, tuna predation was likely to have been even smaller. In addition, we used a cautionary approach that considered the high uncertainty around parameters, such as tuna abundances (i.e., using a confidence interval of ±95%) and energetic densities (i.e., using the range between minimal and maximal values). Although no such uncertainty was included for the abundance of prey species in the area, values are thought to be underestimated rather than overestimated (e.g., due to undetected biomass in unsampled nearshore areas, Brehmer et al. 2006), thereby overestimating predation pressure. However, even if an additive underestimation of predation resulted from the errors that were not included (e.g., on the residence time), predation ratios would still remain far too low to be considered as important. For example, this tuna top-down control of prey populations can be compared with the top-down effect exerted by fisheries. Between 1995 and 2013, on average, 13% of the anchovy and 9% of the sardine population abundance was fished annually, which is at least 6 times higher than the quantity consumed by tuna. Thus, despite errors due to reasonable uncertainty, our results clearly excluded predation pressure by juvenile ABFT as the main cause for the recent decline in sardine and anchovy biomass in the Gulf of Lions.

Effect on the size distribution

If tuna were to consume only the largest individuals, an effect on the size distribution of the prey species might have occurred. However, tuna appear to be opportunistic and have little prey size selectivity, as evidenced by a weak or inconsistent pattern of size selection between years and among species. Tuna preyed on all available size classes and had similar preference for smaller fish as for larger fish. However, the size distributions of the small pelagic fish found in the stomach contents and those caught in the survey are not exactly comparable due to temporal mismatch between the pelagic survey and when the tuna were caught, as well as the lower size limit on the small pelagic fishing gear (although both were corrected for). For example, anchovy spawns between May and June (in contrast to winter spawning sardine and sprat) and these young-of-the-year fish were too small to be captured by the size-restrictive mesh by the July survey. Tuna were generally captured later, when anchovy had already slightly grown. Also, small discrepancies in the size distributions might result from spatial heterogeneity in size of the small pelagic fish populations and the tuna hunting area (e.g., tuna might hunt in a zone where small pelagic fish are not averaged sized). Thus, we can conclude that observed differences between the two distributions are most likely caused by
factors other than a preferential consumption of certain size classes by tuna and that the size distributions of the small pelagic fish are not likely to have been affected by tuna predation.

**Tuna energy requirement**

Assessing predation pressure is particularly challenging for pelagic fish, as their abundance and the daily energy requirement of their predator are not easily estimated. Here, predation estimates were possible due to the availability of a calibrated model and a large amount of diverse multi-annual data sources, including stomach content samples of ABFT and extensive acoustic and aerial survey data.

The DEB model provided us with energy intake estimates that were otherwise unavailable, as only very few studies have shown the energetic requirements of tuna (e.g. Korsmeyer & Dewar 2001; Mourente & Tocher 2009). We found that tunas between 4 kg and 86 kg (i.e. between 1.5 and 9.2 years) consume about 0.8%M\textsubscript{b} to 2.4%M\textsubscript{b}, i.e. about 174 kcal to 1342 kcal (or 726 kJ to 5617 kJ) daily. The estimates of %M\textsubscript{b} are in the lower range of results from previous studies on other (commonly captive) tuna species (Glencross et al. 2002; Essington et al. 2002; Wexler et al. 2003; Takii et al. 2005; Fitzgibbon et al. 2007). For example, Essington et al. (2002) reported daily consumption rates of 3.5-6%M\textsubscript{b} for 0.5-6 year old yellowfin tuna (*Thunnus albacares*), while Wexler et al. (2003) described rates of 1-10%M\textsubscript{b} for yellowfin of 1-6 kg. For the more closely related southern bluefin tuna (*Thunnus maccocyii*), Fitzgibbon et al. (2007) estimated a daily consumption of 2-9%M\textsubscript{b} for fish of around 10 kg. ABFT individuals in this study were generally larger and were exposed to different ambient temperatures, two factors that greatly alter the energetic requirements of tuna. Smaller fish consume fewer calories but have a higher energetic need relative to their mass and the endothermic system of tuna includes a specific relationship between ambient temperature and metabolic rate (Blank et al. 2007). Additionally, %M\textsubscript{b} depends on the energetic density of the food ingested and captive individuals might have an increased metabolic rate because of stress. But even considering the maximum reported ingestion rate found in literature (0.43 MJ*kg\textsuperscript{-1}*day\textsuperscript{-1}, found for small yellowfin by Wexler et al. 2003; thus theoretically overestimating ingestion values for larger ABFT), the estimated predation pressure of ABFT on small pelagic fish was still relatively low (<10%).

**Atlantic bluefin tuna diet**

In contrast to studies on tuna energy requirements, studies on the diet composition of ABFT are ample (e.g., Karakulak, Salman & Oray 2009; Varela, Rodríguez-Marín & Medina 2013). As the diet of tuna varies significantly between years, seasons, regions and life stages, our results deviated from other studies. For example, other studies from the Mediterranean found more empty stomachs (e.g., migrating adult tuna from the Strait of Gibraltar; Varela, Rodríguez-Marín & Medina 2013) supporting the hypothesis that the Gulf of Lions act as an important feeding area for juvenile tuna (Druon et al. 2011; Fromentin & Lopuszanski 2014). Our results are consistent with other studies that found that ABFT prey composition is diverse but dominated by few species (Fromentin & Powers 2005). However, we found a predominance of sardine and anchovy in the diet (e.g., up to 76%N of anchovy), as opposed to more elevated abundances of cephalopods and/or crustaceans highlighted in other Mediterranean areas (e.g. Sinopoli et al. 2004; Sarà & Sarà 2007; Goñi et al. 2011; de la Serna et al. 2012). Cephalopods were of very limited importance (<4%N) and crustaceans were only rarely encountered (<1%N). This may be partly because tuna sampling for stomach analyses was limited to the nearshore zone around two neighbouring ports. However, ABFT are usually more numerous further offshore (Bauer et al. 2015), where e.g. cephalopods might be more abundant.
Although tuna are generally considered to be opportunistic predators (Crane 1936), the individuals in this study appeared to negatively select sardine and sprat and positively select anchovy (a similar finding was suggested for albacore, *Thunnus alalunga*, in the bay of Biscay; Goñi *et al.* 2011). This is surprising as sprat has a higher fat content than anchovy (Brosset *et al.* 2014). Therefore, this apparent selection may actually be due to a difference in the geographic distribution and/or behaviour of the prey species, or an error in the relative abundance estimates of the prey in the environment (see before) or the stomachs. For example, sardine and sprat in the Gulf of Lions are more coastal than anchovy and depths of 150 m to 200 m are unfavourable to them (Saraux *et al.* 2014). Thus, tuna may prefer deeper waters on the continental shelf, and as such, prey less on nearshore individuals. As tuna for stomach analyses were caught nearshore, an opposite bias may have been expected. Furthermore, sardine and anchovy might be different in terms of behaviour and movement, so that anchovy are when hunted more easily caught. For instance, diurnal differences in densities of both populations have been previously reported (Barange & Hampton 1997; Saraux *et al.* 2014), possibly resulting in a dissimilar predation risk. We also found that when the relative proportion of sardine in the ecosystem increases this does not relate to a concurrent increase in their relative consumption by tuna. This might be because sardine are coastal and when their relative proportion in the ecosystem is higher, they may increase school densities rather than expand their spatial distribution to areas were tuna hunts more intensely (Saraux *et al.* 2014).

In conclusion, we provided an integrative and novel framework for conducting predator-prey analyses. We showed that sardine, anchovy and sprat are important in the diet of tuna, although no sound evidence was found for clear selectivity of size classes. Additionally, tuna removed an extremely small proportion of small pelagic fish from the ecosystem and thus could not have caused the decline in their populations. Therefore, we conclude that the tuna and small pelagic fish stocks in this area could be managed independently.

**Acknowledgements**

We thank the captain and the crew of the RV “L’Europe” as well as all the scientists on board for their assistance during the PELMED surveys. PELMED surveys are cofinanced by Europe through the Data Collection Framework. The aerial surveys were funded by the convention Ifremer - Direction des Pêches Maritimes et de l’Aquaculture (French administration) from 2009 onwards. We are also grateful for the funding of the MERMEX project and France Filière Pêche (FFP) for the stomach analyses. This work is a part of the program Study of the Pelagic ecosystem in the Gulf of Lions (EcoPelGol), financed by France Filière Pêche. M.J. acknowledges support from Japan Society for the Promotion of Science (JSPS) Postdoctoral Fellowship Program for Foreign Researchers no. P13380 and an accompanying Grant-in-Aid for Scientific Research.

**References**


Chapter 4: Prey predator interactions in the face of effective management strategies: changes in Mediterranean small pelagics are not due to increased tuna predation | 128


Supplementary material

Appendix S1 Supplementary material and methods

Tuna abundance
Annual aerial surveys have been performed between June and October from 2000 to 2003 and from 2009 until present in the Gulf of Lions to construct a unique fishery-independent index of tuna density (Fromentin et al. 2003; Bonhommeau et al. 2010; Fromentin, Bonhommeau & Brisset 2013; Bauer et al. 2015). Using the annual estimates of bluefin tuna densities given by Bauer et al. (2015), we calculated the abundance of tuna in the studied area by simply multiplying those annual densities with the surface area of the aerial survey transects. We did not account for the differences in spatial coverage of the small pelagic fish surveys (<200 m) and the tuna surveys (including waters >200 m) as small pelagic fish are primarily concentrated over the continental shelf (Saraux et al. 2014), and an increased survey area would not significantly affect the estimates of abundance or biomass of these species.

Fig. A1 Annual abundance and standard deviation of Atlantic bluefin tuna (Thunnus thynnus) in the Gulf of Lions, estimated from aerial surveys.

Energetic density
To consider the energetic importance of the prey species of interest in the tuna diet, information on the energetic density and body mass distribution of the other main prey species needs to be known as well. Therefore, all prey species that constituted more than 1%N of the tuna diet over a three year period were also examined, accounting for 98.3%N of the prey consumption. Multiple species of mackerel (97.5%N Scomber japonicus and 2.5%N S. scombrus) and cephalopods (mostly Illex coindetii and some other Illex spp., as well as some Todaropsis eblanae) were grouped because individuals
were not often identified to the species level and species-specific otolith length versus body length relationships and energetic densities were not available.

Energetic densities (kJ/g of wet weight) were obtained from the literature for sardine (Rosa et al. 2010; Harmelin et al. 2012; Spitz & Jouma’a 2013), anchovy (Tirelli et al. 2006; Dubreuil & Petitgas 2009; Harmelin et al. 2012; Spitz & Jouma’a 2013), sprat (Hislop, Harris & Smith 1991; Arrhenius 1998; Spitz & Jouma’a 2013), mackerel (Montevecchi et al. 1984; Spitz & Jouma’a 2013) and cephalopods (Lawson, Magalhes & Miller 1998; Eder & Lewis 2005; Ciancio, Pascual & Beauchamp 2007). As energetic densities may change considerably between seasons, places and individuals (e.g., because of differences in length or condition), maximal and minimal values were noted (Table S1) and a uniform distribution between these two values was used, rather than the average, to represent the energetic values of the prey species, thereby accounting for some uncertainty.

References


Appendix S2: DEB model properties

**Basic equations**

Table A1 Dynamic equations of the non-standard Dynamic Energy Budget model developed and validated for Pacific bluefin tuna (*Thunnus orientalis*, Jusup *et al.* 2011) and reparameterised for Atlantic bluefin tuna (*T. thynnus*) for use in this study.

### State and auxiliary variables

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E(t)$</td>
<td>Amount of energy in reserve tissue</td>
<td>J</td>
</tr>
<tr>
<td>$V(t)$</td>
<td>Volume of structural tissue</td>
<td>cm³</td>
</tr>
<tr>
<td>$L(t)$</td>
<td>Structural volumetric length</td>
<td>cm</td>
</tr>
<tr>
<td>$E_m(t)$</td>
<td>Level of maturity</td>
<td>J</td>
</tr>
<tr>
<td>$E_a(t)$</td>
<td>Status of the reproductive buffer</td>
<td>J</td>
</tr>
<tr>
<td>$E_0$</td>
<td>Initial energy reserve of an egg</td>
<td>J</td>
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### Energy fluxes

<table>
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<th>Metabolic process</th>
<th>Energy flux</th>
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<tbody>
<tr>
<td>Assimilation</td>
<td>$\dot{p}<em>A = M_1 {p</em>{Am}} f L^2$</td>
</tr>
<tr>
<td>Utilization</td>
<td>$\dot{p}_C = E \left( \frac{M_1 V}{L} \frac{d}{dt} \ln L \right) = E \frac{M_1 \dot{V} [E_G] L^2 + \dot{p}_S}{\kappa E + [E_G] L^3}$</td>
</tr>
<tr>
<td>Somatic maintenance</td>
<td>$\dot{p}_S = \dot{p}_M + \dot{p}_T = [\dot{p}_M] L^3 + M_2 [\dot{p}_T] L^2$</td>
</tr>
<tr>
<td>Growth</td>
<td>$\dot{p}_G = \kappa \dot{p}_C - \dot{p}_S = \kappa \dot{p}_C - \dot{p}_M - \dot{p}_T$</td>
</tr>
</tbody>
</table>

### Dynamics of state variables, reproduction state

<table>
<thead>
<tr>
<th>State variable</th>
<th>Dynamic equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Energy in reserve</td>
<td>$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$</td>
</tr>
<tr>
<td>Structural length</td>
<td>$\frac{dL}{dt} = \frac{1}{3L^3 [E_G]} \dot{p}_G$</td>
</tr>
<tr>
<td>Maturity level</td>
<td>$\frac{dE_H}{dt} = \dot{p}_R (E_H &lt; E_H^0)$</td>
</tr>
</tbody>
</table>

### Auxiliary functions

<table>
<thead>
<tr>
<th>Auxiliary functions</th>
<th>Functional form</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shape correction function</td>
<td>$M_1(L, E_H) = L/L_b, E_H^0 \leq E_H &lt; E_H^I$ for $L_b/L_b, E_H^I \leq E_H$</td>
</tr>
</tbody>
</table>
Efficiency of internal heat production

\[ M_1(L, E_H) = \begin{cases} 0, & E_H < E_H^1 \\ \frac{E_H - E_H^1}{E_H^y - E_H^1}, & E_H^1 \leq E_H < E_H^y \\ 1, & E_H^y \leq E_H \end{cases} \]

Arrhenius equation

\[ \dot{p}_v(T) = \dot{p}_v(T_0) \exp \left( \frac{T_A}{T_0} - \frac{T_A}{T} \right) \]

Shape factor

\[ \delta_M = \frac{\delta_M^1 (E_H^2 - E_H^b) + \delta_M^2 (E_H - E_H^b)}{E_H + E_H^2 - 2E_H^b}, \quad E_H^b \leq E_H < E_H^y \]

Parameter values

Table A2 Dynamic Energy Budget parameters for Atlantic bluefin tuna (Thunnus thynnus) and their values.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>{\dot{\rho}_{Am}}</td>
<td>Maximum surface-area-specific assimilation rate</td>
<td>124.8</td>
<td>J cm(^{-2}) d(^{-1})</td>
</tr>
<tr>
<td>[E(_G)]</td>
<td>Volume-specific cost of structure</td>
<td>7163</td>
<td>J cm(^{-3})</td>
</tr>
<tr>
<td>\dot{v}</td>
<td>Energy conductance</td>
<td>0.09542</td>
<td>cm d(^{-1})</td>
</tr>
<tr>
<td>{\dot{\rho}_M}</td>
<td>Volume-specific somatic maintenance rate</td>
<td>5.149</td>
<td>J cm(^{-3}) d(^{-1})</td>
</tr>
<tr>
<td>{\dot{\rho}_T}</td>
<td>Surface-area-specific somatic maintenance rate</td>
<td>1877</td>
<td>J cm(^{-2}) d(^{-1})</td>
</tr>
<tr>
<td>(k)</td>
<td>Maturity maintenance rate coefficient</td>
<td>1.362</td>
<td>10(^{-2}) d(^{-1})</td>
</tr>
<tr>
<td>(\kappa)</td>
<td>Fraction of mobilized reserve allocated to soma</td>
<td>0.8222</td>
<td></td>
</tr>
<tr>
<td>(E_H^b)</td>
<td>Maturity at birth</td>
<td>0.2253</td>
<td>J</td>
</tr>
<tr>
<td>(E_H^p)</td>
<td>Maturity at puberty</td>
<td>2.937</td>
<td>10(^7)J</td>
</tr>
<tr>
<td>(E_H^1)</td>
<td>Maturity at the end of the larval stage</td>
<td>2566</td>
<td>J</td>
</tr>
<tr>
<td>(E_H^2)</td>
<td>Half-saturation maturity</td>
<td>7050</td>
<td>J</td>
</tr>
<tr>
<td>(E_H^y)</td>
<td>Maturity at the end of the early juvenile phase</td>
<td>1.629</td>
<td>10(^6)J</td>
</tr>
<tr>
<td>(T_A)</td>
<td>Arrhenius temperature</td>
<td>6398</td>
<td>K</td>
</tr>
<tr>
<td>(\delta_M^1)</td>
<td>Shape factor in the larval stage</td>
<td>0.1475</td>
<td></td>
</tr>
<tr>
<td>(\delta_M^2)</td>
<td>Shape factor in the adult stage</td>
<td>0.2531</td>
<td></td>
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</tbody>
</table>
Age-length and age-weight curves

![Graph showing the relationship between tuna age and length (left) and weight (right), as modelled by the Dynamic Energy Budget model for Atlantic bluefin tuna (Thunnus thynnus).](image)

**Fig A2** Relationship between tuna age and length (left) and weight (right), as modelled by the Dynamic Energy Budget model for Atlantic bluefin tuna (Thunnus thynnus).
Figure S1

Fig. S1 Age-length keys of anchovy (Engraulis encrasicolus), sardine (Sardina pilchardus) and sprat (Sprattus sprattus) calculated from the small pelagic survey data over the period 2008 to 2013. For sprat a linear model \( L(t) = a + b \times t \) was used, where \( L(t) \) is the expected length at age \( t \). For sardine and anchovy seasonal variability was accounted for using Somers’ model (Somers 1988), \( L(t) = L_\infty (1 - e^{k(t-t_0)} - S(t) + S(t_0)) \) with \( S(x) = \left( \frac{C}{2\pi} \right) \sin(2\pi(x - t_s)) \), where \( L_\infty \) is the model asymptote for average length, \( k \) is a measure of the exponential rate of approach to asymptotic length, \( t_0 \) is the theoretical age at which the average length would be zero, \( C \) is the amplitude of the growth oscillation and \( t_s \) is the inflexion point.

Table S1

Table S1 Biological parameter values of major prey species found in the stomach contents of juvenile Atlantic bluefin tuna (*Thunnus thynnus*). The ranges of energetic densities were taken from literature (see Appendix S1: Energetic density). Lengths of sardine, anchovy and sprat were calculated using the linear relationship between otolith (oto) length and individual (ind) fish length ($L_{oto} = a + b \cdot L_{ind}$), and their body mass was obtained by converting these lengths using an annual length weight key ($W_{ind} = e \cdot L^{f}_{ind}$). Direct length measurements were not needed for mackerel and squid, and otolith lengths or beak lower rostral lengths (LRL) were directly converted to weight ($W_{ind} = c \cdot L^{d}_{oto/LRL}$). All relationships were calculated from the small pelagic survey biological data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Energetic density (kJ/g wet weight)</th>
<th>$L_{oto} = a + b \cdot L_{ind}$</th>
<th>$W_{ind} = e \cdot L^{f}_{ind}$</th>
<th>$W_{ind} = c \cdot L^{d}_{oto/LRL}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$a$</td>
<td>$b$</td>
<td>$e$</td>
</tr>
<tr>
<td>Sardine</td>
<td>4.00-14.40</td>
<td>0.46</td>
<td>0.14</td>
<td>2011</td>
</tr>
<tr>
<td>Anchovy</td>
<td>2.67-12.81</td>
<td>0.62</td>
<td>0.18</td>
<td>2011</td>
</tr>
<tr>
<td>Sprat</td>
<td>3.7-12.40</td>
<td>0.98</td>
<td>0.06</td>
<td>2011</td>
</tr>
<tr>
<td>Mackerel</td>
<td>6.00-10.30</td>
<td>0.88</td>
<td>3.09</td>
<td></td>
</tr>
<tr>
<td>Squid</td>
<td>5.01-6.46</td>
<td>7.07</td>
<td>2.24</td>
<td></td>
</tr>
</tbody>
</table>
Chapter 5: Can pathogens alter the population dynamics of sardine in the NW Mediterranean?

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Abstract

Sardine populations worldwide can fluctuate drastically over short periods of time, in terms of both biomass and biological characteristics. Dynamics might be amplified by pathogens, but such a hypothesis has never been considered in the absence of clear macroscopic symptoms. In the Gulf of Lions (NW Mediterranean), an enduring severe decrease in sardine (*Sardina pilchardus*) size, condition and age has been observed since around 2008. Such changes made them commercially far less interesting, so landings dropped dramatically. Surprisingly, recruitment has remained high and these modifications primarily affected the adults, which is rather unusual for small pelagic fish populations. We thus hypothesised that a population dynamics altering disease might be present. Therefore, we sampled nine times about 150 sardines during the period June 2014 – July 2015, and performed necropsy, bacteriological, parasitological, histological and virological studies. All analyses were performed on fish grouped as either lean or fat, as the frequency of occurrence of pathogens was expected to be higher in lean sardines. Only four groups of infectious agents were found: microscopic parasites (during all histological analyses) that were either undetermined or trematodes, Coccidia (parasitic protozoa) observed in one host, *Tenacibaculum* bacteria (23/07/2014 and 16/12/2014) and *Vibrio spp.* (05/07/2015 and 14/07/2015) that were sometimes identified as *Vibrio alginolyticus*. No macroparasites were found, in contrast to what was found for sardine elsewhere. Only *Tenacibaculum* appeared significantly more in larger individuals and could theoretically have caused a population size structure decrease. But none of the agents more frequently occurred in fat or lean fish. Also, no clear damage to any tissue was observed, so the effect of the detected and possibly overlooked infectious agents was estimated to be limited. However, the prevalence and effect of Coccidia might have been underestimated, so further research focussing on this parasite is needed. Interestingly, 54% of the sardines analysed in 2015 had elevated quantities of melano-macrophage centres (macrophage aggregates), indicating a certain, yet undetermined, level of stress. As stress caused by disease was estimated to be rather low, pollution and/or malnutrition might lie on the basis of these formations.

**Key words:** Gulf of Lions, pathology, trematodes, *Tenacibaculum, Vibrio alginolyticus*, Coccidia, melano-macrophage centres
Introduction
Understanding population fluctuations is an important objective in ecology. Therefore, a plethora of studies aimed at linking those fluctuations to external drivers. Concerning exploited fish stocks, studies typically focussed on fisheries and environmental changes, such as sea surface temperature and chlorophyll concentration. Factors like predation and competition are considered less, whereas other potential drivers are often overlooked, such as pollution and disease (mechanisms with a rather lateral control, see Fuiman et al. 2015). But disease outbreaks are rising worldwide (Lafferty, Porter & Ford 2004) and some wild fish populations were significantly altered by them (Yamamoto, Takagi & Matsuoka 1984; Meyers et al. 1986; Sindermann 1990). Although pathogens might cause almost direct mortality of fish (hence altering the population abundance, e.g. Jones et al. 1997), their effect can also be delayed and have for example an impact on the condition, size and age structure of a population. For instance, upon infection a fish might grow slower, lose weight (i.e. obtain a reduced condition) and die subsequently younger, so the population size and age distribution is affected deleteriously. Alternatively, it happens that opportunistic pathogens prevail and aggravate the poor state of health of fish that were already stressed and weakened (Miller et al. 2014).

Sardine is an important species from an ecological and economic point of view. It constitutes a high biomass in a central place of the food web (Rice 1995; Cury et al. 2000) and is commercially very interesting (Palomera et al. 2007). But the species is also known for its worldwide conspicuous population dynamics, i.e., large alterations in population biomass and size can occur (Baumgartner, Soutar & Ferreira-Bartrina 1992; Lluch-Belda et al. 1992; Jarre et al. 2015). Around 2008, the average size, age and body condition of sardine (Sardina pilchardus) in the Gulf of Lions (NW Mediterranean) seriously lowered, so they became commercially less interesting and landings plummeted (Van Beveren et al. 2014). The truncated population state and low catches have endured ever since, and although a part of the changes was explained by some environmental drivers (Brosset et al. 2015), no holistic view of the causes was determined. Recruitment remained high (Van Beveren et al. 2014) and the effect of fisheries and predation was reported to be too low to complete the puzzle (Van Beveren et al. Submitted, Submittedb, 2014). Also, the comparison of French with Spanish landing sizes showed that large sardines did not leave for the Catalan coast, although it is the most probable sink in view of the currentology (south-westwards, (Millot 1990). Thus, the disappearance of large and old individuals indicates that sardines suffer from overmortality (or abnormally high natural mortality). Consequently, disease might synergistically explain the shift in condition and size and age structure. Given the importance of the sardine stock and the potential existence of a harmful infectious agent, this study therefore aims at describing and quantifying the presence of pathogens in the Gulf of Lions sardine population.

However, studies analysing disease outbreaks are usually performed after major alerting indications have been observed (marked lesions, mass mortality, macroscopically visible parasites, etc.). Here, no apparent signals were present. Yet, no veterinary survey has ever been performed on this population, so micro symptoms might have been overlooked. Also, it could be that fish disappear from the population right after symptoms occur, e.g. by imperceptible death (Bakke & Harris 1998) or predation (that can be higher on weaker individuals, e.g. Mesa et al. 1998). Furthermore, hidden sublethal effects of microparasites could be detrimental for a population if they reduce its competing, migrating or spawning abilities (Miller et al. 2014).
This devoid of visual symptoms precluded however a lead to a certain pathogen class. Therefore, an all-embracing study was necessary, that had the capacity to detect a wide range of pathogens. Such an assessment would also provide baseline knowledge on the composition and prevalence of viruses, bacteria and parasites in sardine because studies on sardine pathogens are rather rare. The most well-studied case is the Australian sardine, which was affected by two mass mortalities caused by Pilchard herpesvirus in 1995 and 1998 (Whittington et al. 2008). This herpesvirus was suggested to be introduced with clupeids imported to feed sea-caged tuna (Jones et al. 1997). Most other studies related to adult sardine pathogens focussed on its parasite community for stock delimitation (e.g. Baldwin et al. 2011; Reed et al. 2012) or on a single agent, mostly because of its threat to human health (e.g. anisakid parasites in the Mediterranean; Rello et al. 2008; Piras et al. 2014; Serracca et al. 2014). Thus, despite the enormous fluctuations in the anchovy and sardine populations world-wide (Baumgartner, Soutar & Ferreira-Bartrina 1992; Lluch-Belda et al. 1992), a disease hypothesis has never been proposed to explain part of their dynamics (except for the Australian sardine, where its effect was irrefutable).

We investigated the hypothesis that the observed changes in the Gulf of Lions sardine population could be due to or aggravated by an epizootic disease. Therefore, we assessed the prevalence of pathogens by means of a non-specific traditional veterinary approach (necropsy, histology, parasitology, bacteriology and virology) and performed analyses aimed at the specific detection of two known viruses, namely pilchard herpesvirus (PHV) and betanodaviruses. The latter have a large host range and are highly prevalent in the region, affecting many farmed and wild fish species (Panzarin et al. 2012; Vendramin et al. 2013; Kara et al. 2014). As pathological studies are uncommon and generally incomprehensive (Lafferty 2013), this study also provides a reference line for future work.

**Material and methods**

**Sampling**

From June 2014 to July 2015, about 150 sardines were sampled 9 times at different dates (Table 1), so that various seasons could be considered. These fish originated from research cruises (MEDITS, PELMED) or commercial purse seiners or trawlers that operated in the Gulf of Lions (north-western Mediterranean Sea). From August to November 2014, no experiments were performed because sardines were not targeted by fishermen and no scientific survey took place. On the other hand, in July 2015, two last analyses were started with only eight days in between, so short term differences in results could also be examined and a comparison could be made with July of the previous year (when an infectious agent was first detected). On these two dates, it was also possible to start analyses on board almost as soon as sardines were lifted out of the water (PELMED survey). On all other dates, fish were analysed the day of their catch (usually in the evening) or the following morning. Fish were always kept cold (generally on ice) until being measured (total length), weighted (±0.1 g) and analysed for fat content. Fat content was determined with a Fatmeter (Distell Fish Fatmeter, Kent 1990), an electronic device that measures water content, which is strongly related to fat content. For sardine in the Gulf of Lions, this method has been shown to correctly reflect the individuals true fat content (as measured with a direct method), irrespective of the reproductive period (Brosset et al. 2014). Based on these fat measurements, each time fish were divided into 80 lean fish and 70 fat fish (note that the threshold value changed between sampling events due to the
seasonality of fat content), to test whether or not pathogens might be more prevalent in fish in a relatively weaker condition. Next, 15 lean fish and 15 fat fish were taken for necropsy and parasitological and bacteriological investigation (all three experiments were performed on the same 30 fresh individuals). Only on 31/03/2015 one fat sardine was discarded from the three analyses because of its damaged state (human induced). Straight after, a viral culture was started on 20 lean and 10 fat new fresh individuals. All other analyses (histology, PCR for detecting betanodaviruses and pilchard herpesvirus) were performed afterwards on conserved tissue (fixed or frozen) from 15 lean and 15 fat sardines. During two events (31/03/2015 and 14/04/2015) not enough sardine were available to perform all analyses, hence the same individuals were used for both PCRs (herpes and betanodavirus). On two occasions, histology was either not done (24/06/2014) or only on a limited number of individuals (5 fat fish and 5 lean fish, 26/02/2015) because sampled sardines were not in a good enough state to obtain a sound conclusion. All studies for pathogen detection were done by the Laboratoire Départemental Vétérinaire de l’Hérault (Montpellier, France), except the histological part (Oniris laboratory, Nantes, France) and the PCR for betanodaviruses (Anses laboratory, Plouzané, France).

Additionally, on 6/10/2015 a new study was started whereby sardine were captured and transferred to a basin for ex situ experiments. After a first mortality wave due to capture and transport that took place during the first three days, the mortality rate significantly decreased. The remaining fish were examined for the presence of disease when dying or exhibiting negative signals, suggesting an imminent death. Therefore, on 11/10/2015 a necropsy and parasitological analysis including microscopic examinations were performed (skin, gills, kidney, spleen, gonads, intestines and liver) on one fresh sardine which after four days of capture was evaluated to approach death. Given that the veterinary rapport of this fish was of high importance to the interpretation of the other results, it was included in this study.

Necropsy, parasitology and bacteriology

To start, a necropsy was performed on each individual to detect macroscopically visible lesions or other symptoms of disease. Tissue containing such indications recurrently was frozen or fixed in formaldehyde, so further analyses or comparisons could be made later on. Next, microscopic observations were made of a sample of the gills, skin, fins and intestines. Parasites were photographed, measured and conserved when of interest. Additionally, for 5 fish (preferentially those that already showed marks of disease), a bacteriological analysis was performed on each organ presenting lesions and the anterior kidney because of its low contamination risk (no direct contact with the external environment). Samples were streaked on marine (favouring heterotrophic marine bacteria) and CNA (colistin-nalidixic acid, favouring Gram-positive bacteria) agar and incubated at 20±2 °C during 10 days. Present colonies were identified using the Maldi-Tof (matrix assisted laser desorption/ionisation time-of-flight analyser) technique and conserved at -80 °C.

Histology

Histopathological examination of tissue was done to identify damage at the cellular level. Therefore, 30 individuals were sampled for their anterior kidney, spleen, gills, muscle, eyes, brain, intestine, liver, stomach and heart. All tissues were fixed per individual in 10% formaldehyde. However, since April the complete individual was conserved, after the abdomen was opened to maximise formaldehyde penetration. Specimens were embedded in paraffin (automated process executed
overnight) and sectioned into 3 to 4 µm slices with the help of a microtome. Certain paraffined tissue (gills and eyes) was decalcified before being sliced to facilitate the process. Sections were posed on a glass slide and dried at 30 °C during approximately 20 minutes, after which they were deparaffined, rehydrated with water and stained using the standard hematoxylin-eosin-safran (HES) protocol.

**Viral culture**

Per sardine, a piece of kidney, spleen, brain and gill (organs with a relatively high probability of infection) were sampled in a sterile environment. Those were grinded and filtered so that e.g. bacteria were removed. This was done separately for the gills (external tissue) and all other tissue (internal organs). A part of each filtrate was stored at -80 °C. Two 24-well plates were used for inoculation with the two samples (gills and internal organs), of which 3 concentrations were prepared: $10^{-1}$, $10^{-2}$ and $10^{-3}$. Three types of cell cultures were available: EPC (epithelialoma papulosum cyprinid), RTG (rainbow trout gonad) and CHSE (Chinook salmon embryo). Plates were incubated at 14 °C and 21 °C and checked twice every 7 to 10 days, so the experiment lasted around 14 to 20 days.

**PCR for the pilchard herpesvirus (PHV)**

For the PCR analyses, on each date six batches (3xlean and 3xfat) of five heads (including the gills) were stored at -80 °C until analysis. To start, about 30 mg of grinded gills from five individuals were used for DNA extraction with the Nucleospin tissue kit (Macherey-Nagel) following the manufacturer’s instructions. Subsequently, a real-time PCR was used according to Crockford et al. (2008) using primers PHVRltF and PHVRltR.

**PCR for betanodaviruses**

On each of the nine dates, six batches of five heads (3xlean and 3xfat) were conserved at -80°C until processed. At two different periods, total RNA was extracted from pieces of eyes and brain and submitted to a generic real-time RT-PCR specific of betanodaviruses, as already published (Baud et al. 2015).

**Statistics**

During some periods infectious agents or a recurrent histological structure were detected. We analysed if there was an influence of the host’s continuous variables size and fat content (or their interaction) on the presence or absence of the pathogen classes and the histological structure. Therefore, we performed for each a binomial GLMM (generalized linear mixed model) with a logit link and date as a random factor using the Lme4 package in R (Bates et al. 2015). Per date, the fat content and fish size were scaled to avoid bias from seasonal differences. Only the fish of the sampling events during which the bacterium, parasites or structure were detected were considered. Models were selected based on AIC (Akaike information criterion). When models were within 2 AIC units of the lowest AIC value, the most parsimonious one was selected (Arnold 2010).
Results
In total, 1289 sardines ranging between 7.7 cm and 17.3 cm (12.42±1.29 cm) and between 3.4 g and 36.0 g (13.03±4.36 g) were analysed for the presence of an infectious agent. Results are summarised in Table 1.

Necropsy, parasitology and bacteriology

During necropsy, no marked anatomical indications of disease were detected. A complete absence of symptoms was observed in the lymphoid organs and urogenital system. For the digestive system, it was only noted once (24/07) that the liver was of a light colour and of fluctuating consistence. More regularly, a preservation caused (moderate) congestion of the intestinal serous membrane was observed (25/06, 23/07, 16/12), something that also occurred in the respiratory system of one individual (23/07). Concerning parasitology, parasites were absent from the surface of all usually investigated organs, i.e. the gills, skin, fins and intestines.

Table 1 Summary of the results per date and per method (NA=Not Available). A test was considered negative (Neg.) if no absolute evidence of the presence of an infectious agent was found. For histology and bacteriology, the percentage of occurrence of microparasites (Paras.) and Trematodes (Trem.) is also given. Note that trematodes count as microparasites and that some microparasites might have been trematodes, but could not be officially identified as such.

<table>
<thead>
<tr>
<th>date</th>
<th>bacteriology</th>
<th>histology</th>
<th>PCR noda</th>
<th>PCR herpes</th>
<th>Cell culture</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>24/06/2014</td>
<td>Neg.</td>
<td>NA</td>
<td>Neg.</td>
<td>Neg.</td>
</tr>
<tr>
<td>2</td>
<td>23/07/2014</td>
<td>Tenacibaculum (23%)</td>
<td>Paras. (67%), Trem. (30%)</td>
<td>Neg.</td>
<td>Neg.</td>
</tr>
<tr>
<td>3</td>
<td>16/12/2014</td>
<td>Tenacibaculum (7%)</td>
<td>Paras. (77%), Trem. (20%)</td>
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<td>Neg.</td>
</tr>
<tr>
<td>5</td>
<td>31/03/2015</td>
<td>Neg.</td>
<td>Paras. (87%), Trem. (47%)</td>
<td>Neg.</td>
<td>Neg.</td>
</tr>
<tr>
<td>6</td>
<td>14/04/2015</td>
<td>Neg.</td>
<td>Paras. (83%), Trem. (33%)</td>
<td>Neg.</td>
<td>Neg.</td>
</tr>
<tr>
<td>7</td>
<td>21/05/2015</td>
<td>Neg.</td>
<td>Paras. (80%), Trem. (47%)</td>
<td>Neg.</td>
<td>Neg.</td>
</tr>
<tr>
<td>8</td>
<td>05/07/2015</td>
<td>Vibrio (87%)</td>
<td>Paras. (90%), Trem. (40%)</td>
<td>Neg.</td>
<td>Neg.</td>
</tr>
<tr>
<td>9</td>
<td>14/07/2015</td>
<td>Vibrio (63%)</td>
<td>Paras. (60%), Trem. (47%)</td>
<td>Neg.</td>
<td>Neg.</td>
</tr>
</tbody>
</table>

During bacteriological analyses two bacteria could be detected (Fig. 1). *Tenacibaculum spp.* were found on fish from 23/07/2014 and 16/12/2014, with a respective prevalence of 7 and 2 individuals out of 30 (23% and 7%). These bacteria were found in the heart, the brain and the anterior kidney, but never in all organs simultaneously. A binomial GLM showed that infections were independent on the host’s fat content, but were more often present in larger individuals (length was retained by AIC selection as a significant variable, Table S1 and Table S2). The bacteria could not be identified as any of the 21 described species of the genus (16S rDNA sequencing), among which the opportunistic *Tenacibaculum maritimum* (color, culture and Gram aspects). Furthermore, *Vibrio spp.* were present in the anterior kidney of sardines sampled on 05/07/2015 and 14/07/2015 (Fig.1) with a prevalence of respectively 87% and 63% (26 and 19 individuals). During 05/07/2015, 46% of the *Vibrio spp.* were determined as *Vibrio alginolyticus*. The infected individuals were not of particular size or condition (binomial GLM, Table S1).
Lesions were globally scarcely encountered: one sardine had a focal granulomatous fibrosing lesion on the heart (05/07/2015), two sardines had one on their muscle tissue (23/07/2014 and 16/12/2014) and two others had a (peri)hepatic lesion that might have corresponded to an autolysed parasitic structure (23/07/2014). Histological lesions compatible with a known viral origin (e.g., herpesvirus and betanodavirus) were never noted, nor were there inflammatory or other lesions associated with the observed parasites.

In general, microparasites (often trematodes) were always detected (Table 1, 220 analysed sardines), with their occurrence ranging between 60% and 90% of all sardines analysed per date. There was no clear seasonal trend in occurrence, as these percentages fluctuated considerably. For example, the maximal and minimal percentages of occurrence were both observed during July 2015, when two analyses were executed exceptionally within 9 days. Also, infection was independent of fish condition.
or size (binomial GLM, Table S1). Therefore, we will discuss findings without emphasising the difference between fat or size classes.

We found that about half of the infected sardines were host to a small quantity of trematodes (Table 1), which could however not be determined to the species level. Nonetheless, trematodes (dimension: around 100x275µm) from the digestive system were described by their thick eosinophilic cuticle, spicules, absence of coelom and the absence or presence of brownish eggs (present on all but the first sampling date for histological analyses), whereas another trematode found in the brain had again an eosinophilic cuticle (with 4 external extensions) and the absence of coelom, but also the presence of a digestive tube and genital tissue (23/07/2014). In the liver of 45 sardines (20%), some parasitic elements were observed between the hepatocytes: one to four parasitic structures of about 15 micron long with a fine cell wall and an interior vermiform hypereosinophilic element (present on all dates). Unfortunately, those elements could not be identified. In 9 of those individuals, no actual parasite was observed. Their presence was also again independent of fish condition or size (binomial GLM, Table S1). Places of occurrence of parasites (trematodes or unidentified parasitic elements) in the 220 analysed sardines were the anterior kidney (1x), muscle (1x), brain (5x), oesophagus (73x), stomach (48x), pyloric caeca (84x), intestines (24x) and liver (24x). Hence, no parasites were found in the skin or eyes.

Microscopic examination of the liver from the one sardine analysed on 10/10/2015 revealed that it was highly infested by oocysts of undetermined Coccidia (Fig. 2). This individual did not have any macroscopically visible symptoms of disease on the skin, gills, kidney, spleen, intestine or gonads.

![Fig. 2 Photo of coccidian Oocysts in the liver of a sardine (Sardina pilchardus) analysed on 11/10/2015 (magnification: 1000x with immersion oil).](image-url)
In contrast, melano-macrophage centres (macrophage aggregates) were found in the spleen of 81 sardines, mostly in slightly to moderately elevated quantities (no exact counting was performed). They were encountered on all dates in 2015, with a frequency of occurrence ranging between 17% (14/04/2015) and 100% (26/02/2015, when only 10 fish were analysed). However, 22 of them also occurred in sardines in which no sign of an infectious host was found. Thus, their presence was not necessarily connected to an infestation. Such histological structures were also not associated to sardines of particular size or condition (binomial GLM, Table S1). Additionally, telangiectasia (dilatation of lamellar vessels) was found in the gills of four hosts (three times at 16/12/2014 and once at 05/07/2015), and an ectopic oocyte (cardiac cavity) was encountered in 11 sardines, spread over 5 sampling events (twice in an individual that did not show any other signs of infection).

**Viruses: cultures and PCRs**

Viral cultures gave negative results for all the batches tested. The more specific PCR analyses directed towards pilchard herpesvirus and the betanodavirus were also always negative.

**Discussion**

This study investigated the pathogenic community of sardine of the Gulf of Lions, in search of a cause of the observed decline in their size, age and body condition. To our knowledge, no study exists that was based on such a wide aspecific approach to determine the diversity and patterns of occurrence of infectious agents, nor were pathogens already linked to their population dynamics. This is in spite of the well-known and extreme sardine population fluctuations (Checkley et al. 2009). Surprisingly, no macroparasites and viruses were detected, and only relatively few bacteria and microscopic parasite species were found. Nevertheless, microscopic parasites were highly prevalent, one sardine was infected with hepatic microparasitic Coccidia oocysts and two bacteria were detected each during two different months; *Tenacibaculum spp.* and *Vibrio spp.*, the latter sometimes identified as *Vibrio alginolyticus*.

*Vibrio spp.* (gram-negative bacteria) were highly prevalent in sardines sampled in July 2015, during both occasions. This genus dominates seawater ecosystems and is the main bacterial causative agent of many marine animal diseases, although most are non-pathogenic (Xie et al. 2005). But about one fourth of the detected Vibrio spp. were identified as *Vibrio alginolyticus*, an important opportunistic and widespread pathogen of marine species (Carli et al. 1993), of which the influence on human health as well has been known since long (Schmidt, Chmel & Cobbs 1979; Blake, Weaver & Hollis 1980; Matsiota-Bernard & Nauciel 1993). To give some examples of its opportunistic character, *V. alginolyticus* was found in corals (Zhenyu et al. 2013), shrimp (e.g. *Penaeus monodon*, Lee et al. 1996), deep-sea echinoids (*Paleopneustes cristatus*, Bauer & Young 2000) and several fish species (Colorni, Paperna & Gordin 1981; Molitoris et al. 1985; Noguchi et al. 1987; Balebona et al. 1998; Yan et al. 2007; Wang et al. 2014). Some notion also exist of the capacity of *V. alginolyticus* to infect sardine (e.g. from the Atlantic coast of Morocco, Elotmani & Assobhei 2004), but no study truly questioned their effect on this host species. As many strains exist, virulence is highly variable (Noguchi et al. 1987; Xie et al. 2005). Its prevalence can also depend on environmental variables (Huang et al. 2015). For example, in the North Sea human infections increased because of a temperature rise (Schets et al. 2006) and in Liguria (NW Med), their presence in rock pools was also temperature and salinity dependent (Carli et al. 1993). However, infected individuals appear usually to be recognisable from symptoms, micro-or macroscopically established (Esteve & Herrera 2000;
Here, no damage to sardine tissue was observed, neither microscopically (histology) nor macroscopically (necropsy). Additionally, *Vibrio* spp. did not occur more often in lean or larger fish, hinting that they might not cause overmortality of large individuals or reduce fish condition, although infections could be recent and thus not yet have had an effect. Therefore, *Vibrio* spp. are unlikely to have caused the recent changes in the sardine population. Yet, *V. alginolyticus*, as other pathogens (Miller *et al.* 2014), was often associated with species under stress (i.e., cultured species, see Colorni, Paperna & Gordin 1981; Balebona *et al.* 1998; Wang *et al.* 2014). Thus, although the effect of vibrios is unlikely to be pronounced, they might be an indicator of stress. However, they could also simply be opportunistic species, or result from post-mortem contaminants. Further analyses are necessary to determine their exact effect.

*Tenacibaculum* spp. (family Flavobacteriaceae) had a relatively weak frequency of occurrence during only two months, but these two sampling periods were highly spread, so the bacterium might actually be present during several months, i.e., at least from July to December. Also, some of the species within the genus are renowned for their great impact on fish (e.g. Faílde *et al.* 2013). Moreover, *Tenacibaculum* is the only pathogen that had a significantly higher presence in larger individuals. A very harmful but low prevalent species of *Tenacibaculum* might thus theoretically cause overmortality of large fish. But for *Tenacibaculum* the same is valid as for the Vibrios; the extremely few observed damage to tissue points toward agents that might not be harmful enough to be a prominent factor altering the physical status of sardine. Given that the strain did also not correspond to any known *Tenacibaculum* profile, this might indicate the opportunistic character of the bacterium. In contrast, microscopic parasites occurred most frequently; they were always present, and in all internal types of tissue. However, they are likely to be insignificant from a pathological point of view for the same reasons as previously stated (no lesions, not significantly more present in leaner fish).

We also detected high numbers of hepatic oocysts from coccidian parasites (Apicomplexa) in one sardine. These intracellular microparasites have already been found in liver tissue of sardine elsewhere in the Mediterranean (e.g. Kalfa-Papaioannou & Athanassopoulou-Raptopoulou 1984) and can have a considerable effect on both cultured and wild fish populations (Anderson & Gordon 1982) as they may affect fish condition and cause mortality (Gestal & Azevedo 2006). Also, its effect on fish is not necessarily associated with clear macroscopically visible symptoms (e.g. Kalfa-Papaioannou & Athanassopoulou-Raptopoulou 1984). But despite its potential concealed harmfulness, its detection might seem scarcely noteworthy because only a single individual was infected. However, it may be that the undeterminable hepatic parasitic structures observed in 20% of all fish analysed histologically were actually coccidian parasites in an early non-infectious developmental stage. In such case, (sub)lethal effects might only have occurred after this early phase, and coccidioses could thus have been overlooked. On the one hand, this might have been because individuals generally died before the disease could have been established. On the other hand, it might be that the infectious oocyst stage was not observable on tissue that had been stored on formaldehyde, as was used for the general histological analyses (and the standard necropsy and parasitological analysis performed on fresh fish were not done for the liver). Thus, there is definitely a need to perform additional analyses so the prevalence and harmfulness of this pathogen can be assessed, despite their possibly early phase being non-selective for species of a given size or body condition.
Apart from the detected agents, the high prevalence of hepatic melano-macrophage centres (MMC, in 37% of all sardines histologically examined) is also of particular help in illuminating the current sardine situation in the Gulf of Lions. These centres, also called macrophage aggregates, are focal accumulations of macrophages, generally found in the spleen and kidney of teleost fish. What makes them interesting, and particularly so for our case, is their association with environmental stress (Agius & Roberts 2003). Their characteristics (accumulation, proliferation, size, number, etc.) are not only dependent on their age (Brown & George 1985), but also vary with infectious diseases (Agius 1979), starvation (Agius & Roberts 1981) and environmental contaminants (Couillard & Hodson 1996; Fournie et al. 2001; Alcaro et al. 2012). Hence, they can be used as biomarkers (Wolke et al. 1985; Wolke 1992). For example, the number and area of MMCs in red mullets (*Mullus barbatus*) from the polluted zone in front of Barcelona (NW Mediterranean) was significantly higher than what was found for mullets sampled next to a small national marine reserve that is part of the Gulf of Lions (Carrasson et al. 2008). Thus, the accumulations of MMCs in about one third of all sardines examined during 2015 might indicate some level of stress. However, we did not quantify the MMCs precisely and no baseline scenario was identified, so it was impossible to conclude on their exact implication. Nonetheless, it should be noticed that 27% of the sardines that had MMCs did not show any trace of an agent, that tissue damage was limited and that MMC presence was not size and thus unlikely age dependent (although their quantity per species still might be). Thus, the presence of MMCs might be little related to age and disease, but rather to factors such as pollution and/or a bad nutritional status. Indeed, a change in plankton quantity and/or quality was already previously suggested to be of potential importance to the shift in the sardine population (Van Beveren et al. 2014) and the Gulf of Lions contains substantial concentrations of pollutants (Gomez-Gutierrez et al. 2007; Bodiguel et al. 2008; Harmelin et al. 2012).

Surprisingly, only four infectious agents were found. In an early general report of sardine in the Gulf of Lions, several parasite types had been reported, some of which were noted to be very abundant in our sampled region (Lee 1961). Studies on adult sardine assessing parasites elsewhere (studies on viruses and bacteria are extremely rare), always found a higher prevalence and diversity. In South Africa, sardines were even reported to be amongst the most heavily infected fish (Reed, Mackenzie & van der Lingen 2012). Parasitic copepods, nematodes, trematodes, coccidian, cestodes, monogeneans, etc. have all already been encountered. Whether studies were aimed at investigating parasite communities for stock delimitation or human risk assessment, most studies found for example Anisakids nematodes. Studies reporting their presence in the Mediterranean are plentiful (summarised by e.g. Cavallero et al. 2015). To our knowledge, only one study looking at 750 sardine from the Ligurian coast did not find any (Serracca et al. 2014). The reason why such a low presence of pathogen species was found is hard to explain. It could be that for parasites, intermediate host species (e.g. such as cetaceans for anisakids) are insufficiently present in the sampled area. Also, some infections depend on variables such as season, fish size and depth. Our sardines were mainly obtained from local fishermen catching them nearshore, thus at relatively shallow depths. However, seasonality and fish size were relatively well covered (except for the period August to November 2014). Also, pathogens might have died if fish were not fresh enough. But even when fish were handled directly after being caught (5/07/2015 and 14/07/2014) instead of after some hours, no bigger diversity was found (i.e., only *Vibrio spp.* and the microscopic parasites including trematodes that were always present). Furthermore, the lowest prevalence of microscopic parasites was found during one of the sampling dates, when analyses were done on exceptionally fresh fish.
The analyses performed were not exhaustive, so some pathogens might have gone undetected. Not all bacteria and viruses are cultivable on respectively the two agars and three cell lines used, despite those media being able to isolate a wide variety of unanticipated agents, including mixed cultures. For example, the epithelial carp cells (EPC) we worked with have been used for the isolation of the viral hemorrhagic septicemia virus (VHSV) from sardine and other marine species (e.g. halibut, Atlantic cod, turbot), but their detection level was highly variable among hosts (Dopaz et al. 2002; Arkush et al. 2006). Cultures could also be falsely negative for the detection of an early stage infection, as sufficient pathogen loads can be required to obtain a positive assessment (Miller et al. 2014). Furthermore, not all parts of the body were considered for each analysis. Although the organs most probable to be affected were selected, pathogens or their symptoms might—although unlikely—still have occurred elsewhere. Next, the pathogenicity of certain agents might have caused sardine to die and disappear from the population before they can be observed (Bakke & Harris 1998, see possibly Coccidia previously). This might have occurred for the adult population, but also for the eggs or larval stage. For instance, examples are available of sardine egg infection leading to at least 20% mortality (Hollande & Cachon 1952; Lee 1961; Stratoudakis, Barbosa & Meneses 2000). But we only analysed and discussed the adults, because if eggs and/or larvae would have suffered from overmortality, this would not have resulted in the observed decrease in adult fish condition and size. Hence, diseased eggs, larvae or early juveniles would be unable to explain the observed population changes. Thus, although our approach was aimed at detecting the widest possible range of adult pathogens, it is impossible to give information on the full scope.

Despite the impossibility to consider all pathogens still a very wide range was searched for, and this practically all year round. Consequently, although we cannot be entirely conclusive about the existence of a population restructuring disease in the sardine population of the Gulf of Lions, the likeliness that such a sufficiently harmful and prevalent agent is present has subsided. This is especially true given that during necropsy and histological analyses almost no damage was found to the tissue of adults, even at a histological level. Thus, even the role of potentially unnoticed pathogens becomes questionable. Also, if pathogens would be the key factor for the current size and condition decrease, we expected them to mainly infect lean or large fish. But only Tenacibaculum spp. appeared to infect relatively larger individuals. However, given the high prevalence of some agents and the hepatic parasitic elements encountered in 20% of the histologically examined sardines that might be early stage Coccidia (further research is needed), we do not exclude that pathogens might still exercise a certain synergetic effect. Of additional great interest is that we detected frequently occurring MMC accumulations. This might indicate that individuals are exposed to a certain amount of stress. Therefore, pollution and non-pathogen related diseases such as malnutrition could perhaps better explain the current decrease in sardine “health”.

Acknowledgments
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References


## Supplementary material

### Table S1

Table S1 All candidate models (binomial GLMMs) for each response variable, with the sampling date as a random effect. The final model is indicated in red. AIC = Akaike Information Criterion.

<table>
<thead>
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<th>Response</th>
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<th>Deviance</th>
<th>AIC</th>
</tr>
</thead>
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<td>fat * size + (1</td>
<td>date)</td>
<td>44.67</td>
</tr>
<tr>
<td></td>
<td>fat + size + (1</td>
<td>date)</td>
<td>45.73</td>
</tr>
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<td></td>
<td>fat + (1</td>
<td>date)</td>
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<td></td>
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<td>date)</td>
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<tr>
<td></td>
<td>(1</td>
<td>date)</td>
<td>50.42</td>
</tr>
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<td>66.55</td>
</tr>
<tr>
<td></td>
<td>fat + size + (1</td>
<td>date)</td>
<td>66.59</td>
</tr>
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<td></td>
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<td>date)</td>
<td>66.59</td>
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<td></td>
<td>size + (1</td>
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<tr>
<td></td>
<td>(1</td>
<td>date)</td>
<td>50.42</td>
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<td>date)</td>
<td>200.64</td>
</tr>
<tr>
<td></td>
<td>fat + size + (1</td>
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<td>fat + (1</td>
<td>date)</td>
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<tr>
<td></td>
<td>fat + size + (1</td>
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<td></td>
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<td>(1</td>
<td>date)</td>
<td>234.71</td>
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<td></td>
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<td></td>
<td>(1</td>
<td>date)</td>
<td>214.40</td>
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</tbody>
</table>

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Table S2 Results of the binomial GLMM relating fish size and condition to the presence or absence of Tenacibaculum \(N_{\text{individuals}}=60\).

<table>
<thead>
<tr>
<th>Response</th>
<th>Factor</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
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<td>0.58</td>
<td>-3.44</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Size</td>
<td>0.76</td>
<td>0.36</td>
<td>2.12</td>
<td>0.03</td>
</tr>
</tbody>
</table>
General discussion

The objective of this PhD was to study the origin of the large fluctuations in small pelagic populations in the Gulf of Lions (GOL), after some anomalies had been observed which resulted in a fisheries crisis. To do so, we first unravelled a part of the biology of these species in the area, so the changes could be better understood and potentially important drivers could be identified. Then, not only specific bottom-up drivers (instigating changes in production) were considered, but also top-down regulating factors (controlling death rate) were taken into account, so they could be excluded or not. Here, a final discussion is given on all the population level changes that were observed, and the most probable hypotheses that might explain them. Finally, we provide based on the current knowledge a most likely theory of what could have happened.

Population level changes

We have observed a change in several aspects of the small pelagic population structure and dynamics since 2007/2008 (Table 1). To start, we confirmed in chapter 1 that fish size decreased. Specifically, the size structure of sardine is generally bimodal, but since 2008 the second peak representing the largest individuals has progressively disappeared. Anchovy on the other hand has a unimodal size distribution. Simultaneously with sardine, its median size gradually shifted towards smaller individuals. For sprat it was harder to draw a conclusion about a size trend because of insufficient data during some years, but an indication was found that its size also started to reduce around the same time.

<table>
<thead>
<tr>
<th>Species</th>
<th>abundance</th>
<th>biomass</th>
<th>body condition</th>
<th>size</th>
<th>age</th>
<th>growth</th>
<th>L50</th>
<th>fecundity</th>
</tr>
</thead>
<tbody>
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<td>Sardine</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anchovy</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
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<td>sprat</td>
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<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

Since 2008, sardine and anchovy have displayed a clear decline in body condition as well (chapter 1). Precisely, sardine condition decreased with age during 2008-2013, in contrast to the positive relation between condition and age perceived before (Brosset et al. 2015). Thus, older and larger sardine and anchovy were most impacted, perhaps leading to their early death and consequently causing an alteration of their size and age structure. Although sprat too did not have an optimal body condition (chapter 1), they appeared to still be in better condition than the other two small pelagics (Brosset et al. 2014). Additionally, for sardine we also noticed a significant decrease in growth and age structure (chapter 1). This was not observed for anchovy and undetermined for sprat due to a lack of data and the few existing age classes for this species. Length at maturity (L50, body length at which 50% of the individuals are mature) was also determined annually for sardine (2003-2013) and anchovy (2002-
2013) in their spawning period. For both species, around 2007/2008 a decrease was observed in this parameter (P. Brosset, pers. comm.).

Between 2005 and 2007 the inverse happened, i.e. most of the discussed parameters indicated a very healthy population. Given that these three years stand out when looking at the last two decades, this result is as thought-provoking as the 2007/2008 population alterations. However, as the most recent changes endure and entail unfavourable economic and ecological consequences, we focus on this shift during our final and general discussion.

**The EcoPelGol project**

In order to provide a final discussion on what could be the responsible factors for the recent changes in the ecosystem, it is helpful to first briefly consider other studies that were published inside the EcoPelGol framework, that started about three years ago (a full summary is out of the scope of this work). Although not all of them directly asked the question “how are the populations of small pelagics in the Gulf of Lions controlled?” they all contributed to the understanding of their population dynamics, thereby at least backing-up the answer to this question. In chronological order, a first study by Brosset *et al.* (2014) investigated multiple methods to analyse pelagic fish condition. A second paper focussed on the spatial structure and distribution of sardine, anchovy and sprat in the GOL during 2003-2012 (Saraux *et al.* 2014). Using the acoustic survey data of PELMED (see chapter 1 and 3), it was concluded that for example sardine and sprats are more coastal than anchovy, all three species globally strongly overlap but that biomass density differed at local scale. Thirdly and lastly, Brosset *et al.* (2015) also looked at the inter- and intra-annual fluctuations of body condition of all three species, and linked those to environmental and biotic variables. Additionally, for example differences in condition between age-classes were examined. But as the EcoPelGol project is not yet finished, other work outside this PhD is still on-going. For example, the diet of the three small pelagics of interest is investigated in terms of niche breadth, position and overlap (stomach and isotope analyses) over a period sufficiently long to assess amongst other things if changes occurred concomitantly to population changes. Also, ocean colour information is used to assess changes in the phytoplankton community in the Gulf of Lions. Further effort will be directed towards the assessment of the reproductive capacity of individuals, temporal fluctuations in small pelagic body condition on a Mediterranean scale, etc.

**The main hypotheses**

The information of all chapters and other studies is combined to give an updated view of the current knowledge on the possible drivers. A summary is given in Figure 1.

**Fisheries**

Prior to this study, the GFCM (General Fisheries Commission for the Mediterranean) already literally stated that the system was not controlled by human activity (GFCM 2007), although in their report no specific arguments underpinning this statement were given. In this study, we also assumed fisheries to be unlikely as the prime driver of the observed changes. As stated in chapter 1, the yearly ratio of landings to ecosystem biomass (known as harvest rate, a proxy for exploitation, Fig. 2) was during the last 20 years generally lower than 0.2. Importantly, exploitation was also higher before a biomass increase had taken place (sardine) or during years when biomass had already decreased (anchovy), in contrast to what would have been expected if fishing was the only cause of the recent
decline. For anchovy, high fishing pressure exerted during the low biomass years, might have nonetheless prevented the population from rebuilding. However, fishing pressure decreased quickly after. The number of vessels also decreased when fish size started to decrease. Between 2011-2014, only about 10 vessels were targeting sardine and/or anchovy, some of which only during part of the year (GFCM 2007, 2014). To compare, at the start of the crisis (2007) at least 62 vessels were still active (GFCM 2007). Secondly, during the last years the size structure of the landings (Fig. 3) was also skewed towards smaller individuals, despite fisheries usually targeting large and old fish (Berkeley et al. 2004b). Thus, fishing is unlikely to be responsible for the disappearance of larger fish.

Thirdly, in the end of chapter 1, we concluded that body condition decreased in parallel for anchovy, sardine and sprat. But fisheries generally do not alter fish condition. Also, fisheries would be unlikely to have influenced the condition of all three species simultaneously, as exploitation levels of sardine and anchovy were not identical and basically non-existent for sprat. A fourth argument for the unlikeliness of the prime importance of fisheries was provided in chapter 3, when we looked at fish landings. Although we did not assess the effect of fisheries directly, a historical perspective allowed
us to still better grasp its influence. For example, after decades of exploitation, the populations were still able to build a relatively high biomass, i.e. ten times higher than the maximal landings during the last 150 years.

Thus, although no direct analysis was made to assess the effect of fisheries, we still obtained a better understanding of its pressure on small pelagics. Based on four motives (the exploitation ratio, the landing sizes, the temporal changes in biological traits and the history of the landings) we could conclude that although small pelagic fisheries were strongly present in the area and might have affected the targeted populations, they are unlikely to be responsible for the major changes that happened during the last decade.

Fig. 2 Fishing harvest rate (%) over approximately the last two decades.

**Predation**

An increase in predation might have resulted in a restricted biomass of sardine and anchovy in the ecosystem. Importantly, this might have affected the largest and oldest individuals if size selective feeding occurred. Also, because of prey-selective feeding this effect could perhaps have been somewhat smaller for sprat. Beyond direct mortality, increased predation risk could also strongly affect prey behaviour, such as foraging or spawning (Lima & Dill 1990; Brown & Kotler 2004). For example, tuna and Chilean Jack Mackerel can spawn in oligotrophic waters to avoid predation (Barbieri *et al.* 2005; Cubillos *et al.* 2005), notwithstanding the direct nutritional disadvantage for their offspring. Specifically, the energetic costs of the prey might be increased to avoid risk (e.g. by introducing small changes in habitat, Brown & Kotler 2004), thereby possibly lowering their condition to some extent. However, predation should happen on the adult phase, as recruitment remained high and a raised consumption of eggs (e.g. through a jellyfish or intra-guild predation increase, see respectively Fuentes *et al.* 2010; Brotz & Pauly 2012 and Bachiller *et al.* 2015) would not alter the size and age structure of the populations. Thus, theoretically the total sardine and anchovy ecosystem biomass, size structure and condition could be affected by stronger predation on the adults, whereas sprat could remain relatively untouched. Accordingly, predation could hypothetically explain parts of the fluctuations observed in the small pelagic populations. For example, for the Black Sea it was already proposed that bonito (*Sarda sarda*) might influence the anchovy population (see introduction, Sahin *et al.* 2008). And although bottom-up control was considered to be more likely (see chapter 1), this hypothesis still remained interesting to dig into.
Therefore, in chapter 3 we looked at the predation pressure of bluefin tuna on sardine, anchovy and sprat in the GOL. We specifically considered bluefin tuna as predator, given that they were estimated to be among the most important predators of small pelagic fish (chapter 3). Tuna was also of specific interest because of its great increase in abundance in the GOL over the last recent years (Bauer et al. 2015), which resulted from effective management strategies implemented in 2007 (quotas, fishing season restrictions, etc.). Hence, this rise happened simultaneously with the deleterious changes in the sardine and anchovy populations. From this chapter, we could conclude that the tuna predation effect was negligible, as maximally 2% of each population was consumed annually between 2011 and 2013. Also, bluefin tuna did not feed preferentially on certain size classes, hence is unable to alter the size structure of the populations. Thus, bluefin tuna alone could not have caused the observed changes (see discussion chapter 3).

But many other predators are present, such as marine mammals, predatory fish, sharks, seabirds and marine turtles (Cardona et al. 2015). However, for most of these, sardine and anchovy are only of minor importance (see Cardona et al. 2015). Also, they generally have relatively low population biomasses, might consume small pelagics in the GOL only for a limited period of the year, and are geographically restricted (e.g. to the surface, such as some seabirds). But the effect of dolphins could be contemplated, as they have a relatively high energetic requirement (related to e.g. their large body-volume, see Piercey et al. 2013; Rechsteiner, Rosen & Trites 2013) and some species are known to be present year-round (e.g. Cotte et al. 2010). Most frequently occurring striped dolphins can attain a high density over the continental shelf (Bauer et al. submitted; Cotte et al. 2010). At the densities reported by Cotte et al. (2010) based on ferry transects (0.38 dolphins km$^{-2}$), their abundance (estimated at 7752) does not reach that of tuna in the GOL area (roughly 10000-30000 during 2009-2012). Bauer et al. (submitted) who analysed the same aerial survey data as for the calculation of regional tuna abundance estimates (see chapter 4) reported even lower dolphin densities (max 0.15 dolphins km$^{-2}$), and thus concluded that tuna was by far more abundant. Even if we assume that striped dolphin total population biomass is higher than that of tuna because their average weight is more important (but weight data is not sufficiently available), they also feed predominantly on cephalopods (e.g. Würt & Marrale 1993). Thus, they are unlikely to exert a very large pressure on the small pelagic populations. The second most common dolphin species, bottlenose dolphins, are limited in number when compared to tuna (at least 10 times less, Ripoll et al. 2001; Labach et al. 2011; Gnone et al. 2011), so even their total biomass might be smaller (and hence their energetic requirement). Additionally, this species consumes mostly hake (Blanco & Salomón 2001), so the effect on the small pelagic populations is also estimated to be restricted. Of lesser importance are Risso’s dolphins, who feed chiefly on oceanic cephalopods from the middle slope (Astruc 2005; Blanco, Angeles Radian & Antonio Raga 2006). Likewise, infrequently observed pilot whales prefer open and deep waters (Bauer et al. submitted; Cañas, Sagarminaga & García-Tiscar 2002) and are predominantly squid-eaters (Relini & Garibaldi 1992).

But the effect of all predators might be accumulative, and the pressure on the small pelagics therefore underestimated. Yet, predation is estimated to be of very limited importance in this study. First, fisheries pressure is much higher than tuna pressure (chapter 3). All predators together would need to have an effect at least six times higher than what is only exerted by bluefin tuna to match fisheries. Second, sardine and anchovy are minor prey for some of the predators (e.g. Cardona et al. 2015). Third, most of the predators showed a population decline or stagnation, rather than an increase. For example, in late 2007 (when sardine and anchovy biomass, size and condition started to
decrease), an epizootic resurgence in the Spanish Mediterranean striped dolphin populations was observed (Raga et al. 2008), which might have affected the largest dolphin population of the GOL as well. In any case, no increase in their density was seen between 2009-2012 (Bau er et al. submitted). Thus, it could be reasoned that if formerly their effect was larger or at least identical, today their effect could not have caused such great changes.

A spatial shift
In 2011, the GFCM also stated that there might be “some migration of fish in and out of the area” (GFCM 2007). A (temporal) spatial shift in the distribution of the sardine and anchovy might explain why their biomass is not as elevated as in some preceding years (such as 2004-2005 for sardine and 1999-2001 for anchovy). But such a displacement might also result in a lowering of abundance, something that was not observed. Therefore, particularly a displacement of the largest and oldest individuals might help to explain the current phenomenon. However, this would still not explain the decrease in fish condition, neither the sprat outburst. Therefore, this hypothesis should also go hand in hand with one or more other theories. For example, it could be that the condition of fish decreased because of a change in the environment (see Brosset et al. 2015), and that this change in environment (being detrimental for sardine and anchovy) pushed sardine and anchovy to migrate to neighbouring more favourable environments (vote with the fins hypothesis, Landa 1998), whether or not for their whole life cycle (e.g. only as adults for feeding and not for spawning). For example, a subtropicalization of the North Sea resulted in the arrival of sardine and anchovy in more northern waters from the 1990s onwards (Beare et al. 2004b; a; Montero-Serra, Edwards & Genner 2015). Although temperature appeared to be the main force, a probably related change in food might also have played a role. North Sea herring for instance might have moved further north because its main food sources declined (Corten 2001). Likewise, in the Canary and California current relatively long-term migrations of sardine or anchovy to more southern or northern areas were already seen (see McFarlane & Beamish 2001; Aristegui et al. 2009; Demer et al. 2012). Additionally, the intensity of seasonal migration can highly vary between years (e.g. sardine in the California current, Zwolinski & Demer 2012).

Here, displacement would be described as movement to a zone outside the scientific survey study area, as abundance, biomass and biological parameter estimates were made only for this zone. Therefore, two hypotheses could be put forward: fish moving outside the GOL and fish displacement inside the GOL to areas that were not taken into account during the pelagic survey.

Migration outside the GOL
The idea of sardine and anchovy migration to neighbouring shelf areas was the one originally thought of by the GFCM (2007). Likely, they could have moved to the Spanish South coast, especially as there is a general strong south-westward circulation in the GOL (Millot 1990; Nicolle, Garreau & Liorzou 2009) and the continental shelf is broader than the one of the Ligurian coast (Italy). As the Spanish equivalent of the French pelagic survey took place in November-December instead of July until 2008, it is however difficult to compare abundances, biomass and fish sizes between regions. Nevertheless, the annual size distribution of the landings can still be paralleled. For France, the landing sizes follow roughly the same trend as the size distribution observed during July surveys. Thus, landed size distributions are a reasonably proxy for the size distributions of the wild populations. Only the frequencies of the smallest fish are perhaps biased because of the used mesh sizes, but given that we are primarily interested in the larger fish, this does not pose a problem. From
a comparative analysis (Fig. 3) it becomes clear that Spanish landed pelagic fish (data received from Ana Giráldez) were also smaller during recent years. This was also statistically verified (Wilcoxon signed rank test), as a significant difference (p<0.05) was always found between the periods (average: 2002-2004, good: 2005-2007 and poor: 2008-2013), for each species and region. This is especially true for anchovy, whose landings by Spain were formerly somewhat larger than the French ones. Inversely, landed sardine was usually smallest in Spain. However, sardines in Spain still reached a minimum size during the recent years. The converging of the size distributions of both areas for both species might stress similarities between the French and Spanish populations, or a close connection between both. As we found evidence that sardine and anchovy in Spain are also smaller, there might have been a driver that acted on a larger scale, that is, the NW Mediterranean basin rather than just the Gulf of Lions. Hence, without excluding migration between areas itself, it can still be concluded that large individuals did not move to Spain.

Fig. 3 Comparison of the annual size distributions of sardine and anchovy landed in Spain (blue) and France (red). Vertical lines indicate the median size of each distribution.
Migration inside the Gulf of Lions

The abundance and biomass of the small pelagics were assessed with a scientific survey (PELMED, see chapter 1) assessing the area of the Gulf of Lions at depths between 20-200m. The upper boundary is related to a reduced pelagic biomass from this depth onwards, i.e. no sprat is found at depths >200m and the zone between 150-200m is unfavourable for sardine (Saraux et al. 2014). On the other hand, the lower boundary is established by the draught of the ship, the numerous fishing deployments close to the coast and technical limitations. For example, the cone of the acoustic echosounder only assesses fish biomass directly underneath the vessel, so that in shallow waters it scans a very small volume (the volume is proportional to the depth cubed).

An earlier study however showed that a significant proportion of small pelagic biomass might occupy shallow areas (<20m), leading to underestimations (Brehmer et al. 2006). This might especially be true for sardine, that favours nearshore waters (Saraux et al. 2014). But to explain the current pattern principally larger sardines should have been undetected, which would be unlikely given that predominantly the smallest fish live closest to shore, even during low biomass years (Saraux et al. In Prep). Additionally, an increase in large coastal sardine should have been reflected in the landings. Also, to our knowledge, no such observations have been made by local fishermen.

During the aerial surveys directed towards the detection of bluefin tunas, some small pelagics were also already observed in the deeper waters in the Gulf of Lions (S. Bonhommeau, pers. comm.). But these areas remain else unassessed in terms of small pelagic abundance and biomass. No scientific study has been directed specifically to deep waters and fishermen remain mostly on the continental shelf due to their one-day trip obligation, so no further information is available. However, the area is known to be generally unfavourable for sprat and sardine, so both species are unlikely to shift to this zone (Saraux et al. 2014). Furthermore, at the scale of the Mediterranean basin, sardines were shown to have a high probability of being present in relatively shallow waters (<65m depth) during summer (when the pelagic survey of the GOL takes place), and even during winter they do not migrate to much greater depths (up to 100m, Tugores et al. 2011). Although anchovy can in general be found in somewhat deeper waters, they also have a higher probability of occurrence at depths shallower than 200m (Giannoulaki et al. 2013). However, these studies were based on acoustic data and did not take into consideration waters deeper than 200m. In contrast, in the bay of Biscay a large proportion of the anchovy population can sometimes be found in oceanic waters of the shelf (Boyra et al. 2005). However, these were mainly juveniles and this peculiarity was suggested to be the result of a predator-avoidance mechanism (Irigoin et al. 2007). In the GOL, we expect the largest fish to be located in the deeper waters, and predation pressure is not assumed to be extremely high (see previous paragraph). But it appears that such risk-avoidance might have brought about the major decrease in fish condition, perhaps more detrimental for the species than the actual predation pressure.

Thus, the migration flux to the outside or within the GOL (whether to the coast or deeper waters) is unlikely to have been strong enough to explain the far-reaching changes that have been observed. However, as no detailed study has been directed to this problem, the exact intensity of migration remains unknown.
**Disease**

The disappearance of large and old individuals (and thus biomass) might have been caused by an abnormally high natural mortality. A disease could well have caused such overmortality, as well as a decrease in fish condition. On the other hand, another factor might have led to the body condition decrease (e.g. pollution, see next section), so that individuals were less immune and thus more susceptible to disease. Very few studies tried to explain sardine and anchovy population dynamics based on this hypothesis (see chapter 1). This was basically only done in Australian waters (Jones et al. 1997; Whittington et al. 2008), and only when extreme sardine mortality waves were observed that were undeniably related to disease. Hence, this hypothesis is rather unique and might therefore give an unexpected outcome, potentially being of high relevance to future studies in other areas where such hypothesis has never been considered.

We performed an all-embracing study (Chapter 4) looking for several pathogens, such as bacteria, parasites and viruses (whether or not specific ones). Although some infectious agents were detected (microparasites, Coccidia and both *Tenacibaculum* and *Vibrio* bacteria), they were not associated with clear symptoms of disease (lesions, etc.), even on a histological level. But this study was not exhaustive, so an agent might have been overlooked and further research focussed on Coccidia is needed. However, the presence of a sufficiently prevalent and harmful agent that can significantly alter the population biomass and structure could be estimated as less likely. Particularly the complete lack of symptoms almost all year-round (only fall was excluded) underpins this assumption. On the other hand, at a cellular level indications of stress were found, which might have resulted from malnutrition or pollution.

**Pollution**

Pollution or a decreased water quality could have had the same effect as a pathogen, namely a decrease in fish condition and a consequent overmortality. Pollution could also have weakened fish, so that they became for example more susceptible to disease or even predation, the latter however likely not resulting in a change in population dynamics (see previously). Oppositely, a pollution effect might have been triggered by a change in environmental condition, so an association between both might need to be considered. This is because the concentration of contaminants (e.g. PCBs) in the GOL can be linked to weather conditions, which determine the contaminant flux through continental input, sediment suspension and hydrodynamic transport (Tiano 2014; Tiano et al. 2014). Given that the GOL contains considerable concentrations of pollutants (Harmelin et al. 2012) and is the Mediterranean area most polluted by PCBs (Gomez-Gutierrez et al. 2007; Bodiguel et al. 2008), this hypothesis would be worthy of a detailed examination. But in contrast to previous hypotheses, no illuminating analyses have yet been done or their results are still unknown (see COSTAS project, Tronczynski et al. 2013). Thus, more information is needed before a conclusion can be stated. However, some ideas can be put forward.

Pollution might have an effect on many fish species, either directly or indirectly. Indirectly, planktonic species could be impacted (Tiano 2014), potentially resulting in a community and/or abundance change (Arfi, Champalbert & Patriti 1981; Uriarte & Villate 2005). Such an event might produce changes higher up the food chain, such as at the level of the small pelagic fish. However, a study on the aspects of PCBs (including multiple congeners) in the GOL indicated that PCB biomagnification in plankton is relatively low, and concentrations are not correlated to the plankton biomass in the system (although such relation might have been masked; Tiano et al. 2014). Thus, PCB concentration...
might not have increased if food would have decreased (so a synchronous effect of both would have occurred), nor will PCBs accumulate greatly in the primary food source of the small pelagic fish.

Directly, pollutants might change fish physiology after ingestion (Heath 1995), whether or not after bioaccumulation or biomagnification of the contaminants along the trophic web. However, for the few pollutants (PCB, PBDE, Hg and $^{137}$Cs) in anchovy and sardine of the GOL looked at so far (see Harmelin et al. 2012), no exceptionally high levels were found when compared to other European regions (Naso et al. 2005; Bocio et al. 2007; Martí-Cid et al. 2007). The Mediterranean also harbours important concentrations of microplastics, but concentrations in the GOL were not higher than elsewhere (Balearic Islands, Sardinia and Corse, Faure et al. 2015). This indicates that it might be necessary to look at a mixture of pollutants, as the combined effect of numerous weakly present ones might become an influential cocktail. Also, the body condition of sprat was during the last years better than for sardine and anchovy (Le Bourg et al. 2015). However, pollutants might be accumulated less by sprat than by anchovy and sardine. For example, as sprat is on average smaller and younger, metal concentrations might be lower, given that they depend on fish size and age (Canli & Atli 2003; Polak-Juszczyk 2009). Additionally, to our knowledge, no other (trophically higher) fish species were reported to be in significantly lower condition. Although because of biomagnification of PCBs and most metals through the food web (e.g. Rasmussen et al. 1990; Mason, Laporte & Andres 2000; Barwick & Maher 2003), an effect on the sardine and anchovy predators (and the succeeding trophic levels) could be expected.

**Competition**

Density-dependent mechanisms also influence population dynamics (Hixon & Carr 1997), and can be caused by either predation (previously discussed) or competition. For example, negative density-dependence takes place when population growth becomes limited by increased predation and competition. Indeed, based on previous studies on sardine and anchovy elsewhere, density-dependent mechanisms are probable to be present in each population (e.g. Jacobson & Maccall 1995; Lindegren et al. 2013). Predation was discussed previously, but another yet to analyse aspect is inter- and intraspecific competition for a given resource, which may be food or space.

First, inter-specific competition is considered. Sardine, anchovy and sprat in the GOL show a clear overlap in both their diet and territory (Brosset et al. In Prep; Pethybridge et al. 2014; Saraux et al. 2014; Le Bourg et al. 2015). For example, Pethybridge et al. (2014) concluded based on lipid biomarkers that there is a high degree of dietary overlap between sardine and anchovy, albeit the presence of seasonal differences in their competition for resources. No competition with sprat was noticed, but a rather small sample size was taken. However, Le Bourg et al. (2015) showed based on stomach content and stable isotope analyses that the trophic niche of all three species overlapped. While some competition for food and space might thus usually be present, an increase in competition may have caused for example the decrease in fish condition and growth. For example, another study that concentrated on the Baltic pelagic ecosystem provided evidence that pelagic fish growth might be reduced by inter-specific competition (Casini, Cardinale & Hjelm 2006; Casini et al. 2011). But as the total abundance and biomass of small pelagics in the ecosystem was not particularly higher during 2007-2011 (see Fig. 1 from the introduction), there is no reason to believe that inter-specific competition would have increased, if resources remained stable and the relative strength of inter-specific-competition was not higher between sprat and both sardine and anchovy than between the two latter. Thus, it is clear that by itself this theory can hardly explain all observed
changes. If competition has increased, environmental changes would most likely lie on the basis of the observed changes. That is, they would have altered the resources and/or available space. Therefore, a competition increase might not only by itself explain changes in for example fish condition, but might also point towards other drivers. Interestingly, there is some evidence that interspecific-competition did indeed rise. Clearly, resource competition can only increase if a change in diet is also observed (although the latter does not evidence the former). Le Bourg et al. (2015) already noted based on a comparison with literature that there are some differences between the periods 1995-1996, 2007-2008 and 2011-2012. Additionally, another study in progress that directly quantifies the temporal evolution in niche overlap also supports this hypothesis (Brosset et al. In Prep). Thus, competition might be a non-ignorable co-acting factor responsible for the observed changes if resources became limited, which did indeed happen according to our main hypothesis (see further).

In contrast, given their much higher numbers, intra-specific competition between sprat individuals might very likely have been amplified. However, such competition could not have attained extremely high levels, as this might have impeded the population from becoming as successful. Nevertheless, it might be the reason why sprat is not in optimal “health” during the last years (chapter 2). Also, this might be the reason why the sprat population decreased again in 2013 and 2014 (see Fig. 2 of the general introduction). Such a theory is strengthened by the example of the Baltic Sea, where the growth and condition of an also rapidly enlarged sprat population fluctuated greatly, which was principally attributed to intra-specific competition (Möllmann et al. 2005).

Environmental changes
From the beginning of this study onwards, environmental changes were thought to be highly potential drivers of the small pelagic ecosystem change, given the reduction in size, condition and growth of sardine and anchovy and the significant role of the environment in the restructuration of the small pelagics communities elsewhere in the world (see chapter 1).

Unfortunately, no sufficiently long time series were available of sardine, anchovy and sprat biomass or abundance to make a straightforward connexion with several environmental variables. However, 10 years long monthly time series of sardine and anchovy condition were available. In a study from within the EcolPelGol framework (Brosset et al. 2015), these data were used to illuminate that the condition of sardine in the Gulf of Lions was negatively related to temperature and positively to the WeMO (Western Mediterranean Oscillation) index and the mesozooplankton and diatom concentrations. Anchovy on the other hand was linked positively to mesozooplankton concentration and river runoff from the Rhône. In chapter 2, the landings instead of the body condition of sardine and anchovy were also linked to environmental indices (chapter 2). This data is although more approximate (landings rather than biomass), annual and far much longer (1865-2013). A model on these historical time series showed again the importance of the WeMO, but this time for anchovy instead of sardine (although the effect remains positive). Also, both sardine and anchovy landings were related to the AMO, but respectively positively and negatively. However, this index is considered less important for explaining the recent changes (see discussion chapter 2).

Final hypothesis
Before trying to formulate a most likely hypothesis at present, some things should be reminded of. First, recruitment remained high during the last years, so important drivers did not cause a
recruitment failure. This contrasts to most declines in small pelagic populations seen worldwide, for which this was one of the prime causes. Also, in 2005-2007 sardine and anchovy were on average larger, fatter and older. This could (but might not) have been caused by the same mechanism, which should then show similar short-term alterations. Next, as in other Mediterranean areas, sardine and anchovy did not fluctuate inversely during the last years and no evidence exists (e.g. in the historical landings) that they ever did in this region, in contrast to what was observed in multiple oceanic ecosystems (Lluch-Belda et al. 1992), although perhaps only for a certain time-span (Baumgartner, Soutar & Ferreira-Bartrina 1992; Finney et al. 2002). This stresses the inherent difference, in terms of the species themselves as well as their environment, between this small up-welling area and the large renowned ones from which most studies on anchovy and sardine arose.

Although there is no single driver that clearly popped out, we clarified the potential role of several elements (Fig. 1). Those factors are not mutually exclusive and some might work synergistically. Hypotheses inquiring about the role of top-down processes are generally unconvincing. Fisheries appear to be the most plausible of them, but were considered as a potential cofactor rather than an ultimate cause. Specifically, fishing might make populations more prone to climate changes, as their response ability might be destabilized (Anderson et al. 2008; Planque et al. 2010). For example several studies show the dependence of stocks productivity on the combination of climate and exploitation (e.g. Rouyer et al. 2014). Also, a spatial shift itself is not a driver, but a result of either top-down or bottom-up control (e.g. Montero-Serra, Edwards & Genner 2015). And as top-down control was estimated to be rather limited, the hypothesis of bottom-up is strengthened. Indeed, the effect of several environmental drivers has also already been confirmed (Brosset et al. 2015, chapter 2). However, a sound understanding of the exact mechanisms is still lacking.

As already hypothesised from chapter 1 onwards, a change in the zooplankton abundance, quality and/or phenology (e.g. timing of blooming) might explain a large part of the observed changes. This idea was reinforced during subsequent analyses, in or outside this PhD. A zooplankton change might have caused the decrease in sardine and anchovy condition, whereby especially the older individuals are affected (Brosset et al. 2015). This weakening could have caused a restricted attainable maximal size and an early death of the older and larger individuals mainly through starvation (rather than e.g. facilitated predation, as derived from chapter 3), altering the age and size structure of the populations. Indeed, sardine and anchovy condition was related to oceanic and biotic factors so that a high productivity regime corresponds to a better body condition (Brosset et al. 2015). That is, an optimal condition is attained when the concentration of mesozooplankton (and also diatoms for sardine) is elevated and when the WeMO is in its positive phase, characterised by low SST and strong Rhône runoff and wind mixing. The effect of SST and Rhône runoff on the condition of respectively sardine and anchovy was also established directly (Brosset et al. 2015). Both factors increase productivity, the latter by increasing nutrient input and the former by changing the upwelling intensity (lower when warmer) and (in)dependently the development of cold-water or larger copepods (fewer when warmer, Roemmich & McGowan 1995; Halsband-Lenk, Hirche & Carlotti 2002; Hinder et al. 2014). Even the long-term landings of anchovy were positively related to the WeMO in the Gulf of Lions. Along the neighbouring Spanish coast, landings of sardine and anchovy were also respectively influenced by the WeMO and river outflow (see introduction), stressing again the importance of productivity. But additionally to for instance the WeMO’s recent enduring average low, an overall trend in the NW Mediterranean also favours a non-productive regime. Namely, temperature has been increasing, whereas wind stress and water mixing has been declining (Calvo et
Such changes could have diminished the food concentration, quality and/or phenology to an extent that they altered the sardine and anchovy population as observed.

But currently no proof exists that a zooplankton change really did take place in the Gulf of Lions, making it hard to validate this hypothesis. Besides the modelled concentrations of several plankton classes (see Brosset et al. 2015), which only span the last decade, little information is available. Studies on the planktonic community of a longstanding sampling point at the entrance of Villefranche Bay, east of the Gulf of Lions, are only up to 2006 (García-Comas et al. 2011; Vandromme et al. 2011; Berline et al. 2012). However, they indicated that winter physical forcing could be the most significant factor for production (García-Comas et al. 2011; Vandromme et al. 2011). Specifically, production is favoured when strong winter vertical mixing took place, during wet and cold years. Unfortunately, published information on the GOL hydrodynamics is also limited in time or space (Schaeffer et al. 2011). But this result confirms that indirectly, the WeMO (for which winter values were taken in chapter 2) and SST might indeed influence productivity in this area.

Thus, assuming that zooplankton or pelagic fish biomass is indirectly related to certain available parameters (chlorophyll a concentration, Rhône river outflow, SST and the WeMO), looking at those proxies (Fig. 4) might also help evaluating this hypothesis. Although fragments of these series were already previously used (chapter 2; annually and without chl a, Brosset et al. 2015; monthly for 2002-2011), we did not yet discuss them fully, i.e. on a monthly time scale spanning at least two decades. One reason for this is that population biomass data points are annual (July) and few, so no sound connexion can be established with those parameters. Furthermore, chlorophyll data is derived from satellites and only available from 1998 onwards. To discuss the final hypothesis exhaustively, the mentioned series are plotted here and analysed for their breakpoints (using the same methods as in chapter 2). Before doing so, they were decomposed and their seasonal trend was removed (Fig. 4). This is however only an introductory examination and more meticulous analyses should be carried out. Only two breakpoints were found around 2007/2008. Precisely, both the last breakpoint of the WeMO (05/2008, CI: 05/2006 - 06/2010) and the chlorophyll time series (12/2008, CI: 11/2007 - 01/2009) have a confidence interval that includes 2007/2008. However, for the WeMO the direction of change is opposed to the expected (an increase instead of a decrease). But the last chlorophyll breakpoint does truly indicate a nutrient decrease, although this appeared to start too late (especially as a change in fish size should to a certain extent be delayed). When considering the general trend (seasonal variation was removed) in all variables, again no conspicuous evidence appears. Nonetheless, it seems that all four variables indeed evolved so that productivity might supposedly be lower, although this trend is more apparent for some (e.g. river discharge and the WeMO) than for others (e.g. Chla). But those variables are only proxies, and a relationship between zooplankton or small pelagic fish biomass and the four discussed parameters might not be as straightforward. For example, in Villefranche bay zooplankton fluctuated oppositely to phytoplankton (and thus chlorophyll a), perhaps caused by a top-down control of the grazers (Vandromme et al. 2011). Thus, a modest inspection of perhaps important ecosystem-scale factors only faintly endorses the idea of a zooplankton change caused by environmental change. However, I could also be that a change in zooplankton is triggered by for instance pollution, rather than climate or physical changes.

The problem of a zooplankton data lack can also be partially circumvented by looking at the diet composition of sardine and anchovy over a 20-year period, assuming that changes in diet potentially
reflect changes in the plankton community of the ecosystem (Brosset et al. In prep). Indeed, Le Bourg
(2015) already noted that such changes might have taken place. Also, given the prey-selectivity of
sardine and anchovy, a minor change in the dominant zooplankton species could have a great effect
on these small pelagics (Van Ginderdeuren et al. 2013). Many examples also exist of areas where
a change in zooplankton community, caused by environmental fluctuations, spread through the pelagic
foodweb (Beaugrand et al. 2015). It is again possible to take the example of the Baltic Sea, where
herring (Clupea harengus) condition and growth decreased mainly because of a decline in the
abundance of a specific copepod genus, an effect that was amplified by the strong competition with
the increased sprat stock (Möllmann et al. 2003, 2005; Rönkkönen et al. 2004).

Fig. 4 Decomposed monthly time series (1992-2014) of environmental indices that were shown to be of importance, or
from which it is expected that they might be. Blue dotted lines indicate breakpoints. The Rhône outflow (m³/s) was
measured at the Beaucar/Teascon (source: Compagnie Nationale du Rhône), SST (°C) and Chlₐ (mg/m³) calculated from
satellite sensors (source: respectively AVHRR and SeaWiFS) and the WeMO index downloaded from

Zooplankton changes might not only clarify the anchovy and sardine population alterations in terms
of abundance, size, age and condition, but could thus also explain why sprat prospered. Under past
circumstances, anchovy and sardine were flourishing and might have inhibited the sprat population
from increasing through spatial and/or trophic competition (Brosset et al. In Prep; Saraux et al. 2014;
Le Bourg et al. 2015). When food quality and quantity possibly changed, the ecosystem state might
have become more benign for sprat, allowing its expansion. Specifically, their competitors weakened
(smaller and low condition fish) while plankton quantity and quality was still sufficiently high to at
least avoid a significant decrease in condition. To be precise, the body condition of sprat was
although not optimal during the last years (see chapter 1) still better than for the other two species
(Brosset et al. 2014). This could be explained by the larger prey size spectrum of sprat, as well as e.g.
a higher mobility between feeding areas than anchovy (Brosset et al. In Prep; Le Bourg et al. 2015).
Sprat could also have other trophodynamic advantages in view of the prevailing conditions, such as a
faster clearance rate, a higher assimilation efficiency or lower energetic costs for feeding (see van der
Lingen, Hutchings & Field 2006 for the trophodynamic differences between sardine and anchovy).
In summary, we believe that the most likely key to our puzzle entails a decline in the zooplankton quantity and quality (size spectrum and composition). This drop might have been caused by a decreased (probably winter) vertical mixing of the water column. Indeed, not only is currently the winter WeMO index, a proxy for e.g. SST and river runoff, in a negative phase and thus favouring water column stability, most environmental factors show a long-term trend that further stimulates the decrease in vertical mixing. An environmentally induced zooplankton quality and quantity decrease might have led to an energetic shortage for anchovy and sardine, whose feeding apparatus and strategy might not have been adapted to the imposed changes. This could have been reflected in a decreased growth and body condition. Given their poor “health”, both species might have died oversoon or have grown too slow to attain a large size, so that their populations were not replenished with older and larger individuals anymore. Sprat, being a trophic generalist and having its competitors weakened, could have profited from this situation and bloomed. Intra-specific competition of sprat might explain their suboptimal “health”. Additionally, the situation could have been magnified by e.g. fisheries or pollution (affecting fish condition directly or indirectly by influencing the plankton community). The major aspects of this hypothesis shows several points in common with for instance the mechanism behind the Baltic sprat versus herring dynamics (see previously, Möllmann et al. 2005; Casini, Cardinale & Hjelm 2006), and examples throughout this work (especially provided in chapter 1 and during the discussion of the individual drivers) underpin the possibility of each of the process steps.

Perspective

Despite the increased understanding of the dynamics and biology of the three small pelagic populations, still many questions remain. For example, not all discussed hypotheses were fully analysed. The effect of pollution is scarcely known, so the concentration of pollutants inside individuals might be quantified and their effect evaluated. Pollution might influence the small pelagic fish indirectly as well, because of its potential (synergetic) effect on the plankton community and/or quality (e.g. Uriarte & Villate 2005). Also, the interactions between at least the three pelagic species might be considered using a population-dynamics model. Such model might give insight into level of competition between them. Furthermore, the effect of fisheries is still not completely assessed. The presence of disease and baseline data on the pathogen community was only defined for sardine, so the study might be repeated for anchovy or sprat.

Additionally, experiments with sardines and anchovy in captivity (already planned within Ecopelgol) could underpin the plankton as well as other hypotheses, as such studies already proved to be successful (e.g. Vanderlingen 1994; Garrido et al. 2007). For example, the effect of temperature and food regime on fish growth and condition could be tested. Feeding on small and large copepods could be compared, as well as a copepod versus diatom diet. In light of our principal hypothesis, a significant effect of diet on sardine condition should be observed. Moreover, the effect of toxic compounds (heavy metals, pesticides, etc.) on fish biology could be tested by artificially controlling their concentrations. Ecotoxicology could amongst other things help in understanding the consequences of the pollutant concentrations that might be established in the wild populations.

But especially analyses concentrating on the plankton hypothesis deserve the requisite attention. Despite the absence of a planktonic time series for the Gulf of Lions, two promising alternatives exist. First, the Villefranche data (see “final idea”) might be further explored (http://www.obs-
Changes in plankton composition (in terms of classes and sizes) and abundance could be analysed over a longer time span (including the recent years). Several techniques exist to verify if changes occurred in composition, whether or not together with small pelagic population fluctuations (e.g. ordination and classification techniques, statistical tests such as the Mantel test, etc.). Trends and breakpoints might be analysed using for example similar time series analyses as in chapter 3, applied to aggregate series (e.g. considering total copepod biomass) or individual plankton series (i.e., separating classes and sizes as far as possible). Second, one could work with satellite sea colour data (e.g. from MODIS). Using an already available algorithm (see PHYSAT, Alvain et al. 2005; Navarro et al. 2014) and in-situ data (e.g. the seaBASS dataset and PELMED, see chapter 1 and 3), satellite image pixels might be linked to a dominant phytoplankton functional type, such as nanoeukaryotes, Prochlorococcus, Synechococcus, diatoms, Phaeocystis-like and coccolithophores. Such work is currently already in progress within the Ecopelgol project. Alterations in phytoplankton might be related to zooplankton abundance or composition, either through bottom-up control or top-down control of one trophic compartment on the other (e.g. Ryther & Sanders 1980; Vanni 1987; Mallin & Paerl 1994). Thus, a phytoplankton change might have gone in parallel with a modification of zooplankton abundance and/or composition, in turn controlling the small pelagic populations. But despite these several possibilities that should still be looked into, this work is one great step towards the understanding of the small pelagic dynamics in the Gulf of Lions.

References


Annex

Publications

Published


Submitted


In preparation

Conference presentations

International Statistical Ecology Conference (ISEC, July 2014, Montpellier)

Bayesian mixture modeling to assess year-to-year fluctuations in age structure of Mediterranean anchovy and sardine

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Keywords: small pelagic fish, \textit{Engraulis encrasicolus}, \textit{Sardina pilchardus}, ageing, population dynamics

Abstract:

Since 2009, the Gulf of Lions has shifted to a different regime, characterised by both a lower anchovy (\textit{Engraulis encrasicolus}) and sardine (\textit{Sardina pilchardus}) biomass. To better understand these changes, we investigated the magnitude and the timing of variations in growth, body condition and size and age structure of anchovy and sardine since 1992, using scientific pelagic trawl data. To circumvent usual difficulties in the ageing procedure, mixture models have been applied to decompose size structures into a mixture of Gaussian curves representing age categories. We developed a Bayesian framework that combined the use of size distributions with independent priors, i.e. age-length keys from otolith readings. These finite mixture models were run using the R package 'Rstan' (Stan Development Team 2012). The model provided consistent results, despite the typical absence of multiple distinct peaks in the size structure. For anchovy and sardine a period with per age larger individuals and mostly higher proportions of oldest ages was detected around 2005-2007, in contrast to the most recent years that were characterized by the rarity of old/large fish. The distinguished periods are similar to our findings for growth, condition and size structure. In particular, we conclude that the disappearance of larger individuals since 2011 is due to the combination of both slower growth and the loss of the oldest fish. The analyses of the investigated biological parameters allowed us to obtain a deeper insight into the population structure and dynamics, as well as their current “state of health”.

References

Can an increasing tuna population in the western Mediterranean influence small pelagic abundance and size?

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Keywords: small pelagic fish, \textit{Engraulis encrasicolus}, \textit{Sardina pilchardus}, ageing, population dynamics

Abstract:

Over the last years, significant changes have been observed in the sardine, anchovy and sprat populations of the Gulf of Lions. Since 2007, the biomass of sardine and anchovy has decreased, whereas the commercially uninteresting sprat population showed a remarkable upsurge, resulting in important economic losses for fisheries. Also, the size distribution of all three species shifted simultaneously to smaller individuals. In contrast, tuna abundance tripled during these years because of a successful recovery plan. So could there be a top-down effect? Using energetic modelling (DEB model), trophic ecology (stomach analyses) and two population censuses (of tuna and the small pelagics) as pillars, the proportion and size classes of the small pelagic populations consumed by tuna were investigated. During 2011, 2012 and 2013, the most important prey in terms of abundance was mostly anchovy (between 39 and 75%), followed by sardine (between 12 and 39%). On the other hand, sardine constituted generally the largest part of biomass consumed (between 30 and 57%), except in 2011 when anchovy was more important (61%). Over all years, both species also occurred in over 85% of all stomachs analysed. However, no apparent evidence was found for the preference of certain prey size classes. We also calculated that tuna consumed around 2-20% of the anchovy, 1-3% of the sardine and 0-2% of the sprat population. In comparison, fisheries removed annually between 4 and 30% of the anchovy and between 1 and 42% of the sardine population during the last 20 years. Thus, the predation effect of tuna on the sardine and sprat population remained extremely low, whereas the anchovy population might during certain years and in combination with other factors to some extent be influenced by tuna.