Mediterranean Institute for Advanced Studies, IMEDEA (CSIC-UIB)

Department of Ecology and Marine Resources

Fish Ecology Group

Selection drivers of life-history traits in marine coastal fishes

PhD Thesis

A Thesis submitted for the degree of Doctor of Philosophy

Department of Biology

University of the Balearic Islands

By:

Josep Alós Crespí

Advisors:

Dr. Miquel Palmer Vidal & Dra. Beatriz Morales Nin

University Advisor:

Dr. Gabriel Moyà Niell

University of the Balearic Islands, April 2013

[Blank page]

[… There has been surprisingly little consideration of human-induced selection in the wild until recently. Even more surprising perhaps is the absence of any detailed consideration of this effect by Darwin because he had such a passion for hunting as a young man …]

Fred W. Allendorf, 2009

Selection drivers of life-history traits in marine coastal fishes is a PhD thesis submitted for the degree of Doctor of Philosophy by Josep Alós Crespí

Josep Alós Crespí
(PhD Candidate)

I certify that I have read this dissertation and that, in my opinion, it is fully adequate in scope and quality as a dissertation for the degree of Doctor of Philosophy

---

Dr. Miquel Palmer Vidal
(Principal Advisor)

I certify that I have read this dissertation and that, in my opinion, it is fully adequate in scope and quality as a dissertation for the degree of Doctor of Philosophy

---

Dra. Beatriz Morales Nin
(Co-Advisor)

I certify that I have read this dissertation and that, in my opinion, it is fully adequate in scope and quality as a dissertation for the degree of Doctor of Philosophy

---

Dr. Gabriel Moyà Niell
(University Advisor)

Approved for the University Committee on graduate studies

Abstract

Humans have non-randomly harvested animals since the origin of our species, resulting in both ecological and evolutionary changes of wild populations. Considering this fact, this Thesis tested the hypothesis that recreational fishing is a non-random selection process for some life-history traits of costal sedentary fishes. This Thesis provides both empirical and theoretical evidence demonstrating how the variability existing in wild populations could be the outcome of fishing-induced selection in marine coastal fisheries.

Selection operates at the individual level. Therefore, the existence of inter-individual variability is a necessary condition. As a first step, two life-history traits were selected that may be a priori good candidates for being fishery-selected: growth and reproduction. The wild variability in these traits of *Serranus scriba* were estimated using novel methodological and theoretical approaches based on the use of calcareous structures of fishes (otoliths), robust statistical tools and histological microscopy techniques.

This Thesis demonstrates how recreational fishing can cause local depletion and is size-selective per se. Fishing mortality is not necessarily linked to harvesting because some individuals may be released after being fished for voluntary (catch-and-release) or

mandatory (minimum legal size) reasons. The potential survival rate of individuals released by anglers was estimated for the first time in a Mediterranean marine coastal fish, with special emphasis on *Serranus scriba*. Post-release mortality rates are generally low but can be critical depending on the species' environmental context and fishing gear. This Thesis also provides management options for sustainable exploitation by offering tools to decrease the post-mortality levels.

The major achievement of this Thesis is the empirical demonstration of a fishing-induced selection process against individuals with larger growth ability after maturation and lower reproductive investment, in accordance with life-history theory. The theoretical and empirical expectations of this selection have been studied in wild populations subjected to different exploitation pressures and different levels of population connectivity and gene flow. Individuals from highly exploited populations are smaller, have lower growth rates after maturation and invest more energy in reproduction than fish from no-take marine protected areas, where natural selection drives these life-history traits in the opposite direction. Elsewhere, it has been demonstrated that most of those life-history traits are heritable and that consistent fishing-induced selection over time can induce evolution. The plausibility of this fact is discussed under the perspective of yield sustainability for the first time in the Mediterranean.

This Thesis concludes by hypothesising on the outcomes of fishing-induced selection from a behavioural perspective. A simulation analysis based on a spatially explicit individual-based model in which fish and fishers move within an empirically supported scenario was performed. The results show a consistent selection toward individuals that

show less exploratory behaviour. It is suggested that fishing-induced selection is most likely related to a wide range of potentially correlated traits, including life history, behavioural and physiological traits, thus exposing a wide range of fascinating hypotheses to be tested in further research.

Overall, this Thesis establishes the basis of the fisheries-induced selection in marine coastal fishes in the Mediterranean and discusses its implications for a proper resources management, aimed to enhance sustainable fisheries and therefore mitigate the plausible negative ecological and evolutionary effects of fishing.

Resumen

Los humanos hemos recolectado animales de manera no estocástica (azar) desde el origen de nuestra especie causando diferentes efectos ecológicos y evolutivos en las poblaciones salvajes. Teniendo en cuenta este hecho, esta Tesis testa la hipótesis de que la pesca recreativa no es un proceso de azar para algunos rasgos de la historia vital de los peces. Esta Tesis proporciona evidencias, tanto empíricas como teóricas, que demuestran que la variabilidad existente en estos rasgos de las poblaciones salvajes puede ser fuente de selección por pesca en pesquerías marinas costeras.

Los procesos de selección operan a nivel individual. Por lo tanto, es una condición necesaria la existencia de variabilidad individual dentro de las poblaciones. Como primer paso, se seleccionaron un número de rasgos de historia vital candidatos para ser fuente de selección: crecimiento y reproducción. La variabilidad salvaje de estos rasgos se determinó utilizando novedosas aproximaciones basadas en el uso de estructuras calcáreas (otolitos), herramientas estadísticas robustas y técnicas de histología microscópica en *Serranus scriba*.

Esta Tesis demuestra como la pesca recreativa puede generar una disminución en la biomasa además de ser talla-selectiva. La mortalidad por pesca no tiene porque estar necesariamente ligada a recolección debido a que los peces pueden ser voluntariamente

(captura y suelta deportiva) o obligatoriamente (tallas mínimas legales) devueltos al agua una vez pescados. La tasa potencial de supervivencia de individuos retornados al medio se ha estimado por primera vez en peces marinos costeros que habitan el Mediterráneo, con un especial énfasis en *S. scriba*. Las tasas de mortalidad son en general bajas, pero pueden llegar a ser críticas dependiendo del contexto ambiental y el arte de pesca. Esta Tesis también proporciona recomendaciones para la explotación sostenible a través de herramientas para maximizar las tasas de supervivencia.

El mayor logro de esta Tesis es la demostración empírica de un proceso de selección por la pesca que actúa en contra de fenotipos con mayor capacidad de crecer después de l maduración sexual y una menor inversión en reproducción que sigue las reglas generales de la teoría clásica de historia vital. La teórica y empírica respuesta de esta selección ha sido estudiada en diferentes poblaciones salvajes expuestas a diferentes niveles de explotación y conectividad genética entre poblaciones. Los individuos que habitan poblaciones altamente explotadas son de menor talla, tienen una limitada capacidad de crecer y tiene una mayor inversión en reproducción que los individuos que habitan reservas marinas totales, donde la selección natural juega el papel opuesto. Existen evidencies claras que los rasgos de historia vital estudiados tienen un alto componente heredable que expuesto a un selección constante puede desencadenar un proceso evolutivo. La posibilidad de este hecho se discute en el marco de la explotación sostenible de los recursos pesqueros.

La presente Tesis termina considerando una perspectiva de la selección inducida por pesca en peces marinos costeros mas relacionada con el comportamiento. Se ha realizado un ejercicio de simulación usando un modelo basado en el individuo espacialmente

explicito donde peces y pescadores se movían siguiendo diferentes pautas de comportamiento con base empírica. Los resultados mostraron una consistente selección a favor de fenotipos con un grado de exploración y de actividad menor. Esto sugiere que el proceso de selección por pesca esta probablemente causada por un rango de rasgos potencialmente correlacionados que incluyen rasgos de historia vital, comportamiento y fisiología generando multitud de hipótesis para ser testadas en investigaciones futuras.

En resumen, esta Tesis establece las bases de los procesos de selección por pesca en peces marinos costeros del Mediterráneo, y discute sus implicaciones para una correcta gestión para potenciar la pesca sostenible y mitigar así los posibles efectos negativos de base ecológica y evolutiva causados por la pesca.

Acknowledgements – Agradecimientos - Agraïments

Although my name is printed on the cover of this Thesis, the singular form of the first person does not appear within its chapters. I do this to be grateful to my advisors and collaborators, and to the support of my family, colleagues and friends.

Miquel i Beatriu (IMEDEA), Gràcies per donar-me la oportunitat de realitzar aquesta Tesis Doctoral amb vosaltres. Puc afirmar que he estat molt afortunat de treballar i aprendre al vostre costat. La vostre supervisió, tant personal com humana, la vostre confiança, i els vostres consells, han donat a la meva jove carrera investigadora una excel·lent oportunitat per millorar la meva iniciativa, el meu pensament independent, les meves qualitats de recerca i humanes y el treball en un grup. He gaudit molt amb vosaltres i sempre estaré agraït per el suport incondicional que he rebut per la vostre part. Esper que el futur ens depari multitud de bons moments, tant científics com personals, com els que hem viscut durant aquest quatre anys.

Ignasi, Miquel, David, Carlos, Itzi, Sílvia, i tot el personal del IMEDEA. Sense la vostre ajuda, ànims i suport, aquesta Tesis no hagues estat possible. Moltes gràcies per les sortides de camp, les *brain-storming* sessions, les ajudes amb els mostreigs, així com el vostre temps explicant-me tècniques pròpies de la vostre línia d'investigació. Ignasi, per tu gràcies especials per la multitud de *coffee-breaks* fets, quantes idees bones han sortit d'aquests moment. Gràcies també per introduir-me en el mon dels primers estadis de desenvolupament vital del peixos, és un món apassionant. A tots, gràcies i desitjo poder desfruitar de moltes més ensaïmades amb tots vosaltres els divendres a mig dia. Gotzon i Toni (IMEDEA) gràcies per la vostre ajuda en la pare de conectivitat i donar un caire de multi-disciplinitat a la meva Tesis.

Biel (UIB), Salud (IEO) i Toni (UIB), moltes gràcies per introduir-me en el món de la recerca quan només era un estudiant de Biologia a la UIB. Biel, gràcies especials per ser el Ponent de la Univeristat d'aquesta Tesis. Part del meu instint de recerca és gràcies a vosaltres i a tots els que varem compartir aquella època al laboratori de Biologia Marina. A tota la gent que m'ha ajudat i ha recolzat aquesta Tesis de la Direcció General de Pesca (Govern Balear), moltes gràcies. Toni, Xisco, Amàlia, Elena, M. del Mar, Juanita, Imma, gràcies per la vostre ajuda i el vostre suport en algun moment durant el transcurs d'aquesta Tesis. Pedro i Irine de la Reserva Marina de Palma, moltes gràcies per la vostre col·laboració, podeu estar orgullosos de la feina que esteu fent a la reserva.

No puc oblidar la multitud de pescadors recreatius anònims, coneguts, amics i familiars que han col·laborat en el marc d'aquest estudi. Moltes gràcies a tots i cada un de vosaltres. Una bona part del treball es per vosaltres, perquè pugem seguir gaudint la nostre activitat d'oci durant molts d'anys.

A mis amigos y colegas del IIM, Fran, Alex, Gonzalo y David, sois un equipo increíble, tanto como investigadores como personas. Gracias por los ánimos y por la multitud de comentarios positivos hechos en este trabajo. Una parte de este trabajo es vuestra también, y recordad, nosotros somos jóvenes, hay que luchar por el futuro.

To my international collaborators, thanks a lot. Robert (IGB), viel von dieser Arbeit ist auch deins, Danke. Thomas (IGB), vielen Dank für deine Kommentare und deine Hilfe während meines Aufenthaltes in Berlin, Danke für all die erstaunlichen Tage Fischen. Sue, Luiz, Gabe and Elena (FWC), thanks for your hospitality and your help. Joel and Sara (FWC), thanks, it was awesome enjoy with you a redfish sampling season. Especial thanks for the fishing trips Joel, the fishing weekend down to the Florida Keys was awesome and I will never forget it.

Finalment, Àngela, tu has esta la meva inspiració. Quan he estat disgustat, cansat o desmoralitzat, tu sempre m'has donat ànims per seguir. Necessitaria més d'una Tesis per enumerar totes les vegades que m'has ajudat amb paraules positives i d'ànims. Gràcies per tot, realment soc molt afortunat de tenir-te devora. Jimmy, gràcies per aquesta portada, i gràcies per tots els sopars i bon moment s amb la teva dona, la teva filla i na petita, podem dir que una part d'aquesta Tesis és també per sa paina. Marta i Tomàs, aquest treball també està dedicat a vosaltres.

Mamà, tu ets la més important, tot aquest treball és per i gràcies a tu. Tu vares ser la persona que ens vares encoratjar i espitjar a estudiar a jo i al meus germans quan érem uns nins, inclús en situacions molt complicades. No hi va haver excuses per donar-nos tot el teu esforç i temps, sacrificant-te tu mateixa com a conseqüència. Aquí estan els resultats del teu esforç. Mamà, ara seré Doctor en Ecologia Marina fent i desfruitant del que mes m'agrada, na Marta és una eminent Advocada i en Tomàs és un reconegut cuiner. Tot el teu esforç ha estat recompensat, i sempre estarem agraïts. No te podem tornar el teu temps, però si que podem fer-te protagonista dels nostre èxits, per que realment són teus també. Mamà, aquest treball està dedicat a Tu.

List of manuscripts published

Alós, J., Palmer, M., Balle, S., Grau, A. M., and Morales-Nin, B. 2010. Individual growth pattern and variability in *Serranus scriba*: a Bayesian analysis. ICES Journal of Marine Science, 67: 502-512. (Chapter 2)

Alonso-Fernández, A., Alós, J., Grau, A., Dominguez-Petit, R., and Saborido-Rey, F. 2011. The Use of Histological Techniques to Study the Reproductive Biology of the Hermaphroditic Mediterranean Fishes *Coris julis*, *Serranus scriba*, and *Diplodus annularis*. Marine and Coastal Fisheries, 3: 145-159. (Chapter 3)

Alós, J., Alonso-Fernández, A., Catalàn, I., Palmer, M., and Lowerre-Barbieri, S. (in press). Individual variability in the factors that affect reproductive potential in *Serranus scriba*. Scientia Marina. (Chapter 3)

Alós, J., and Arlinghaus, R. 2013. Impacts of partial marine protected areas on coastal fish communities exploited by recreational angling. Fisheries Research, 137: 88-96. (Chapter 4)

Alós, J. 2008. Influence of anatomical hooking depth, capture depth, and venting on mortality of painted comber (*Serranus scriba*) released by recreational anglers. ICES Journal of Marine Science, 65: 1620-1625. (Chapter 5)

Alós, J., Palmer, M., Grau, A. M., and Deudero, S. 2008. Effects of hook size and barbless hooks on hooking injury, catch per unit effort, and fish size in a mixed-species recreational fishery in the western Mediterranean Sea. ICES Journal of Marine Science, 65: 899-905. (Chapter 6)

Alós, J., Arlinghaus, R., Palmer, M., March, D., and Alvarez, I. 2009. The influence of type of natural bait on fish catches and hooking location in a mixed-species marine recreational fishery, with implications for management. Fisheries Research, 97: 270-277. (Chapter 7)

Alós, J., Arlinghaus, R., Palmer, M., Catalan, I., Basterretxea, G., Jordi, A., Alonso-Fernández, A., et al. (submitted). Recreational harvesting can induce

evolutionary change of life-histories of an exploited marine fish at surprisingly restricted geographical scales. Evolutionary Applications. (Chapter 8)

Alós, J., Palmer, M., and Arlinghaus, R. 2012. Consistent Selection towards Low Activity Phenotypes When Catchability Depends on Encounters among Human Predators and Fish. Plos One, 7: e48030. (Chapter 9)

List of tables

List of figures

Contents

Chapter 1 Human harvesting and fisheries-induced selection of wild fish populations

1.1 Introduction

Humans have harvested fish from the wild since the origin of our species (Allendorf and Hard, 2009; Stenseth and Dunlop, 2009). Today, marine ecosystems are experiencing an accelerated loss of populations, and the current and future trends for global fisheries remain controversial (Worm *et al.*, 2006). Up to 63% of the assessed fish stocks worldwide are overexploited and require rebuilding through reducing exploitation rates (Worm *et al.*, 2009). However, the solution for restoring fisheries is neither easy nor non-controversial (Pauly *et al.*, 2003). In all cases, preventing overexploitation usually demands sophisticated management systems (Worm *et al.*, 2009) and eco-evolutionary approaches (Palkovacs, 2011).

Overexploitation may imply not only fishing-mortality rates exceeding the maximum sustainable yield (Worm *et al.*, 2006) but also unbalanced harvesting (Jørgensen *et al.*, 2007). The latter process can constrain the potential recovery rates of exploited populations (Garcia *et al.*, 2012). Unbalanced harvesting means that fishing is almost never random (Heino and Godo, 2002). Individuals of, for example, a certain size, sex

or behaviour are more likely to be removed from the population (Jørgensen *et al.*, 2007). This biased removal may result in genetic change if the expression of the selected phenotype has some genetic basis (Allendorf *et al.*, 2008). Therefore, detecting and managing fishing-induced selection is a key issue for preventing potential negative effects and ensuring sustainability (Kuparinen and Merilä, 2007).

The basis of natural or fishing-induced selection is the same: there must be some inter-individual variability in specific phenotypic traits (Grimm and Railsback, 2005), and such a phenotypic variability must be, at least in part, heritable (Allendorf *et al.*, 2008). Under these circumstances, trait-selective fishing mortality will produce a selection differential (i.e., fish displaying some specific life-history traits will be more prone to be fished), which in turn may result in fisheries-induced evolution of a wide range of heritable traits (Law, 2000).

However, despite the relevance of this topic due to the potential risk for fishing sustainability, only a few studies have directly analysed the existence and consequences of the selection differentials exerted by fishing on different life-history traits (Enberg *et al.*, 2009). The results of those studies support the hypothesis that fishing-induced selection favours individuals with smaller body size (Jørgensen *et al.*, 2009). It is even plausible that fishing-induced evolution could cause a more complex pattern favouring smaller fish with reduced growth rates and increased reproductive investment that mature sexually at a younger age and smaller size (Hutchings, 1993; Matsumura *et al.*, 2011; Rijnsdorp, 1993). While such traits may provide a benefit to individuals and reduce their exposure to fishing gear, they may penalise fitness at the (wild) population level in a process called maladaptive evolution (Olsen and Moland, 2011). Fishing-

induced and natural selection interplay in this scenario, and such interplay will ultimately determine the evolutionary trajectory of a population in response to fishing pressure (Edeline *et al.*, 2007; Matsumura *et al.*, 2011).

Any fishing gear is size-selective *per se* (Heino and Godo, 2002). In consequence, it is commonly accepted that fishing should favour the survival of individuals exhibiting lower growth rates and smaller adult size (Conover and Munch, 2002). Indeed, some studies conducted in a commercial marine fishing context have revealed negative selection differentials on size-at-age in diverse species such as Atlantic cod, *Gadus morhua* (Pérez-Rodríguez *et al.*, 2009; Sinclair *et al.*, 2002; Swain *et al.*, 2007), and plaice, *Pleuronectes platessa* (Rijnsdorp, 1993). Similarly, a classic laboratory experiment in *Menidia menidia* revealed that size-selective mortality may favour slow-growing fish (Conover and Munch, 2002). However, most of the studies of fishing-related selection differentials have been conducted in a commercial fishing context where size-selectivity is well documented (Law, 2000).

In contrast, (Uusi-Heikkilä *et al.*, 2008) argued that vulnerability to fishing may be more complex: fishing-related selection might operate on a wide range of traits, either positively or negatively and co-varying with vulnerability to fishing. This relation could be the case of recreational fisheries, where in addition to the existence of a bias for harvesting the larger individuals (Lewin *et al.*, 2006), fish must actively interact with the fishing gears (Uusi-Heikkilä *et al.*, 2008). Given this fact, it should be expected that the fish vulnerable to fishing would be those with not only faster growth but also bolder behaviour (Uusi-Heikkilä *et al.*, 2008). However, the links among life history,

physiological and behavioural traits can generate unexpected selection patterns, and the direction of the selection differentials is an open (and hot) topic (Cooke *et al.*, 2007).

Literature about this topic is still scarce and does not show a clear pattern of the direction of fishing-induced selection on life-history traits. On the one hand, authors such as (Saura *et al.*, 2010) reported a decline in body length and weight per generation (a decrease in the growth rate) because of recreational fishing pressure in the Atlantic salmon, *Salmo salar*. On the other hand, a line of fish more vulnerable to fishing exhibited a lower growth rate after only three generations of artificial selection for either high or low vulnerability in largemouth bass, *Micropterus salmoides* (Redpath *et al.*, 2009). The theoretical framework justifying such a pattern is that vulnerable fish seem to display a more accelerated metabolic rate, the energetic cost of which is compensated by greater energy intake through an increased feeding rate (Redpath *et al.*, 2009; Redpath *et al.*, 2010). Thus, the results reported for recreational fishing are contradictory and cast doubt on the a priori expectation that more-vulnerable fish should necessarily encompass the faster-growing individuals within a population.

Indeed, (Matsumura *et al.*, 2011) showed that selection differentials on the growth rate of a recreationally exploited population of pike (*Esox lucius*) might either be positive or negative depending on the management strategy adopted. The adult body size was predicted to either decline or increase in response to recreational fishing mortality depending on which size classes of fish experienced the highest mortality. In the absence of management regulations, the model proposed by (Matsumura *et al.*, 2011) predicts selection against individuals with faster growth rates. At the same time, fish with a larger size of maturation and smaller reproductive investment were selected by

fishing. The fishing outcomes may be the result of a multi-trait correlation (Mollet *et al.*, 2010), including a trade-off between growth and reproduction (Roff, 1992), that determines a specific life-history strategy that maximises individual fitness.

Therefore, there is a need for more detailed studies to better understand whether recreational fishing constitutes a non-random selection process with respect to key life-history traits (Audzijonyte *et al.*, 2013). In the case of non-random fisheries, the putative fishing-induced selective drivers should be qualified and quantified, and their potential ecological and evolutionary effects should be evaluated (Kuparinen and Merilä, 2007). Then, balanced fishing that distributes mortality across the widest possible range of the selected traits should be incorporated into conventional management plans to mitigate the undesirable consequences of fisheries-induced evolution (Garcia *et al.*, 2012). This lack of information especially in marine costal species is the strategic objective of this Thesis.

1.2 Objectives of the Thesis

The main objective of this PhD Thesis was to analyse the plausibility and consequences of fishing-induced selection on hereditable life histry traits related to recreational fishing in the Mediterranean. A marine coastal species, *Serranus scriba* (Linnaeus, 1758), was selected as a case study because this species is highly exploited by the recreational fishery in the Mediterranean. As in many cases, the variability of the life-history traits of the wild populations of this species with low interest for commercial fisheries is poorly known. Thus, the first sub-objective was to accurately describe the variability in the species' growth and reproductive potential. The second sub-objective was to explore the

different sources of recreational fishing mortality of *S. scriba*. The study of fishing effects was extended to estimate sources of fishing mortality, such as post-release mortality, and to provide management tools to mitigate the negative effects of fishing. The third sub-objective was to test the hypothesis that fishing can be selective for some specific life-history traits independently of fish size and to identify how different wild populations respond to these selective forces when gene low is limited. The fourth sub-objective was to test the hypothesis that behaviour could be a fishing-induced selection driver as well. Finally, the implications of the results for better management (i.e., aimed at enhancing sustainable fisheries and avoiding plausible maladaptive effects of fishing) are discussed.

1.3 Structure of the Thesis (chapter-by-chapter)

This PhD thesis is structured in 10 chapters. The contents and structure of the chapters *one-by-one* are detailed below for clarity.

Chapter 1 introduces the *state of the art*, including an outline of the topic, a general description of the problem and its magnitude, and a review of the most important references. This chapter also lists the main objectives and the hypothesis of this PhD Thesis

Chapter 2 provides an accurate description of the individual growth of *S. scriba* in a wild population using a novel theoretical approach.

First *Chapter 3* provides a description of the reproduction biology of *S. scriba* using microscopy histological techniques. Second, it shows the variability and the main factors affecting the individual reproductive potential in wild populations of *S. scriba*.

Chapter 4 review the literature and provide evidences that recreational fishing is a source of mortality on the *Posidonia oceanica* fish community with, especial emphasize on *S. scriba*. This chapter also shows possible benefits of management trough partial Marine Protected Areas.

Chapter 5 explores alternative sources of fishing mortality induced by the mandatory (minimum legal size) or voluntary release of *S. scriba* made by recreational anglers. This chapter identifies the most important post-release mortality factors that affect survival of *S. scriba*.

Following the results obtained in *Chapter 5*, the *Chapters 6* and *7* suggest science-based management tools to reduce the fishing mortality induced by mandatory or voluntary release.

Chapter 8 demonstrates how recreational fishing selects for certain phenotypes in terms of life history traits independently of fish size. Also, this chapter demonstrated how the matching population's genetic connectivity and the selective forces, the optimal life history strategy of harvested populations of *S. scriba* can be explained.

Chapter 9 shows the results of a simulation analysis sugesting how behaviour may be modulated by fisheries-induced selection. Most coastal fish seems to move according to home range behaviour and empirical data on between-fish variability of such behaviour was used to test if fishing can be selective for some movement charcateristic. Results were clear and the life history/behavioural relationship emerge as an excellent opportunity for further research.

Finally, *Chapter 10* provides the general conclusions of this PhD Thesis.

The references cited throughout this PhD Thesis are included at the end followed by the appendixes including additional information.

Chapter 2 Describing between-individual variability I: Individual growth pattern and variability in *Serranus scriba*

Alós, J., Palmer, M., Balle, S., Grau, A. M., and Morales-Nin, B. 2010. Individual growth pattern and variability in *Serranus scriba*: a Bayesian analysis. ICES Journal of Marine Science, 67: 502-512.

Chapter 3 Describing between-individual variability II:

Reproductive biology of *Serranus scriba* and variability of

reproductive potential

Alonso-Fernández, A., Alós, J., Grau, A., Dominguez-Petit, R., and Saborido-Rey, F. 2011. The Use of Histological Techniques to Study the Reproductive Biology of the Hermaphroditic Mediterranean Fishes *Coris julis*, *Serranus scriba*, and *Diplodus annularis*. Marine and Coastal Fisheries, 3: 145-159.

Alós, J., Alonso-Fernández, A., Catalàn, I., Palmer, M., and Lowerre-Barbieri, S. (in press). Individual variability in the factors that affect reproductive potential in *Serranus scriba*. Scientia Marina.

Chapter 4 Evidence of fishing mortality in small-bodied coastal fish: basis for further analysis of the benefits of partial Marine Protected Areas

Alós, J., and Arlinghaus, R. 2013. Impacts of partial marine protected areas on coastal fish communities exploited by recreational angling. Fisheries Research, 137: 88-96.

Chapter 5 Post-mortality levels of voluntary and/or mandatory *Serranus scriba* released by recreational anglers: influence of hooking injury, capture depth and venting

Alós, J. 2008. Influence of anatomical hooking depth, capture depth, and venting on mortality of painted comber (*Serranus scriba*) released by recreational anglers. ICES Journal of Marine Science, 65: 1620-1625.

Chapter 6 Effects of hook size and barbless hooks on hooking injury, catch per unit effort, and fish size in a mixed-species recreational fishery in the western Mediterranean Sea

Alós, J., Palmer, M., Grau, A. M., and Deudero, S. 2008. Effects of hook size and barbless hooks on hooking injury, catch per unit effort, and fish size in a mixed-species recreational fishery in the western Mediterranean Sea. ICES Journal of Marine Science, 65: 899-905.

Chapter 7 The influence of type of natural bait on fish catches and hooking location in a mixed-species marine recreational fishery, with implications for management

Alós, J., Arlinghaus, R., Palmer, M., March, D., and Alvarez, I. 2009. The influence of type of natural bait on fish catches and hooking location in a mixed-species marine recreational fishery, with implications for management. Fisheries Research, 97: 270-277.

Chapter 8 Recreational harvesting can induce evolutionary change of life-histories of an exploited marine fish at surprisingly restricted geographical scales

Recreational harvesting was sometimes considered neither persistent nor efficient enough to be of concern for management. In particular in marine environments the impacts of recreational anglers were usually considered negligible. However, consistent selection acting on certain phenotypes should lead to adaptation of life-history strategies whenever gene flow is low. Following this argument one would expect characteristic adaptations of exploited life-histories to recreational fishing pressure in coastal fish as long as population connectivity is low and evolutionary change conceivable to materialize. Here we provide compelling evidence of recreational fishing can induce evolution of fast-life-histories in a small coastal fish as surprisingly small geographical scales. We first show that recreational fishing indeed preferentially captures fish with low reproductive investment and large adult size. Secondly, using oceanographic particle motion models we identify subpopulations of *Serranus scriba* that were reproductively isolated. We finally found fish life histories in exploited sites to be substantially different from unexploited sites. Individuals characterized by high reproductive investment and

small adult size were much more prevalent in exploited compared to unexploited sites suggesting evolutionary adaptations to recreational harvesting that was unlikely be caused by site-specific environmental factors. We propose that recreational harvesting changes life histories also in open marine systems at small geographic scales. A possible meta-population structure is therefore important to consider when managing coastal fisheries, even for small bodied, geographically restricted fish that are a targeted by anglers mainly.

Keywords: Bayesian approach, bi-phasic growth model, life-history traits, fisheries-induced evolution, meta-population structure, recreational fishing, sustainable yield

8.1 Introduction

When fishing exploits a naturally reproducing fish stock, exploitation is almost never random. Indeed humans selectively target certain species (e.g., top predators) and specific phenotypic traits and underlying genotypes within species (e.g., larger sized fish) (Law, 2000; Jørgensen *et al.*, 2007; Allendorf and Hard, 2009; Laugen *et al.*, 2012). Elevated and/or non-random harvesting can generate selection on certain traits and result in fisheries-induced adaptive changes of maturation or growth, which may be of relevance to management (Jørgensen *et al.*, 2007). Whether adaptive changes in life-histories are evolutionary (i.e., adaptive genetic) or merely phenotypically plastic is controversially debated for many stocks (Browman *et al.*, 2008; Jørgensen *et al.*, 2008). Available literature nevertheless supports the hypothesis that fisheries-induced evolution

(FIE) should select for "fast life-histories" characterized by small size and age at maturation and high reproductive investment, which should collectively reduce adult body size (Jørgensen *et al.*, 2007; Law, 2000) and elevate adult natural mortality (Jørgensen and Fiksen, 2009; Jørgensen and Holt, 2013).

The potential for FIE happens has been mainly discussed in the context of commercial fisheries where positive size-selection is well documented (Law, 2000; Sharpe and Hendry, 2009). More complex exploitation patterns with respect to traits selective by fishing are conceivable for passive fishing gears such as trapping or recreational angling (Uusi-Heikkilä *et al.*, 2008). In fact, in many recreational harvesting situations, selection on behavioural or physiological traits should be prevalent in addition to directly or indirectly correlated life-history traits (Alós *et al.*, 2012; Cooke *et al.*, 2009; Cooke *et al.*, 2007; Redpath *et al.*, 2009; Redpath *et al.*, 2010; Wilson *et al.*, 2011; Sutter *et al.*, in press). The resulting complexity of selection pressures on a range of traits suggests that selection differentials are not necessarily to be expected to have the expected sign. For example, it has often been found intuitive to think of selection on body size in fishing context (Conover and Munch, 2002). Indeed, in recreationally exploited Atlantic salmon and Chinook salmon, negative selection differentials on body size were reported (Saura *et al.*, 2010; Kendall and Quinn, 2011). By contrast, (Redpath *et al.*, 2009) found that largemouth bass selectively captured by anglers were smaller than those surviving exploitation, likely because food limitation met with a correlation between metabolism and vulnerability to fishing. Therefore, the evolutionary impact of recreational harvesting on life-history cannot be easily foreseen and more stock-specific analyses that represent local fishing conditions and patterns are needed. To our

knowledge, no study on recreationally exploited fish stocks exists that has attempted to sort this question out in marine environments.

To support the hypothesis of FIE two not mutually exclusive conditions have to be met. First, any phenotypic changes has to be due to fisheries, and second, at least part of the phenotypic change has to have a genetic basis (Kuparinen and Merilä, 2007). A range of approaches have been put forward to study FIE in these two dimensions. First, theoretical modelling of FIE (e.g., (Dunlop *et al.*, 2009; Matsumura *et al.*, 2011) has shown that fishing exploitation can be strong enough to cause selection differentials and fisheries-induced adaptive change to be plausible. Naturally, inference of models to the wild are limited, and models will also never conclusively answer whether evolution has truly happened in nature (Audzijonyte *et al.*, 2013). Second, many observational studies using time series of phenotypic data from the wild have been conducted to study evidence for FIE (e.g., (Rijnsdorp, 1993; Swain *et al.*, 2007). The main issue of this approach is to disentangle genetic from plastic change in life-histories and sophisticated statistical approaches to control for some of the most important environmentally-induced plastic responses on phenotypes have been developed (e.g., the popular probabilistic maturation reaction norm approach, (Heino and Dieckmann, 2008). Clearly, observational studies cannot discount conclusively the potential for non-fishing factors to affect phenotypic change (Audzijonyte *et al.*, 2013), and usually such studies also lack the molecular tools needed to study genetic changes caused by fishing. There are, however, some few observational studies that have used molecular techniques to study historical samples from exploited stocks, which suggest genetic change has taken

place (Ãrnason *et al.*, 2009; Jakobsdóttir *et al.*, 2011; Pukk *et al.*, 2013). The third and final popular approach to the study of FIE has been experimental in the laboratory or in experimental facilities such as ponds (e.g.,(Conover and Munch, 2002; Philipp *et al.*, 2009). The strength of these studies is that they can provide cause-and-effect evidence and that phenotypic change has a genetic basis (e.g., through common-garden experiments) (Conover and Baumann, 2009), but the inference to wild conditions is highly difficult.

A final approach that joins many of the benefits outlined in the three approaches above is a comparative field approach that studies phenotypes of fish striving in similar environmental conditions but differ by historical exposure to harvesting pressure (e.g., (Bevacqua *et al.*, 2012; Drake *et al.*, 1997). Whenever there is no contemporary natural gene flow among sub-populations, differential fishing slection should generate sub-populations that adapt their life-histories to the local selective pressures (Hutchings, 1993; Reznick *et al.*, 1990). Some comparative field approaches has some history in freshwater systems, where spatial segregation and limited natural gene flow (Haugen and Vøllestad, 2001; Drake *et al.*, 1997). However, meta-populations with historically connected fish species are increasingly identified in the open ocean and marine systems (Mora and Sale, 2002), which constitutes a good opportunity to study evolutionary consequences of fisheries in wild fish stocks. In fact, although marine coastal environment has been traditionally assumed that are open and operate as genetically open systems (Roberts, 1997), recent development matching genetics and oceanography suggests that marine fish populations are not as open as expected (Palumbi and Warner, 2003) even at spatial-scales of a few km (e.g., (Carreras-Carbonell *et al.*, 2007; Jones *et*

al., 2005; Taylor and Hellberg, 2003). Small-scale meta-populations in the marine environment would render a field approach useful to provide evidence of FIE change in the wild (Pukk *et al.*, 2013). The Mediterranean Sea offers a suitable model system for population's connectivity because oceanic fronts and local hydrodynamic conditions can generate patterns of isolation within sub-populations in many coastal species (Schunter *et al.*, 2011). Physical processes can induce an increase of local self-recruitment and increase the vulnerability of local populations to human impacts such as fishing (Galarza *et al.*, 2009). Therefore, the local depletion of adult individuals due to fishing activity could therefore change the genetic architecture of the sub-population due to contemporarily restricted gene flow from nearby areas (Roberts, 1997).

Capitalizing on this idea, in this Chapter we adopted a multidisciplinary approach linking an individual, function-based estimation approach to infer life-history traits (annual reproduction investment, theoretical maximum size, age of maturation and immature growth rate) and high resolution hydrodynamic modelling to test if between-population differences in life-history traits can be adequately explained by variation in fishing and population connectivity. Our study is based on a comprehensive analysis of life-history traits in nearby areas at small geographical scales subjected to varying historic fishing pressure (from intense harvesting to no-take) combined with the results from a high resolution numerical model that allowed estimating the connectivity of the studied fish populations. Our hypotheses was that historic recreational fishing pressure has led to life-history adaptations towards "fast life histories" in a small marine fish with limited gene flow among spatially close coastal areas.

8.2 Material Methods

To generate compelling evidence for fisheries to be the most parsimonies explanation for phenotypic change in an open marine environment, at least three lines of evidence have to be accumulated: *i*) one needs to show that the particular gear under investigation induces selection differentials on heritable traits (e.g., body size or maturation), *ii*) one has to provide evidence of restricted gene flow among local populations and *iii*) one has to test the predicted changes in phenotypes among stocks experiencing differential fishing pressures and exclude non-fishing related factors as drivers of change as far as possible. We have compiled all three lines of evidence using a small-bodied coastal fish exploited by recreational fisheries as a model species.

8.2.1 Species case-study

Serranus scriba (Figure 8.1), is a small-sized Serranid that inhabits shallow seagrass meadows (*Posidonia oceanica* and *Cymodocea nodosa*). Its reproductive behaviour is characterized by simultaneous hermaphroditism with relative short-life-span whcih achieves sexual maturity during its first or second year (Alonso-Fernández *et al.*, 2011). It is characterized by daily-batch egg releases (with peak spawning season in May and June in the Mediterranean), indeterminate fecundity and asynchronous oocyte maturation development (Chapter 3 of this PhD Thesis). *S. scriba* is of no importance to commercial fisheries, but the species is highly appreciated by recreational anglers. In fact, the species is among the most intensively harvested (both in terms of numerical abundance and biomass yield) by the small-scale recreational boat anglers in the NW Mediterranean (Morales-Nin *et al.*, 2005).

8.2.2 Harvesting selection experiment

The first question to be answered was whether recreational angling is selective for life-history traits such as annual reproduction investment, theoretical maximum size, age of maturation and immature growth rate. Our empirical approach was based in exploring the potential direction of selection by comparing the life-history of individuals sampled using an experimental active method (random sample of the population using experimental beam trawl) and the dominant fishing gear used in the area (passively fished hook-and-line fishing) similar to those performed by (Wilson *et al.*, 2011) to explore selection of fish personality. We selected an experimental area of 1.1 km² (average of the movement area used by *S. scriba*, (March *et al.*, 2010)) located at the south of Mallorca Island (Figure 8.1). During May (peak of the spawning season), individuals of *S. scriba* from this population were sampled using either the experimental beam trawl (active method) or hook-and-line (passive method) at the identical within-day (mid-day) and spatial-scale.

We conducted three different fishing hauls using the experimental beam trawl (see details of the method in (Deudero *et al.*, 2008) to obtain a large enough sample (n = 50). We also conducted a number of experimental angling sessions done at the experimental area to obtain a hook-and-line sample (n = 165). The experimental angling sessions were done following protocols described in Chapter 7 of this PhD Thesis. All individuals were processed fresh, measured (total length, mm), weighted (total weight, g), and their sagitta otoliths were dissected for estimation of the individual life-history traits using a function-based assessment approach that infers the traits from an

individual growth curve (see for details below). Additionally, the gonads of a sub-sample

for each sampling method (n = 54) were used for direct measurement of reproduction

investment (batch-fecundity) following the method based on the automated image

analysis described by (Alonso-Fernández *et al.*, 2009).
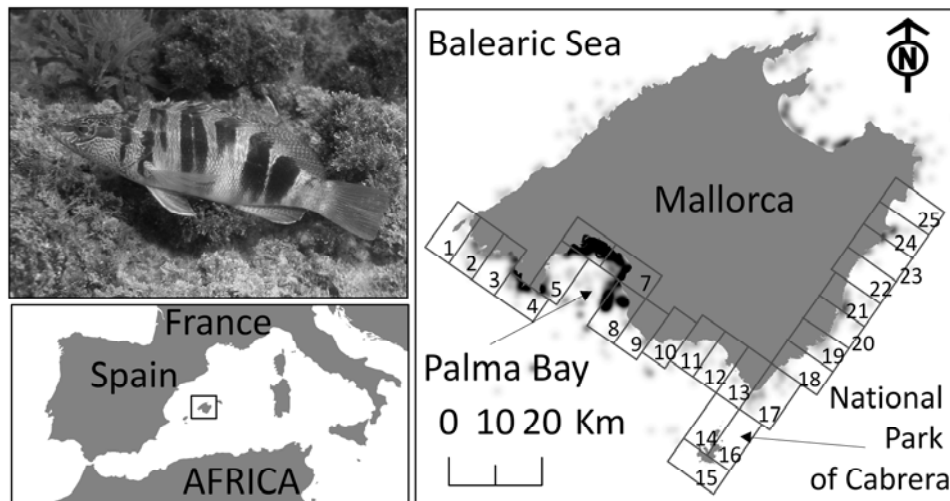
Figure 8.1 Picture of *Serranus scriba* (Family: Serranidae) (top left panel). Map locating the Mallorca Island in the Balearic Sea (NW Mediterranean) (bottom left panel).The spatial location of the 25 sites of eggs releasing is showed in the right panel highlighting the high exploited (recreational fishing) area located in Palma Bay and the waters of National Park of Cabrera where recreational fishing is not allowed (No-take MPA). Black-white gradient represents to be the spatial distribution of the recreational fishing effort in the Mallorca Island proyected in a raster of 250 m x 250 m of (n = 1,430). Recreational anglers were censed by the coastal guards (data obtained in a work-package of the Project CONFLICT).

8.2.3 Sub-populations, connectivity and local harvesting pressure

After identifying the direction of possible selection operating on life-history traits, sub-

populations of *S. scriba* were identified that should show adaptations in such traits due

to historic harvesting pressure. The ideal populations to study should experience

different historic fishing intensity and have limited gene flow among each other. It is

under these conditions that distinct life history adaptations should be expected. We thus

selected the sub-populations of *S. scriba* in the present study following two criteria: *i*) limited gene flow and *ii*) contrasting historical and contemporary harvesting pressures. We first explored the gene flow approximated by the population's connectivity and subsequently we selected reproductively isolated sub-populations exposed to contrasting harvesting pressure (old no-takes marine protected areas, MPA, and a highly exploited area, see below) to test whether life-history changes in life-histories have taken place. Based on life-history theory and the results of the potential selection pressures caused by angling from section 8.2.2, we predicted fish subjected to high harvesting pressure to have evolved smaller maturation age and size, higher reproductive investment and smaller adult size, i.e., a faster life-history (Matsumura *et al.*, 2011).

Similar to many other coastal fish inhabiting seagrass meadows, early life-stages of *S. scriba* are pelagic with dispersal characteristics and gene flow linked to the dominant coastal flow patterns during the spawning season. To estimate the degree of the sub-population's connectivity, we selected 25 areas (see spatial distribution in Figure 8.1) potentially inhabited by adults of *S. scriba* (any seagrass or rocky bottoms with < 30 m depth) along the inner-shelf region of the SE coast of Mallorca (Figure 8.1). The self-recruitment and the direct and indirect connectivity of each sub-population of *S. scriba* were calculated following the procedures of (Basterretxea *et al.*, 2012). Briefly, the Lagrangian trajectories (Watson *et al.*, 2011) of weekly releases of passive tracers (virtual eggs) during the peak reproductive season were numerically simulated using a high resolution (200 m) three-dimensional density-resolving model of the hydrodynamics of the southern Mallorca through a previously-validated Princeton Ocean Model (POM).

The flow fields produced by surface wind forcing were obtained from the 12-hourly wind maps from an historical data-base of ten years (2000-2009, data from the coastal meteorological station of the Palma de Mallorca airport, accessed February 2012: http://www.aemet.es/).

The pelagic larval duration (PLD) was assumed to be 28 days (Macpherson and Raventos, 2006) and the floatability of the eggs was assumed to be positive following the results obtained in the experiment provided in Appendix III. The virtual eggs were homogeneously distributed in each area, and a reflective boundary condition was used to prevent particles from moving onto land. We assumed individual larvae to have been recruited to a particular area if they were found in the inner-shore habitat (defined by each area) at the end of the PLD simulation. Degree of self-recruitment (mean and s.d.) was defined as the number of particles remaining in area j at the end of the prescribed PLD period divided by the numbers of particles initially released in area j per each releasing period (Basterretxea *et al.*, 2012).

The probability that a particle is transported from one area to another one by the end of the PLD (28 days) was considered the direct connectivity. Direct connectivity estimates provide a good indication of the relationship between self-recruitment and dispersal from and to other areas during one hatching cycle. In this sense, it is indicative of organism dispersal (Basterretxea *et al.*, 2012). Hereditable components of phenotypic variation can also be exchanged through indirect transport involving several generations. The indirect connectivity reflects the probability of this transport across generations (Casabianca *et al.*, 2011) and is dependent on the existence of suitable habitat corridors

that allow the survival of intermediate populations between the source and the receiving population. Indirect connectivity (IC) between paired populations was calculated as:

$$IC = \sum_{n=1}^{N} DC^n$$

(1),

where N is the number of hatching cycles, DC identifies the direct routes and DC^n includes all the routes requiring n-*1* steps (or n direct routes). It is important to note that indirect connectivity conveys a temporal term that provides information on the velocity of the exchange. In the case of phenotypic variations this may be relevant because longer routes of exchange, involving a higher number of generations, may imply loss of the hereditable signal.

Patterns of population's connectivity showed how the local self-recruitment processes of the early life-stages of *S. scriba* were dictated by the coastal morphology at the spatial-scale studied. Two main areas, the inner part of Palma Bay (IPB) and the National Park of Cabrera (NPC) were markedly different from the others showing the highest percentages of self-recruitment (Figure 8.2 and 8.3). In comparison to an open population (OP, Figure 8.2), the final position of the virtual eggs released suggested a notorious high degree of retention of eggs in these two main areas (Figure 8.2). Direct connectivity between these two populations (IPB and NPC) areas was low (Figure 8.3), indicating low potential gene flow. These two areas also showed low degree of direct connectivity with the OP (Figure 8.3). When longer term dispersal was analyzed (indirect connectivity based in 50 years) the effect of along shelf connections between the IPB and NPC remained low (Figure 8.3). Therefore, while the populations in OP

were considered to have certain degree of heritable exchange, IPC and NPC were considered to relatively mutually isolated, which constitutes a good opportunity to study the potential for life-history change due to fishing in IPC with NPC serving as a control.

Apart of the limited gene flow of both NPC and IPB, these sub-populations were unique because they were the only ones exposed to the minimum and maximum harvesting selection pressure, rendering them an ideal and pretty unique case-study candidates to test our hypothesis. The NPC was declared a sanctuary (no-take MPA) in 1991. It is formed by 19 small Islands and is one of the largest marine protected areas of the Mediterranean Sea (Francour *et al.*, 2001). Since recreational fisheries was abandoned in NPC, top-predator species and potential predators of small individuals of *S. scriba* notably increased its abundance (e.g., *Epinephelus marginatus*, (Reñones *et al.*, 1999). By contrast, the second area IPB (South of Mallorca Island) is the most important recreational fishery in Mallorca Island receiving substantial recreational fishing effort (Figure 8.1).

8.2.4 Recreational-fishing induced life-history adaptation

Studies on FIE depend on assessment of individual traits. Many life-history traits such as maturation decisions or amount of resources invested into reproduction cannot be directly observed or measured on captured fish. Therefore, many studies on FIE have relied on inferring life-history traits from hard structures (e.g., (Swain *et al.*, 2007). The back-calculation of length-at-age using growth marks contained in the otoliths can offer a reliable method to obtain repeated measures over the life-span of the same individual

when there is a strong relationship between fish and otolith size as is often the case (Mollet *et al.*, 2010; Pilling *et al.*, 2002; Brunel *et al.*, 2012). We chose a function-valued approach (Stinchcombe and Kirkpatrick, 2012) to infer key life-history traits from individual growth curves. In this approach, parameters (traits) estimated from individual growth curves were used as data characterizing individual fish. As far as we are aware, this is the first time this method is used in studies on FIE.

We estimated individual life-history strategies in the NPC, IPB and the OP sub-populations to test our prediction that fish in the NPC should be characterized by "slow" life-histories compared to fish in IPB (the exploited area). Samples of adult individuals of *S. scriba* were obtained from each study area: IPB (n = 201), OP (n = 215) and NPC (n = 353). Fish sampling was carried out with the same gears (conventional hook-and-line) at similar habitat characteristics (seagrass meadows of *P. ocenaica*) and depths. All the individuals were processed as described in section 8.2.2 and the gonads from sub-sampled individuals from May and June (n = 53 from the IPB, n = 41 from the OP and n = 79 from the NPC) were used for direct measurement of the reproductive investment (batch-fecundity). Moreover, direct measures of relative abundance (catch per unit effort as index) and the size and age of vulnerable fish were taken using highly standardized fishing sessions with conventional hook-and-line gear. Fishing sessions (IPB n = 54, AP n = 24 and NPC n = 64) were realized using the standardized recreational angling gear described in (Alós *et al.*, 2009) visiting each sub-population on randomly selected days during a year period. Briefly, two anglers (accompanied by a researcher) fished the same time with the same gear (hook size)

using the same effort (30 min) using two different baits (worm and shrimp). At the end of each fishing session the fish were identified and measured (fish sizes: IPB n = 61, OP n =40 and NPC n = 202). The otoliths of a random-sample of the individuals were processed as described below for aging purposes (IPB n = 61, OP n = 27 and NPC n = 179).

We fitted each individual back-calculated length-at-age data from otoliths to the bi-phasic growth model proposed by (Lester *et al.*, 2004) to provide indirect measures of the annual reproduction investment (g), individual maximum theoretical size (L_∞), age of initiation of maturation (T) and immature growth rate (h) (Arlinghaus *et al.*, 2009; Matsumura *et al.*, 2011). The model assumes linear growth in the juvenile phase and a trade-off between the energy allocation to somatic growth and reproduction in adult ages (Lester *et al.*, 2004). The model by (Lester *et al.*, 2004) is a special case of a more general version published by (Quince *et al.*, 2008a; Quince *et al.*, 2008b) and is valid for a length-weight relationship with an exponent b = 3, which is the case in *S. scriba* (see Chapter 3 of this Thesis) and bi-phasic growth pattern (as detected in *S. scriba* in Chapter 2). Somatic growth rate before the age of the onset of maturation (T, years) in the model by (Lester *et al.*, 2004) is given by

$$L_t = h(t - t_1) + \varepsilon \qquad \text{when } t \leq T \qquad (2),$$

where L_t is the length at age t (mm), h is the immature growth (mm year^{-1}), t_1 is the theoretical age at size 0 mm and ε is the Gaussian error.

When the individual takes the "decision" to start investing into reproduction at age T, the somatic growth of the individual is represented by the more classical von Bertalanffy (VB) growth equation with parameters that provide explicit information on the energy allocated to reproduction (g, annual reproduction investment, year^{-1}) as

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) + \varepsilon \qquad \text{when } t \geq T \tag{3},$$

where $L_\infty = 3h/g$, $k = ln(1 + g/3)$ and $t_o = T + (ln(1 - g(T - t_1)/3)/ln(1+g/3)$, and ε is the Gaussian error (Lester *et al.*, 2004).

These two equations provide a biologically meaningful interpretation of the VB growth parameters traditionally used in fisheries science but representing simple mathematical descriptors (Lester *et al.*, 2004). Accordingly, the growth factor k is proportional to reproduction investment ($k \approx g/3$) and reflects the relative investment averaged over the entire reproductive cycle (g) (see also (Charnov, 2008), L_∞ (maximum theoretical body size) is the ratio of net production to reproductive investment ($L_\infty = 3h/g$) and t_0 in the VB growth model is another simple function of T and g (Lester *et al.*, 2004).

The growth model was fitted using a Bayesian approach for each individual. This approach has several advantages for inferring parameters of complex models (Ellison, 2004) and has become popular to estimate individual growth parameters (Helser and Lai, 2004). Two different models were fitted. The first model was applied to the data of either beam or hook-captured fish to estimate the type of selection on life-history traits

exerted by hook-and-line captured fish relative to trawled individuals. The second model was fit to the individual data of the three study populations to infer life-history traits of fish in the three sites (IPB vs. OP vs. NPC). The model was implemented and run using the *runjags* library of the R package (http://www.r-project.org/), which opens JAGS (http://mathstat.helsinki.fi/openbugs/). The model was fitted for individuals of age 5 or older at capture, which improves the accuracy of the method substantially (Alós *et al.*, 2010). Moreover, due the over-dispersed representation of older ages in the unexploited NPC site in the second model, 50 individuals were randomly selected. By this approach, the ages and the number of observations per individual included in the analysis were not different among sites in fitting of the first (Chi-squared independence test, p = 0.46) and second model (Chi-squared independence test, p = 0.1). Therefore, any significant variation in life-history traits among gears or sites was independent of the fish size and the number of samples (ages) per fish including in the fitting. A hierarchical (individuals within a population) structure of minimal prior and hyper-prior knowledge was used and is fully provided in Appendix IV. Three Monte Carlo Markov Chains (MCMC) were run using randomly chosen initial values for the life-history traits and After accepting convergence of the three chains, assessed using Gelman-Rubin diagnostic (Plummer *et al.*, 2006), the number of valid iterations after burning and thinning was 1,000. The feasibility of the Bayesian framework adopted here was assessed through a simulation analysis (Appendix V).

We estimated the potential direction of selection of recreational fishing by comparing the distribution of the individual Bayesian means of each life-history trait for the two sampling methods beam trawl and hook-and-line to test whether angling would

be expected to exert selection on *S. scriba* life-history traits. Subsequently, between-population comparisons in average life-history traits were carried out by comparing the Bayesian population's means of each life-history traits using the Bayesian Credibility Intervals (BCI) (2.5%, 50%, and 97.5% overlapping). Unlike the frequentist's p value, the Bayesian posterior distributions are interpreted correctly as one's belief that there is a p% probability that the parameter of interest lies within the interval (Ellison, 2004). To make robust conclusions, we considered differences in the life-history traits when the BCI did not overlap at all. L_∞ and *h* were expressed in mm as the distance from the otolith centre to the border following the growth path. However, in order to facilitate interpretation, in some cases the scale was translated to fish size (total length) using the regression model provided in Chapter 2.

Between-sampling methods and between-population differences in direct measures of reproduction investment (batch-fecundity), and populations differences in the relative abundance, age and size of vulnerable fish sampled by experimental angling were analysed using frequentist statistics using Generalized Lineal Mixed Effects Models (GLMM, (Zuur *et al.*, 2009). Minimum adequate GLMMs were fitted following a forward step-by-step (by comparing the model with and without the factor through ANOVA) until maximum explanatory power was reached (the *AIC* criterion) (Zuur *et al.*, 2009). The p values for each parameter were estimated through MCMC simulations using the function *pvals.fnc* from the library *languageR* of the R package.
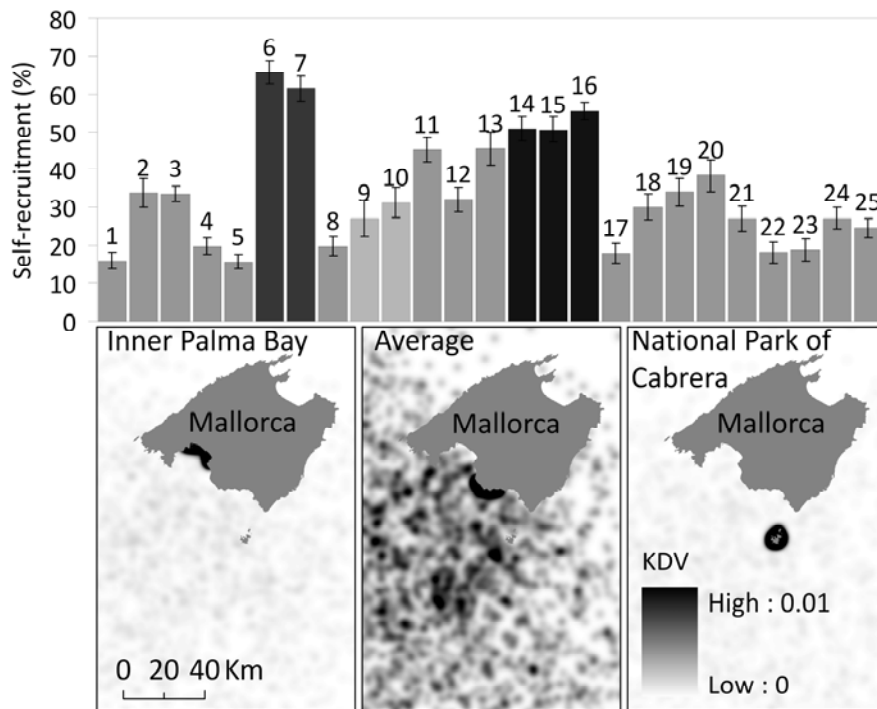
Figure 8.2 Self-recruitment (10 years mean and s.d.) of the 25 sites of eggs release considered in this study (upper panel). The highest values observed in the inner part of Palma Bay (sites 6 and 7) and the National Park of Cabrera (sites 14, 15 and 16) were showed in dark grey and black respectively. An average, in terms of SC, population (sites 9 and 10) is showed in light grey. The bottom panels shows the spatial-plots of a fixed kernel probability distributions (estimated in raster of 250 m x 250 m) of the positions at the end of the PLD duration of the virtual eggs released in each of these three main areas.

8.2.5 Controlling for non-fishing related environmental impacts on life-histories

To help sorting out whether FIE would be the most parsimonious explanation of the observed life-history differences among the three sites investigated in the present study, we also included some environmental data in our study. A 10 year record of satellite (MODIS-Aqua) derived monthly averages of sea surface temperature (SST) and chlorophyll (Chl-a) as measure of productivity was obtained for each of the three sites included in the analyses and compared among them. In all cases (temperature and productivity) chronograms were used to visual inspection for differences.

8.3 Results

8.3.1 Selection pressures on life-history caused by recreational angling

The individual values of maximum theoretical size (L_∞), annual reproduction investment (g), immature growth (h) and age of maturation (T) were successfully estimated for the experimental beam trawl (active gear) and hook-and-line samples (passive gear) (Table 8-1). Mean L_∞ was significantly different between the fish sampled with the two gears (Table 8-1). Similarly, the average g of fish vulnerable to hook-and-line were smaller than those captured in the trawl suggesting that removal of vulnerable fish to angling would exert selection for high reproductive investment (Table 8-1). Results in immature growth rate h and onset of maturation T suggested on average older age of maturation and smaller immature growth in the hook-and-line individuals compared to fish vulnerable to trawls, but in both cases the Bayesian credibility intervals overlapped notably suggesting smaller selection pressures on these traits (Table 8-1). Figure 8.4 shows a box-plot of the individual values of life-history traits estimated for the two fishing treatments. Overall, the results suggested a specific direction of recreational-fishing induced selection, which should favour fish with higher reproductive investment and smaller adult growth capacity under conditions of intensive recreational harvesting.

The results of the direct measures of reproduction investment (batch-fecundity) were in the line of those obtained for the indirect measures of g just described. Accordingly, there were significant differences between the beam trawl and hook-and-line (GLMM; p <0.05, Table 8-2). Individual's sampled using hook-and-line invested less into

reproduction compared to trawl-captured fish (Table 8-2). The relationship between batch fecundity and g estimated from the growth curve was highly significant (GLM, p < 0.01).
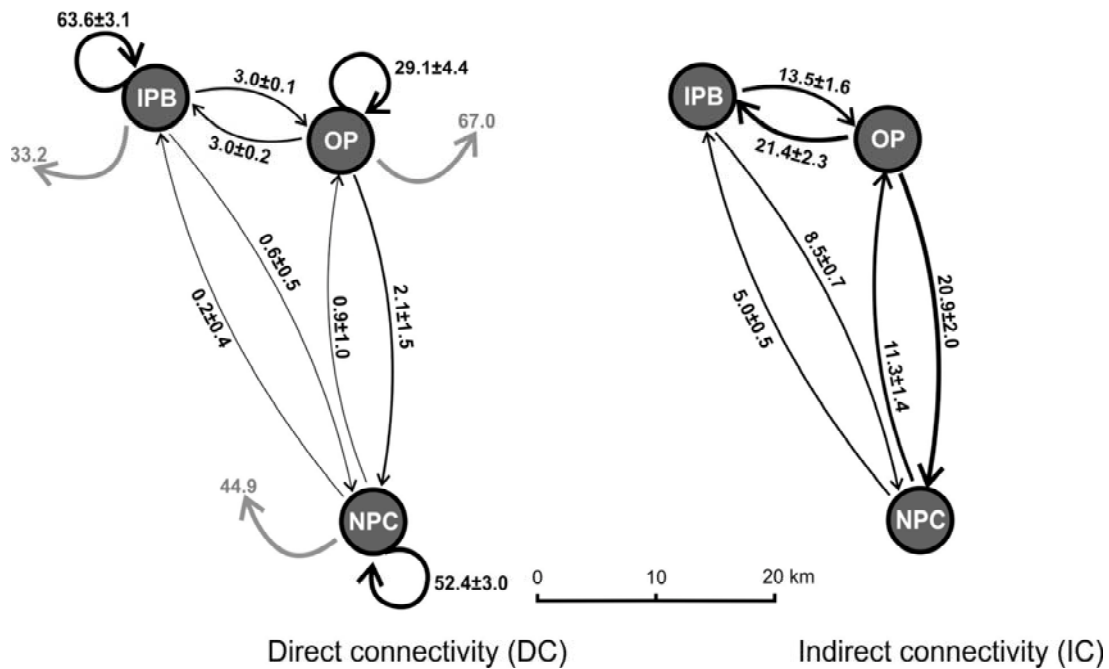
Figure 8.3 Directional flow diagram showing the paired direct and indirect connectivity (black arrows) calculated among the inner part of Palma Bay (PB), the open population (OP) and the National Park of Cabrera (NPC) (each number can be interpreted as a % of eggs released in an specific sub-populations). Indirect connectivity values are the maximum values of connectivity over 50 years. The grey arrows show the connectivity attributed by other sub-populations. 360º black arrows are the self-recruitment values for each specific sub-population.

8.3.2 Population's life-history strategies

The individual values of g, L_∞, T and h were also successfully estimated for the individuals sampled in the three sub-populations studied (IPB, NPC and OP). There were non-overlapping posterior distributions of g between the IPB (Bayesian mean =

0.75 years^{-1}) and the NPC (Bayesian mean = 0.61 years^{-1}). Thus, we accepted the hypothesis of higher reproductive investment in the exploited site IPB relative to the unexploited site NPC (Table 8-3 and Figure 8.5). In contrast, the posterior distribution of the open population OP had intermediate values (Bayesian mean = 0.70 years^{-1}) notably overlapping with the distributions of the other two populations. Results were similar for L_∞, and differences between the Bayesian means of IPB (Bayesian mean = 228 mm of fish total length) and NPC (Bayesian mean = 244.7 mm of fish total length) were significant, indicating lower final size in fish living in the exploited site IPB (Table 8-3 and Figure 8.5). In the case of T and h, the posterior distributions of the three populations were highly overlapped discarding the plausibility of any significant differences (Table 8-3 and Figure 8.5).
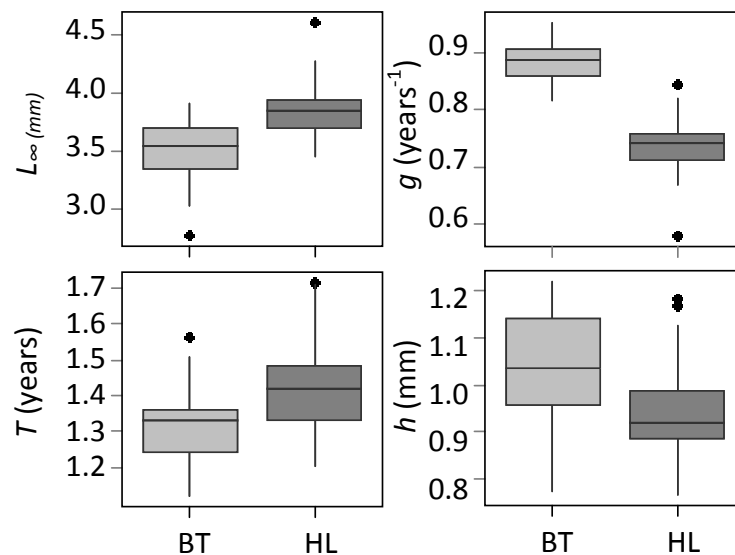
Figure 8.4 Box-plot of the Bayesian individual means of the life-history parameters (reproduction investment, infinite size, age of maturation and immature growth) estimated for the beam trawl (BT in light grey) and hook-and-line (HL in dark grey) individuals.

Individuals sampled in the IPB (high exploited population) also had a significant higher batch-fecundity than those the individuals sampled in the NPC (GLMM; $p < 0.05$, Table 8-2). A summary of the GLMMs performed to explore differences in the population means of relative abundance, fish sizes and ages of vulnerable fish is shown in Table 8-4, which revealed significant effects in all the response variables. The population of IPB was characterized by a significantly lower catch rate as indicator of abundance, and the fish were on average smaller and younger as is typical in exploited sites. By contrast, vulnerable individuals sampled in the NPC were more abundant, larger and older, and the fish in the OP site showed average values (Table 8-4). Daily temperature oscillated in the same way both at a daily and seasonal basis in the IPB and NPC sites suggesting no differences in temperature regimes as to be expected due the close proximity between the two areas (Figure 8.6). By contrast, chlorophyll-a concentrations estimated from the sea-colour images available for the IPB and NPC showed in both cases a clear seasonal periodicity, and the IPB had higher values suggesting being a more productive site than the NPC (Figure 8.6). Therefore, one would have expected larger growth rates in IPB fish, but the opposite was found

Table 8-1 Bayesian posterior distribution (MCMC) of means the life-history traits (reproduction investment in year $^{-1}$, infinite size inn mm of otolith, age of maturation in years and immature growth rate referred to otolith scale in mm year $^{-1}$) for the beam trawl and the hook-and-line samples.

Parameter	Beam trawl					Hook-and-line				
	Mean	s.d.	2.5%	Median	97.5%	Mean	s.d.	2.5%	Median	97.5%
Reproduction investment	0.88	0.12	0.75	0.86	1.11	0.74	0.06	0.68	0.73	0.81
Infinite size	3.50	0.11	3.28	3.50	3.70	3.84	0.07	3.72	3.84	3.95
Age of maturation	1.33	0.08	1.17	1.33	1.45	1.43	0.05	1.35	1.43	1.49
Immature growth	1.03	0.11	0.90	1.01	1.24	0.94	0.05	0.89	0.93	1.01

8.4 Discussion

Recreational fisheries-induced evolution of "fast life-histories" characterized by high reproductive investment and small adult size in the small coastal fish *S. scriba* constituted the most parsimonious explanation of the observed phenotypic data. Four lines of evidence support this conclusion. We have first shown that recreational angling selects for certain life-histories, i.e., those with high reproductive investment and small terminal size. We have secondly shown that oceanographic currents and local hydrodynamics prevented gene flow among spatially closed sites. Therefore, two ingredients of FIE of life histories in the marine environment were met. Accordingly, we found average life-histories in exploited and unexploited sites to mirror the directional changes expected from the theoretical selection pressures exerted by anglers. Finally, the smaller adult growth and larger reproductive investment of fish surviving the exploitation in high intensity sites could not be explained by envrioenmatlel relates factors. Our comparative findings therefore joins previous work in freshwater ecosystems (Drake *et al.*, 1997; Haugen and Vøllestad, 2001; Magnan *et al.*, 2005) that harvesting can result in FIE of fast life-histories characterized by early maturation, high investment into reproduction and small adult growth when gene flow is limited at small spatial scales in marine environments.

Table 8-2 Results of the two Generalized Lineal Mixed effect models (GLMMs) fitted to test the relationship between the direct measure of reproduction investment (batch fecundity) and (A) the sampling method (beam trawl and hook-and-line), and (B) the populations (inner of Palma Bay, average population and National Park of Cabrera). In both models Fish size was also included as fixed factor and Fishing ID as random factor. The GLMM developed for populations also included the temporal variable month. The table shows the parameters include in the final model (the MCMC mean of the parameters, the lower and upper highest 95% credibility intervals (HDP) and the significance of the parameter. Interactions were not significant and were not included.

Log (batch fecundity)	MCMC	HPD 95%		P- value
Parameter	mean	lower	upper	
Selection experiment				
Intercept	5.83	5.00	6.63	<0.001
Fish size	0.02	0.01	0.02	<0.001
Method (hook–and–line)	-1.31	-1.93	-0.68	<0.05
Populations comparisons				
Intercept	5.21	4.67	5.75	<0.001
Fish size	0.02	0.02	0.02	<0.001
Population (inner of Palma Bay)	0.74	0.42	1.08	<0.05
Population (average population)	-0.08	-0.38	0.22	0.87
Month (may)	-1.04	-1.30	-0.77	<0.001

Our findings agreed with theoretical models on recreational-fishing induced selection that proposed selection for high reproductive investment and declines in adult body size of Northen pike (Arlinghaus *et al.*, 2009), and with the empirical findings on recreationally exploited Atlantic salmon (Saura *et al.*, 2010) and Chinook salmon, (Kendall and Quinn, 2011). Because it is likely that the life-history of a fish is correlated to underlying behavioural and physiological traits (Uusi-Heikkilä *et al.*, 2008), it is very likely that the fish surviving exploitation are also characterized by higher shyness and less aggressive foraging (Biro and Post, 2008; Sutter *et al.*, 2012). Because the selection found in our work is expected to drive populations of *S. scriba* to evolve slower capacity to growth after maturation due to higher reproductive investment and because the

adapted individuals are expected to also become harder to catch (Philipp *et al.*, 2009) the resulting outcome is likely to affect fishing communities negatively by affecting reproductive fitness and catchability negatively (Sutter *et al.*, 2012; Johnson *et al.*, 2011). In direct contrast to such recreational harvest-based selection, natural selection in natural environments such as the National Park of Cabrera will drive population in the opposite direction favouring individuals with large expected life-span to avoid gape-limited predation and with low reproductive investment due to the trade off with post maturation growth and to postpone the survival cost of reproduction (Hutchings, 1993; Reznick, 1982; Aikio *et al.*, 2013). In particular, in environments where the abundance of predators of *S. scriba* is high (for example, presence of *Ephinephelus marginatus)*, directional selection on fast (juvenile and adult) growth is to be expected (Edeline *et al.*, 2007). Therefore, the optimal life-history strategy should favour a version of "bigger-is-better" which is characterized by fast early growth, late maturation and moderate to small annual reproductive investment (Edeline *et al.*, 2007; Hutchings, 1993; Olsen and Moland, 2011; Reznick, 1982). This is because the (surviving) individual theoretically would maximize the fitness over a larger the life-span under natural conditions (Charnov, 2005; Roff, 1984).

Table 8-3 Posterior distribution (MCMC populations means, s.d. and Bayesian credibility intervals) of the life-history traits (reproduction investment in year $^{-1}$, infinite size (mm of otlith), age of maturation in years and immature growth rate referred to otolith scale in mm year $^{-1}$) estimated for the three analysed populations (inner of Palma Bay, average population and National Park of Cabrera).

Population			Bayesian credibility intervals		
LH Parameter	Mean	s.d.	2.5%	Median	97.5%
Inner of Palma Bay					
Reproduction investment	0.75	0.04	0.67	0.75	0.83
Infinite size	3.59	0.07	3.45	3.60	3.74
Age of maturation	1.50	0.05	1.40	1.51	1.61
Immature growth	0.89	0.04	0.81	0.89	0.98
Average population					
Reproduction investment	0.70	0.04	0.63	0.70	0.78
Infinite size	3.85	0.07	3.70	3.85	3.99
Age of maturation	1.48	0.05	1.38	1.47	1.57
Immature growth	0.89	0.04	0.82	0.89	0.98
National Park of Cabrera					
Reproduction investment	0.61	0.03	0.55	0.61	0.67
Infinite size	3.88	0.06	3.75	3.87	4.00
Age of maturation	1.55	0.05	1.46	1.55	1.65
Immature growth	0.79	0.03	0.72	0.79	0.85

By contrast and in line with our work, heavy exploitation by anglers would expect to lead to evolution of fast life-histories characterized by early reproduction and large reproductive investment, which results in penalties on adult growth. While these patters were supported in our work in relation to reproductive investment and adult growth, no change in maturation timing was found. However, given that maturation happens in *S. criba* usually at age 1 (Alonso-Fernández *et al.*, 2011) there was no room for maturation evolution in this species. This constraint also likely explains the tendency for exploited fish to growth fast early in life because it pays off to be as large as possible when first reproduction starts and investment into the future (by growing to larger sizes) does not

pay off. The same was found in a theoretical model by (Matsumura *et al.*, 2011) in recreationally exploited northern pike, *Exos lucius*. When size selectivity favoured heavy cropping of very young fish already, selection pressures on fast early immature growth was predicted. The direction of selection changed to negative selection on immature growth when size-selectivity only targeted large mature fishes, e.g., due to a large minimum-size limit (Matsumura *et al.*, 2011).
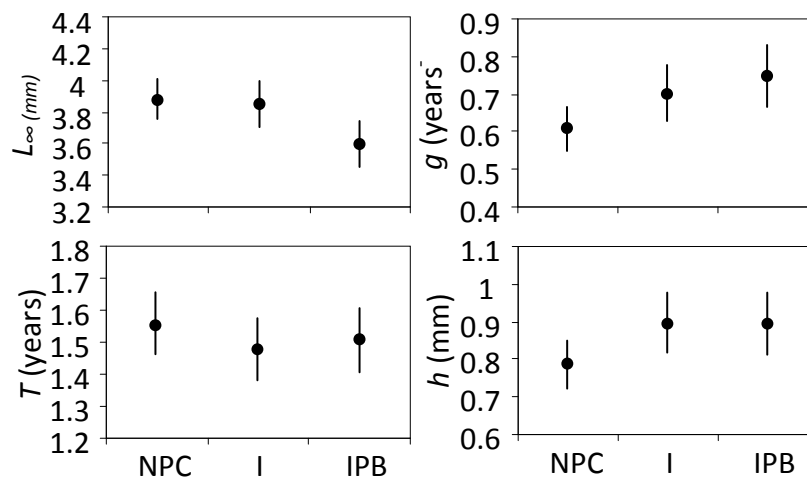
Figura 8.5 Bayesian Credibility Intervals (2.5%, 50%, and 97.5%) of the posterior distribution of the population's means estimated for each LH trait to assess with the differences between-populations

One caveat of any comparative study such as the one performed here is to discount any non-fishing related environmental drivers that might also explain the among-site differentiation in life-history (Kendall and Quinn, 2011). In fact, all differences observed in the life-history in our sub-populations could be related to unaccounted environmental characteristics directly or indirectly related to harvest pressure (Dunlop *et al.*, 2005; McDermid *et al.*, 2010). While we cannot discount that the phenotypic change may be entirely plastic, the bulk of evidences presented here makes this

explanation unlikely. First of all, all life-history traits have some modest heritability and the selection caused by recreational fishing was found pronounced, which should generate selection differentials on heritable traits (Law, 2000). Secondly, the variation in fishing pressure among sites was undisputed and the gene flow among the protected area site and the exploited site was found very small. Thirdly, our control sites (OP) showed intermediate phenotypes to the high exploitation and non-exploitation site. Finally and although cold waters may slower pre-maturation growth and result in older age of maturation and larger longevity in some species (McDermid *et al.*, 2010; Wright *et al.*, 2011), we could discount temperature to vary substantially among our sites. The only environmental driver that did vary among the high and no exploitation sites was the productivity of the system, which was approximated by a 10-years time-series of chlorophyll-a concentration. Although differences were small, there was a consistently higher productivity during the peak of annual productivity in spring in the exploited IPB. Greater resource availabilities should on the one hand increase relative fecundity due to greater resource intake (e.g., (Craig and Kipling, 1983), which might explain the greater annual reproduction investment found in the IPB sites. At the same time, however, growth rate of both immature and mature should profit from higher productivity in the high exploitation, and maximum size should then increase (McDermid *et al.*, 2010). Similarly, the reduced density of fish should additionally elevate growth due to relaxed competition (Lorenzen and Enberg, 2002). By contrast, our life-history traits in relation to growth directly showed the exact opposite response. First, the immature growth rates (*h*) did not differ statistically among sites. Secondly, the theoretical maximum size was significantly smaller in the high exploitation sites

although the environmental plasticity hypothesis should have predicted larger maximum sizes inter alia because relaxed intra-specific competition for prey should have increased the food availability generating fast growth and small reproductive investment (Dunlop *et al.*, 2005). Therefore, we have no environmental factor that may explain the life-history difference and thus have limited supports for a plasticity hypothesis, rendering FIE the more parsimonious mechanism of life-history differentiation in our study. In particular, the high heritability of the life-history traits studied here (Law, 2000), and the limited genetic exchange among populations of very likely common ancestors makes genetic divergence through fisheries-induced adaptive change the most likely explanation.

Table 8-4 Results of the three Generalized Lineal Mixed effect models (GLMMs) fitted to test the relationship between the relative abundance (fish*30min*angler), fish size (mm) and ages (years) of vulnerable *Serranus scriba* sampled in the inner of Palma Bay, the average population and the National Park of Cabrera. The full model (without reduction) includes the fixed factors population, depth (m), angler, bait and month. The abundance GLMM have repeated measures within day and the size and age were repeated measures of fishing sessions within day which were included as random effects. The table

shows the parameters include in the final model (the MCMC mean of the parameters, the lower and upper highest 95% credibility intervals (HDP) and the significance of the parameter.

Parameter	MCMC mean	HPD 95%		P- value
		lower	upper	
Log (Abundance + 1)				
(Intercept)	1.35	0.86	1.87	<0.001
Population (inner of Palma Bay)	-0.64	-1.00	-0.27	<0.01
Population (average population)	-0.30	-0.77	0.16	0.200
Depth (m)	-0.04	-0.06	-0.01	<0.05
Month (Jan)	0.43	0.03	0.81	0.082
Month (Feb)	0.12	-0.26	0.53	0.588
Month (Mar)	0.16	-0.30	0.61	0.570
Month (May)	0.31	-0.12	0.75	0.170
Month (Jun)	0.52	-0.02	1.03	0.076
Month (Jul)	1.16	0.49	1.84	<0.01
Month (Aug)	0.99	0.53	1.43	<0.001
Month (Oct)	0.75	0.00	1.57	0.073
Month (Nov)	0.91	0.15	1.69	<0.05
Log (Fish size)				
(Intercept)	4.83	4.73	4.93	<0.001
Population (inner of Palma Bay)	-0.17	-0.24	-0.10	<0.001
Population (average population)	-0.10	-0.17	-0.03	<0.01
Bait (Shrimp)	0.08	0.04	0.13	<0.01
Depth (m)	0.01	0.00	0.02	<0.05
Log (Fish age + 1)				
(Intercept)	1.33	1.10	1.54	<0.001
Population (inner of Palma Bay)	-0.49	-0.62	-0.36	<0.001
Population (average population)	-0.46	-0.62	-0.29	<0.001
Bait (Shrimp)	0.14	0.04	0.24	<0.05
Depth (m)	0.03	0.01	0.04	<0.01

Cause-and-effect evidence for evolutionary changes (i.e., genetic) in the wild can only unequivocally determined by commen garden experiments (Conover and Baumann, 2009; Enberg *et al.*, 2012). Molecular ecological tools are rapidly emerging but the link of genotypes to complex phenotypes is not straightforward (Ãrnason *et al.*, 2009; Jakobsdóttir *et al.*, 2011; Pukk *et al.*, 2013). In this context, comparative field

studies such as ours may provide a useful compromise to study whether fishing differentially targets certain phenotypes and whether populations with common ancestry and low current gene flow differentiate in their average phenotype in directions expected from theory and in line with selection differentials estimated in the wild. Often, the large effective population size of marine fish has been proposed to constitute barriers to FIE (Cuveliers *et al.*, 2011; Pukk *et al.*, 2013). We have shown, however, that meta-populatoins of the small coastal species *S. scriba* inhabiting Mallorca Island develop reproductively isolated sub-populations on small spatial scales, which are characterized by high levels of local self-recruitment and low direct and indirect connectivity among each other. Those findings are in line with recent literature indicating that contrary to traditional wisdom that considered marine populations to constitute panmictic systems (Roberts, 1997), hydrodynamics and life-history may actually also result in fine meta-population structures with limited gene flow in many marine areas (Cowen *et al.*, 2006; Mora and Sale, 2002; Schunter *et al.*, 2011). This provides conditions for fisheries-induced evolution to happen also in coastal species targeted by recreational fisheries on very small geographical scales.
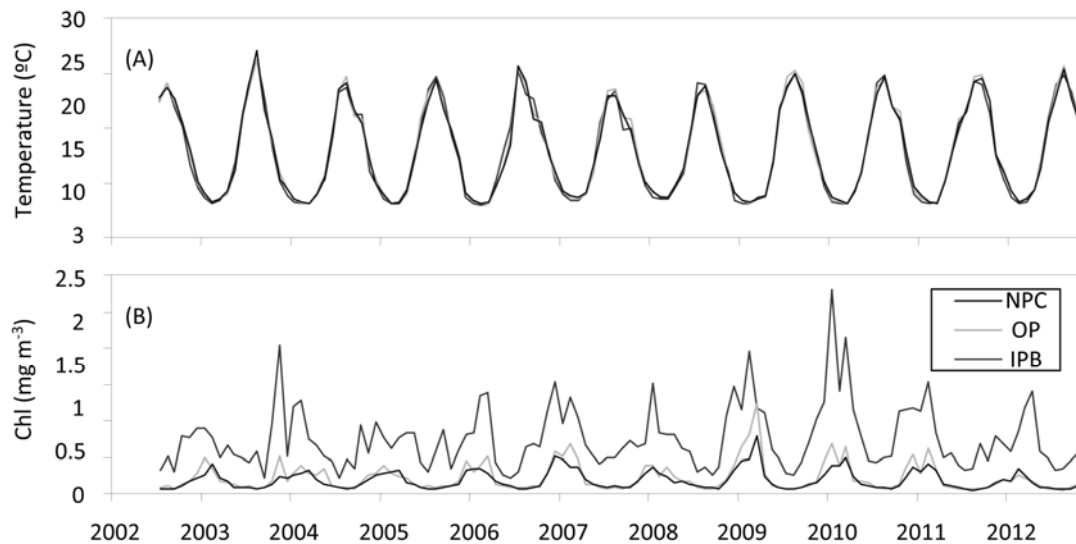
Figura 8.6 Chronograms of ten years of the daily surface temperature (ºC) and concentration of chlorophyll-a (mg m^{-3}) in the inner part of Palma Bay (PB), in the open population (OP) and in the National Park of Cabrera (NPC).

Although we consider our evidence for angling-induced evolutionary change in *S. scriba* to be indirect, we cannot disentangle unequivocally whether the phenotypic change has a genotypic basis. Empirical evidence of FIE in our study species could be generated using common-garden experiments of fish collected of different sites and raised and tested in the laboratory. For example, the offspring from the different populations reared under identical environmental conditions could explain the origin of the differences of S. scriba in the wild (Conover and Baumann, 2009). Until this research becomes available, this Thesis proposes a new paradigm of the potential for widespread FIE of small bodied at small scales in marine coastal fishes. Due the potential negative effects of fisheries-induced evolution, which may affect recovery, productivity and catch per unit effort negatively (Sutter *et al.*, 2012; Enberg *et al.*, 2009), fisheries scientist and mangers may adjust their management polices to prevent or decrease the evolutionary impacts of harvesting for successful fish stock management.

To do so requires understanding the meta-population structure and avoid sub-population specific harvesting as much as possible if avoiding FIE is a management goal.

Chapter 9 A behavioural perspective of fisheries-induced selection in marine coastal fisheries

Chapter 10 General conclusions

1. The *individual* is the optimal level of study understanding life-history traits such as growth and/or reproduction, since *differential mortality* (either natural or fishing-related) happens at such level.

2. The study of the individual growth and reproduction revealed both population-level patterns such as the mating behaviour, and individual-level patterns such as the broad *between-fish variability* on most of the life-history traits or the bi-phasic growth pattern.

3. *Recreational fishing* constitutes a significant source of mortality (additional to the natural mortality). Specifically, it may cause local depletion in highly sedentary species, such those that inhabit *Posidonia oceanica* meadows.

4. Fishing mortality results not only from the direct extraction of biomass but also from indirect morality related with *fish captured and released* but that fails to survive. *Management measures* such as gear modifications or the stipulation of partial Marine Protected Areas should be useful to reduce recreational fishing mortality.

5. The fishing mortality induced by recreational fishing *is not a random but a biased process* in relation to some hereditable life-history traits. Biased harvesting generates *selection differentials* against phenotypes with higher growth capability and lower

reproduction investment in line with the theoretical expectations of optimal life history.

6. The pelagic nature of the early life stages and its hydrodynamic-dependent dispersal characteristics can generate *sub-populations*, even at a small spatial scale (few kilometres). This process can generate reproductively *isolated populations with limited gen flow*.

7. Harvesting should able to *induce fast evolution of life-history traits*. Selected phenotypes in isolated sub-populations of coastal fish exposed to the recreational fishing seems to be characterized by high reproductive investment and small adult size

8. Selection of *behavioural traits* constitutes an overlooked component of the emerging concept of *human-induced evolution*, and it can play a key role in sedentary marine species determining the odds of encounters between fish and fishers.

9. Empirical evidence of fisheries-induced evolution can be only unequivocally detected by *common-garden experiments*. This constitutes an exciting opportunity for further research. Until this research becomes available, this PhD Thesis proposes a new paradigm: the evidence, even at small spatial-temporal scales, *that fisheries-induced evolution on coastal sedentary species exploited by recreational fisheries is plausible*.

10. Due the potential negative effects of fisheries-induced evolution, which may affect stock recovery and productivity, fisheries scientist and mangers should adjust management polices to prevent or buffer the evolutionary impacts of harvesting. This goal requires better understanding the meta-population structure and identifying fishing syndromes or potentially correlated selective traits.

Reference list

Aikio, S., Herczeg, G., Kuparinen, A., and Merilä, J. 2013. Optimal growth strategies under divergent predation pressure. Journal of Fish Biology, 82: 318-331.

Alonso-Fernández, A., Alós, J., Grau, A., Dominguez-Petit, R., and Saborido-Rey, F. 2011. The Use of Histological Techniques to Study the Reproductive Biology of the Hermaphroditic Mediterranean Fishes *Coris julis*, *Serranus scriba*, and *Diplodus annularis*. Marine and Coastal Fisheries, 3: 145-159.

Alonso-Fernández, A., Vallejo, A. C., Saborido-Rey, F., Murua, H., and Trippel, E. A. 2009. Fecundity estimation of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) of Georges Bank: Application of the autodiametric method. Fisheries Research, 99: 47-54.

Alós, J., Arlinghaus, R., Palmer, M., March, D., and Alvarez, I. 2009. The influence of type of natural bait on fish catches and hooking location in a mixed-species marine recreational fishery, with implications for management. Fisheries Research, 97: 270-277.

Alós, J., Palmer, M., and Arlinghaus, R. 2012. Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. PLoS ONE, 7: e48030.

Alós, J., Palmer, M., Balle, S., Grau, A. M., and Morales-Nin, B. 2010. Individual growth pattern and variability in *Serranus scriba*: a Bayesian analysis. ICES Journal of Marine Science, 67: 502-512.

Allendorf, F. W., England, P. R., Luikart, G., Ritchie, P. A., and Ryman, N. 2008. Genetic effects of harvest on wild animal

populations. Trends in Ecology & Evolution, 23: 327-337.

Allendorf, F. W., and Hard, J. J. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. Proceedings of the National Academy of Sciences of the United States of America, 106: 9987-9994.

Arlinghaus, R., Matsumura, S., and Dieckmann, U. 2009. Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). Evolutionary Applications, 2: 335-355.

Ãrnason, E., Hernandez, U. B., and Kristinsson, K. 2009. Intense habitat-specific fisheries-induced selection at the molecular Pan I Locus predicts imminent collapse of a major Cod fishery. PLoS ONE, 4: e5529.

Audzijonyte, A., Kuparinen, A., and Fulton, E. A. 2013. How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies.

Evolutionary Applications: n/a-n/a.

Basterretxea, G., Jordi, A., Catalán, I. A., and Sabatés, A. 2012. Model-based assessment of local-scale fish larval connectivity in a network of marine protected areas. Fisheries Oceanography, 21: 291-306.

Bevacqua, D., Capoccioni, F., MeliÃ , P., Vincenzi, S., Pujolar, J. M., De Leo, G. A., and Ciccotti, E. 2012. Fishery-Induced Selection for Slow Somatic Growth in European Eel. PLoS ONE, 7: e37622.

Biro, P. A., and Post, J. R. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proceedings of the National Academy of Sciences of the United States of America, 105: 2919-2922.

Browman, H. I., Law, R., and Marshall, C. T. 2008. The role of fisheries-induced evolution. Science, 320: 47-50.

Brunel, T., Ernande, B., Mollet, F. M., and Rijnsdorp, A. D. 2012. Estimating age at maturation and energy-based life-history traits from individual growth

trajectories with nonlinear mixed-effects models. Oecologia: 1-13.

Carreras-Carbonell, J., Macpherson, E., and Pascual, M. 2007. High self-recruitment levels in a Mediterranean littoral fish population revealed by microsatellite markers. Marine Biology, 151: 719-727.

Casabianca, S., Penna, A., Pecchioli, E., Jordi, A., Basterretxea, G., and Vernesi, C. 2011. Population genetic structure and connectivity of the harmful dinoflagellate Alexandrium minutum in the Mediterranean Sea. Proceedings of the Royal Society B: Biological Sciences, 279: 129-138.

Conover, D. O., and Baumann, H. 2009. The role of experiments in understanding fishery-induced evolution. Evolutionary Applications, 2: 276-290.

Conover, D. O., and Munch, S. B. 2002. Sustaining fisheries yields over evolutionary time scales. Science, 297: 94-96.

Cooke, S. J., Donaldson, M. R., Hinch, S. G., Crossin, G. T., Patterson, D. A., Hanson, K. C., English, K. K., et al. 2009. Is fishing selective for physiological and energetic characteristics in migratory adult sockeye salmon? Evolutionary Applications, 2: 299-311.

Cooke, S. J., Suski, C. D., Ostrand, K. G., Wahl, D. H., and Philipp, D. P. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. Physiological and Biochemical Zoology, 80: 480-490.

Cowen, R. K., Paris, C. B., and Srinivasan, A. 2006. Scaling of Connectivity in Marine Populations. Science, 311: 522-527.

Craig, J. F., and Kipling, C. 1983. Reproduction effort versus the environment; case histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. Journal of Fish Biology, 22: 713-727.

Cuveliers, E. L., Volckaert, F. A. M., Rijnsdorp, A. D., Larmuseau, M. H. D., and Maes, G. E. 2011. Temporal genetic stability and high effective population size despite fisheries-induced life-history trait evolution in the North Sea sole. Molecular Ecology, 20: 3555-3568.

Charnov, E. L. 2005. Reproductive effort is inversely proportional to average adult life span. Evolutionary Ecology Research, 7: 1221-1222.

Charnov, E. L. 2008. Fish growth: Bertalanffy k is proportional to reproductive effort. Environmental Biology of Fishes, 83: 185-187.

Deudero, S., Morey, G., Frau, A., Moranta, J., and Moreno, I. 2008. Temporal trends of littoral fishes at deep Posidonia oceanica seagrass meadows in a temperate coastal zone. Journal of Marine Systems, 70: 182-195.

Drake, M. T., Claussen, J. E., Philipp, D. P., and Pereira, D. L. 1997. A Comparison of Bluegill reproductive strategies and growth among lakes with different fishing intensities. North American Journal of Fisheries Management, 17: 496-507.

Dunlop, E. S., Baskett, M. L., Heino, M., and Dieckmann, U. 2009. Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. Evolutionary Applications, 2: 371-393.

Dunlop, E. S., Orendorff, J. A., Shuter, B. J., Rodd, F. H., and Ridgway, M. S. 2005. Diet and divergence of introduced smallmouth bass (Micropterus dolomieu) populations. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1720-1732.

Edeline, E., Carlson, S. M., Stige, L. C., Winfield, I. J., Fletcher, J. M., Ben James, J., Haugen, T. O., et al. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. Proceedings of the National Academy of Sciences of the United States of America, 104: 15799-15804.

Ellison, A. M. 2004. Bayesian inference in ecology. Ecology Letters, 7: 509-520.

Enberg, K., Jørgensen, C., Dunlop, E. S., Heino, M., and Dieckmann, U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evolutionary Applications, 2: 394-414.

Enberg, K., Jørgensen, C., Dunlop, E. S., Varpe, Ø., Boukal, D. S., Baulier, L., Eliassen, S., et al. 2012. Fishing-induced evolution

of growth: concepts, mechanisms and the empirical evidence. Marine Ecology, 33: 1-25.

Francour, P., Harmelin, J. G., Pollard, D., and Sartoretto, S. 2001. A review of marine protected areas in the northwestern Mediterranean region: siting, usage, zonation and management. Aquatic Conservation: Marine and Freshwater Ecosystems, 11: 155-188.

Galarza, J. A., Carreras-Carbonell, J., Macpherson, E., Pascual, M., Roques, S., Turner, G. F., and Rico, C. 2009. The influence of oceanographic fronts and early-life-history traits on connectivity among littoral fish species. Proceedings of the National Academy of Sciences, 106: 1473-1478.

Garcia, S. M., Kolding, J., Rice, J., Rochet, M. J., Zhou, S., Arimoto, T., Beyer, J. E., et al. 2012. Reconsidering the Consequences of Selective Fisheries. Science, 335: 1045-1047.

Grimm, V., and Railsback, S. F. 2005. Individual-based Modeling and Ecology, Princeton University Press, Princeton and Oxford,.

Haugen, T. O., and Vøllestad, L. A. 2001. A century of life-history evolution in grayling. Genetica, 112-113: 475-491.

Heino, M., and Dieckmann, U. 2008. Detecting Fisheries-Induced Life-History Evolution: An Overview of the Reaction-Norm Approach. Bulletin of Marine Science, 83: 69-93.

Heino, M., and Godo, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science, 70: 639-656.

Helser, T. E., and Lai, H. L. 2004. A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, Micropterus salmoides. Ecological Modelling, 178: 399-416.

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology, 74: 673-684.

Jakobsdóttir, K. B., Pardoe, H., Magnússon, Á., Björnsson, H., Pampoulie, C., Ruzzante, D. E., and Marteinsdóttir, G. 2011. Historical changes in genotypic frequencies at the Pantophysin

locus in Atlantic cod (Gadus morhua) in Icelandic waters: evidence of fisheries-induced selection? Evolutionary Applications, 4: 562-573.

Johnson, D. W., Christie, M. R., Moye, J., and Hixon, M. A. 2011. Genetic correlations between adults and larvae in a marine fish: potential effects of fishery selection on population replenishment. Evolutionary Applications, 4: 621-633.

Jones, G. P., Planes, S., and Thorrold, S. R. 2005. Coral reef fish larvae settle close to home. Current Biology, 15: 1314-1318.

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., et al. 2007. Managing Evolving Fish Stocks. Science, 318: 1247-1248.

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., et al. 2008. Response. Science, 320: 48-50.

Jørgensen, C., Ernande, B., and Fiksen, Ø. 2009. Size-selective fishing gear and life history evolution in the Northeast Arctic cod.

Evolutionary Applications, 2: 356-370.

Jørgensen, C., and Fiksen, O. 2009. Modelling fishing-induced adaptations and consequences for natural mortality. Canadian Journal of Fisheries and Aquatic Sciences, 67: 1086-1097.

Jørgensen, C., and Holt, R. E. 2013. Natural mortality: Its ecology, how it shapes fish life histories, and why it may be increased by fishing. Journal of Sea Research, 75: 8-18.

Kendall, N. W., and Quinn, T. P. 2011. Length and age trends of Chinook salmon in the Nushagak River, Alaska, related to commercial and recreational fishery selection and exploitation. Transactions of the American Fisheries Society, 140: 611-622.

Kuparinen, A., and Merilä, J. 2007. Detecting and managing fisheries-induced evolution. Trends in Ecology & Evolution, 22: 652-659.

Laugen, A. T., Engelhard, G. H., Whitlock, R., Arlinghaus, R., Dankel, D. J., Dunlop, E. S., Eikeset, A. M., et al. 2012. Evolutionary impact assessment:

accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. Fish and Fisheries: n/a-n/a.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659-668.

Lester, N. P., Shuter, B. J., and Abrams, P. A. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proceedings of the Royal Society of London Series B-Biological Sciences, 271: 1625-1631.

Lewin, W. C., Arlinghaus, R., and Mehner, T. 2006. Documented and potential biological impacts of recreational fishing: Insights for management and conservation. Reviews in Fisheries Science, 14: 305-367.

Lorenzen, K., and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London Series B-Biological Sciences, 269: 49-54.

Macpherson, E., and Raventos, N. 2006. Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes. Marine Ecology Progress Series, 327: 257-265.

Magnan, P., Proulx, R., and Plante, M. 2005. Integrating the effects of fish exploitation and interspecific competition into current life history theories: an example with lacustrine brook trout (*Salvelinus fontinalis*) populations. Canadian Journal of Fisheries and Aquatic Sciences, 62: 747-757.

March, D., Palmer, M., Alós, J., Grau, A., and Cardona, F. 2010. Short-term residence, home range size and diel patterns of the painted comber *Serranus scriba* in a temperate marine reserve. Marine Ecology Progress Series, 400: 195-206.

Matsumura, S., Arlinghaus, R., and Dieckmann, U. 2011. Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits, with an application to northern pike (*Esox lucius*). Evolutionary Ecology, 25: 711-735.

McDermid, J. L., Shuter, B. J., and Lester, N. P. 2010. Life history differences parallel environmental differences among North American lake trout (*Salvelinus namaycush*) populations. Canadian Journal of Fisheries and Aquatic Sciences, 67: 314-325.

Mollet, F. M., Ernande, B., Brunel, T., and Rijnsdorp, A. D. 2010. Multiple growth-correlated life history traits estimated simultaneously in individuals. Oikos, 119: 10-26.

Mora, C., and Sale, P. F. 2002. Are populations of coral reef fish open or closed? Trends in Ecology & Evolution, 17: 422-428.

Morales-Nin, B., Moranta, J., Garcia, C., Tugores, M. P., Grau, A. M., Riera, F., and Cerda, M. 2005. The recreational fishery off Majorca Island (western Mediterranean): some implications for coastal resource management. ICES Journal of Marine Science, 62: 727-739.

Olsen, E., and Moland, E. 2011. Fitness landscape of Atlantic cod shaped by harvest selection and natural selection.

Evolutionary Ecology, 25: 695-710.

Palkovacs, E. P. 2011. The overfishing debate: an eco-evolutionary perspective. Trends in ecology & evolution (Personal edition), 26: 616-617.

Palumbi, S. R., and Warner, R. R. 2003. Why Gobies are like hobbits. Science, 299: 51-52.

Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers, P., and Watson, R. 2003. The future for fisheries. Science, 302: 1359-1361.

Pérez-Rodríguez, A., Morgan, M. J., and Saborido-Rey, F. 2009. Comparison of demographic and direct methods to calculate probabilistic maturation reaction norms for Flemish Cap cod (Gadus morhua). Evolutionary Applications, 2: 291-298.

Philipp, D. P., Cooke, S. J., Claussen, J. E., Koppelman, J. B., Suski, C. D., and Burkett, D. P. 2009. Selection for vulnerability to angling in Largemouth Bass. Transactions of the American Fisheries Society, 138: 189-199.

Pilling, G. M., Kirkwood, G. P., and Walker, S. G. 2002. An improved method for estimating

individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. Canadian Journal of Fisheries and Aquatic Sciences, 59: 424-432.

Plummer, M., Best, N., Cowles, K., and Vines, K. 2006. CODA: convergence diagnosis and output analysis for MCMC. R News, 6: 5.

Pukk, L., Kuparinen, A., Järv, L., Gross, R., and Vasemägi, A. 2013. Genetic and life-history changes associated with fisheries-induced population collapse. Evolutionary Applications: n/a-n/a.

Quince, C., Abrams, P. A., Shuter, B. J., and Lester, N. P. 2008a. Biphasic growth in fish I: Theoretical foundations. Journal of Theoretical Biology, 254: 197-206.

Quince, C., Shuter, B. J., Abrams, P. A., and Lester, N. P. 2008b. Biphasic growth in fish II: Empirical assessment. Journal of Theoretical Biology, 254: 207-214.

Redpath, T. D., Cooke, S. J., Arlinghaus, R., Wahl, D. H., and Philipp, D. P. 2009. Life-history traits and energetic status in relation to vulnerability to angling in an experimentally selected teleost fish. Evolutionary Applications, 2: 312-323.

Redpath, T. D., Cooke, S. J., Suski, C. D., Arlinghaus, R., Couture, P., Wahl, D. H., and Philipp, D. P. 2010. The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish. Canadian Journal of Fisheries and Aquatic Sciences, 67: 1983-1992.

Reñones, O., Goñi, R., Pozo, M., Deudero, S., and Moranta, J. 1999. Effects of protection on the demographic structure and abundance of *Epinephelus marginatus* (Lowe, 1834). Evidence from Cabrera Archipelago National Park (West-central Mediterranean). Marine Life, 9: 2.

Reznick, D. 1982. The impact of predation on life history evolution in Trinidadian Guppies: genetic basis of observed life history patterns. Evolution, 36: 1236-1250.

Reznick, D. A., Bryga, H., and Endler, J. A. 1990. Experimentally

induced life-history evolution in a natural population. Nature, 346: 357-359.

Rijnsdorp, A. 1993. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, (*Pleuronectes platessa*). Oecologia, 96: 391-401.

Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. Science, 278: 1454-1457.

Roff, D. A. 1984. The Evolution of Life History Parameters in Teleosts. Canadian Journal of Fisheries and Aquatic Sciences, 41: 989-1000.

Roff, D. A. 1992. The evolution of life histories: theory and analysis, Chapman and Hall, New York, US.

Saura, M., Moran, P., Brotherstone, S., Caballero, A., Alvarez, J., and Villanueva, B. 2010. Predictions of response to selection caused by angling in a wild population of Atlantic salmon (*Salmo salar*). Freshwater Biology, 55: 923-930.

Schunter, C., Carreras-Carbonell, J., Macpherson, E., Tintoré, J.,

Vidal-Vijande, E., Pascual, A., Guidetti, P., et al. 2011. Matching genetics with oceanography: directional gene flow in a Mediterranean fish species. Molecular Ecology, 20: 5167-5181.

Sharpe, D. M. T., and Hendry, A. P. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evolutionary Applications, 2: 260-275.

Sinclair, A. F., Swain, D. P., and Hanson, J. M. 2002. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Canadian Journal of Fisheries and Aquatic Sciences, 59: 361-371.

Stenseth, N. C., and Dunlop, E. S. 2009. Unnatural selection. Nature, 457: 803-804.

Stinchcombe, J. R., and Kirkpatrick, M. 2012. Genetics and evolution of function-valued traits: understanding environmentally responsive phenotypes. Trends in Ecology & Evolution, 27: 637-647.

Sutter, D. A. H., Suski, C. D., Philipp, D. P., Klefoth, T., Wahl, D. H.,

Kersten, P., Cooke, S. J., et al. 2012. Recreational fishing selectively captures individuals with the highest fitness potential. Proceedings of the National Academy of Sciences.

Sutter, D. A. H., Suski, C. D., Philipp, D. P., Klefoth, T., Wahl, D. H., Kersten, P., Cooke, S. J., et al. in press. Recreational fishing selectively captures individuals with the highest fitness potential. Proceedings of the National Academy of Sciences.

Swain, D. P., Sinclair, A. F., and Mark Hanson, J. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proceedings of the Royal Society B: Biological Sciences, 274: 1015-1022.

Taylor, M. S., and Hellberg, M. E. 2003. Genetic Evidence for Local Retention of Pelagic Larvae in a Caribbean Reef Fish. Science, 299: 107-109.

Uusi-Heikkilä, S., Wolter, C., Klefoth, T., and Arlinghaus, R. 2008. A behavioral perspective on fishing-induced evolution. Trends in Ecology & Evolution, 23: 419-421.

Watson, J. R., Hays, C. G., Raimondi, P. T., Mitarai, S., Dong, C.,

McWilliams, J. C., Blanchette, C. A., et al. 2011. Currents connecting communities: nearshore community similarity and ocean circulation. Ecology, 92: 1193-1200.

Wilson, A. D. M., Binder, T. R., McGrath, K. P., Cooke, S. J., and Godin, J.-G. J. 2011. Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis macrochirus*. Canadian Journal of Fisheries and Aquatic Sciences, 68: 749-757.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314: 787-790.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., et al. 2009. Rebuilding Global Fisheries. Science, 325: 578-585.

Wright, P. J., Millar, C. P., and Gibb, F. M. 2011. Intrastock differences in maturation schedules of Atlantic cod, *Gadus morhua*. ICES Journal of Marine

Science: Journal du Conseil, 68: 1918-1927.

Zuur, A. F., Leno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. 2009. Mixed Effects Models and Extensions in Ecology with R, New York, USA.

List of Appendix

Appendix I

The conventional, deterministic form of the von Bertalanffy model for the size y of a fish at age t reads:

$$y_t = L_\infty{}^* (1- \exp(-k^* (t- t_0))),$$

where L_∞ is the asymptotic size at infinite age, k is the growth parameter, and t_0 is a correction term allowing that the fish has some specific size $y_0 = L_\infty{}^* (1-\exp(k^* t_0))$ at time $t = 0$. Alternatively, $t = t_0$ might be seen as the time when the fish has zero size.

This model corresponds to the solution of the differential equation

$$d_t y = k^* (L_\infty - y), \quad \text{subject to } y(t_0) = 0.$$

The model can be easily extended to the case of non-constant growth parameter $k(t)$, allowing for growth changes. In the general case, the size of the fish at age t is given by

$$y_t = L_\infty{}^* (1- \exp(-Q(t))),$$

where $Q(t) = \int_{t_0}^{t} k(s)\, ds$. If we consider a single spurt occurring at time $t_1 > t_0$, such that the growth parameter changes from $k = k_0$ for $t < t_1$ to $k = k_1$ for $t > t_1$, then

$$Q(t) = k_0{}^* (t- t_0), \qquad\qquad \text{if } t < t_1$$

$$Q(t) = k_0{}^* (t_1- t_0) + k_1{}^* (t- t_1), \qquad\qquad \text{if } t > t_1$$

Hence, the fish size at age t is given by

$$y_t = L_\infty{}^* (1- \exp(-k_0{}^* (t- t_0))), \qquad\qquad \text{if } t < t_1$$

$$y_t = L_\infty{}^* (1- \exp(-k_0{}^* (t_1- t_0) - k_1{}^* (t- t_1))), \quad . \quad \text{if } t > t_1$$

In addition we have fitted a generalization of this model that allows for a change in the growth at a specific moment, t_1, of the life span:

$$y_{ij} = L_{\infty i} * (1 - \exp(-k_{0i} * (t_j - t_{0i}))) + \varepsilon_{ij}, \qquad\qquad \text{for } t_j < t_1$$

$$y_{ij} = L_{\infty i} * (1 - \exp(-k_{0i} * (t_{1i} - t_{0i}) - k_{1i} * (t_j - t_{1i}))) + \varepsilon_{ij}, \qquad\qquad \text{for } t_j > t_1$$

where k_{0i} and k_{1i} are the growth parameters before and after the moment of the change (t_{1i}).

Appendix II

Bayesian implementation of conventional Von Bertalanffy growth model proposed by Pilling *et al.* (2002), Helser and Lai (2004), and Helser *et al.* 2007 imposes structure of the variance covariance matrix of the model parameters. This means that covariance between any pair of parameters is explicitly estimated. It is claimed that this procedure ameliorates parameter estimations.

Here we use a simpler model and covariance is left free (i.e., not explicitly estimated by the model). Obviously, in the case that the individual values (i.e. for any single fish) of a given pair of parameters (e.g., $L_{\infty i}$ and t_{1i}) are well estimated, covariance between them will be well estimated also a posteriori. Demonstration of this was carried out through a simulation experiment. We defined a variance-covariance matrix using the between-parameter correlation (i.e., parameters obtained using the observed data). Then, we generated n sets of growth parameters using the *mvrnorm*() function of the MASS library of the R-package. This $n*5$ (i.e., in the case of 5 parameter model) reflects the known variance-covariance matrix. Then, we generate n growth curves with theses parameters (adding a proper error term, i.e., the observed one) and with the observed length-at-age (i.e., the currently observed age). After that, these n curves, for which we know the individual values of the growth parameters, were submitted to the Bayesian approach described in the text (see Materials and methods). Finally, the estimated growth parameters were compared with the known (simulated) values and they were found to be very similar ($r^2 \approx 0.9$) and unbiased (slope ≈ 1 and intercept ≈ 0). This is shown in the next figure:
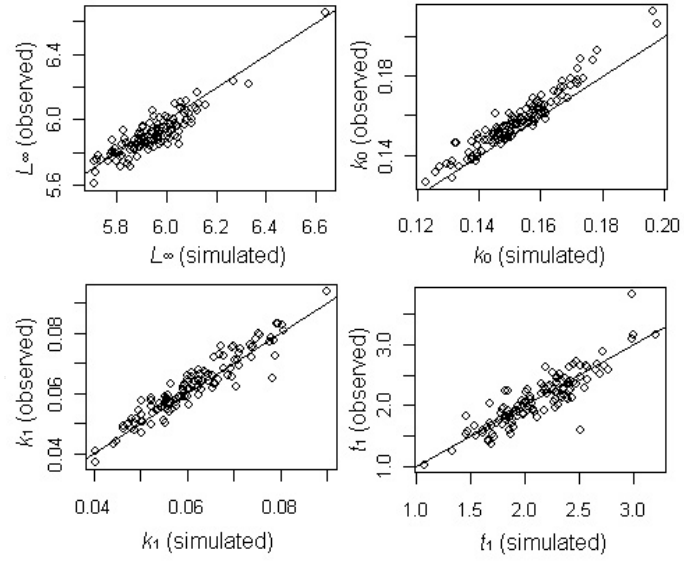
Appendix III

Field experiment to estimate the buoyancy, or specific gravity, of the eggs of *Serranus scriba* during development for dispersal potential

Six adult *S. scriba* individuals of similar sizes (mean and s.d. 145 ± 15 mm) were captured on June 2010 in Palma Bay (Fig. 1 of the manuscript) using conventional hook-and-line recreational fishing gear at depths <20 m and surface water temperatures of approximately 22°C. Individuals were caught early in the morning and transported live in tanks for approximately 30 min to aquaculture facilities (LIMIA, Government of the Balearic Islands). The fish were measured, weighed and placed in a grey cylinder-conical 400 l polyvinyl chloride tank mounted with flow-through UV-sterilised seawater. The temperature and salinity of the system was monitored continuously.

In a previous experiment, the fish did not spawn under similar conditions, likely due the combination of captivity-induced stress and the lack of an appropriate natural spawning environment (J Alós, unpublished data). Therefore, spawning was induced through administration of synthetic agonists of gonadotropin-releasing hormone (GnRHa), which has been successfully used in other species of the Serranidae family, such as Ephinephelus marginatus (Marino *et al.*, 2003). GnRHa stimulates the pituitary synthesis and release of LH and induces ovarian steroidogenesis and oocyte maturation (Mylonas and Zohar, 2000; Zohar and Mylonas, 2001).

Individuals were slightly anesthetised with MS222, and a dose of GnRHa (mean and s.d. of 0.0018 ± 0.0009 ml per g of fish) was inserted in the peritoneal cavity using a hypodermic needle. The fish were allowed to spawn undisturbed in the tank, which was

examined for the presence of eggs every hour. After spawning, the tanks were checked for the presence of fertilised eggs (eggs floating in an intermediate position). Adult individuals were removed from the holding tank, and the water flow and aeration was reduced to prevent damage to the eggs. The temperature and salinity remained constant throughout the experiment (T = 22 ± 0.2°C, salinity = 37.25 ± 0.150).

A sample of approximately 10 eggs was collected every three hours until hatching to estimate changes in buoyancy through development. Egg buoyancy (specific gravity) was measured using the density-gradient column method (Coombs, 1981). Briefly, the method consisted of a 1 m column of water with a stable, constant gradient of seawater salt. The eggs were introduced at the top of the column and settled to a known density level (i.e., the location where the egg is in hydrostatic equilibrium with the surrounding fluid). Glass spheres of a known density were used to calibrate the system (Coombs, 1981; Coombs *et al.*, 1985; Coombs *et al.*, 1990). A temperature-controlled water jacket maintained the apparatus at a stable temperature, similar to the conditions at the time of capture.

Each sub-sample of eggs was introduced into the gradient column. To select a stable density measurement, we recorded the changes in egg density at increasing observational time points (10, 30, and 60 min). The position of the glass spheres in the density column (cm) was recorded at each observational time point and converted to a temperature-corrected specific gravity (g cm-3) (Coombs, 1981). Only fertilized eggs were selected for the experiment. Dead or moribund eggs, which were characterized by

an opaque appearance or rapid sinking to the bottom, were discarded. The sinking or

ascending velocity (w) at each measured time point was calculated based on Stokes' law:

$$w = \frac{gd^2 \Delta\rho}{18\nu}$$

where g is the gravitational force, d is the diameter of the egg, $\Delta\rho$ is the difference

between the density of the environment and the density of the egg and ν is the

molecular viscosity (Sundby, 1997). We were confident that the properties of the egg

remained in agreement with Stokes' law because the diameter of the egg and differences

in density yielded Reynolds numbers < 0.5 (see Sundby, 1997).

Induced spawning occurred between 21:00 and 21:30 on the first night after the

morning hormone treatment (sunset was at 21:21). We successfully measured the

buoyancy of the eggs over five different time periods prior to hatching. The last

measurement was performed after 29.5 h, and 100% of the eggs in the rearing tank had

hatched 32.5 h after fertilisation, which was the morning of the second day after

fertilisation (Fig. 1 of this appendix). The observed mean and s.d. of the egg diameter

was 799 μm ± 32.7 (n=90). The eggs had a single oil globule and a relatively small

perivitelline space (Figure 1 of this appendix).

The mean specific gravity was at neutral buoyancy at the time of the first

measurement, although the eggs remained lighter than the surrounding water for the

remaining duration of the experiment (Figure 1 of this appendix). At 200 min after

fertilisation, the average egg density was close to a neutral buoyancy (5.47×10^{-4} g cm^{-3}), and some of the eggs were becoming heavier at an ambient temperature, which

corresponded mainly to the gastrula stages (Figure 1 of this appendix). The average excess positive buoyancy at the end of the experiment was 2.07 x 10-3 g cm-3, which corresponds to an average ascent velocity of 4.19 m h-1 under homogeneous experimental conditions.

Figure 1 Specific gravity (g cm-3) of *Serranus scriba* eggs through development at 22°C water temperature. A local smoother (95% CI, in grey) has been added to aid in the visualization (function "loess"=local polynomial regression in the library ggplot2 from the R package). Dashed line depicts the specific gravity of the local seawater at the culture temperature. Figure also shows three images of the eggs development at the stages of morula (A, 100 min after fertilization), early (B, 897 min) and late embryo (C, 1,845 min).
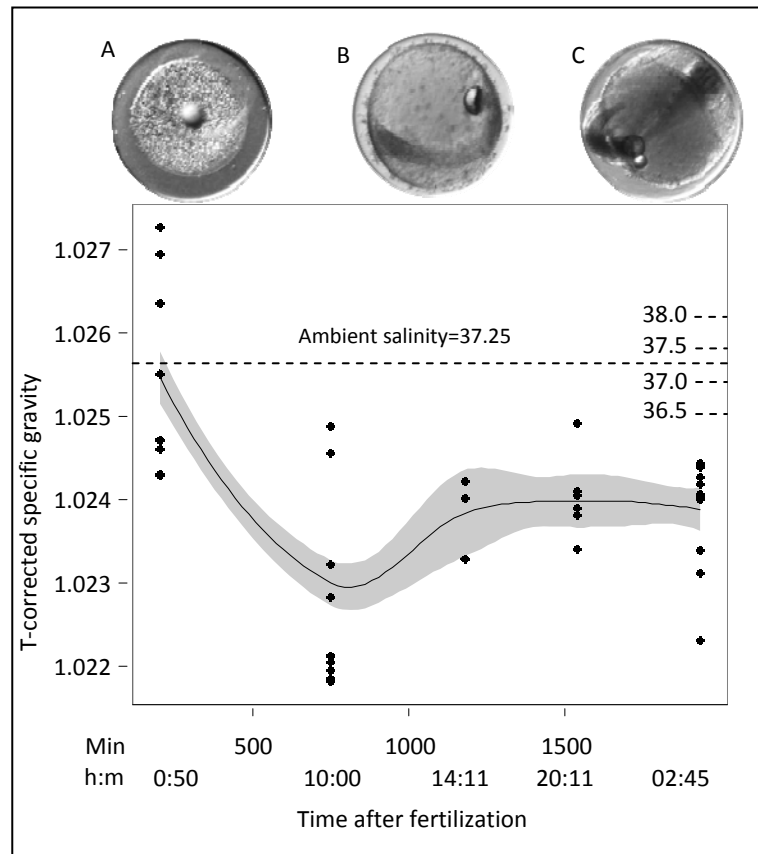
Appendix references

Coombs, S. H. 1981. A density-gradient column for determining the specific gravity of fish eggs, with particular reference to eggs of the mackerel (*Scomber scombrus*). Marine Biology, 63: 101-106.

Coombs, S. H., Fosh, C. A., and Keen, M. A. 1985. The Buoyancy and Vertical Distribution of Eggs of Sprat (*Sprattus Sprattus*) and Pilchard (*Sardina Pilchardus*). Journal of the Marine Biological Association of the United Kingdom, 65: 461-474.

Coombs, S. H., Nichols, J. H., and Fosh, C. A. 1990. Plaice eggs (*Pleuronectes platessa* L.) in the southern North Sea: abundance, spawning area, vertical distribution, and buoyancy. Journal du Conseil: ICES Journal of Marine Science, 47: 133-139.

Marino, G., Panini, E., Longobardi, A., Mandich, A., Finoia, M. G., Zohar, Y., and Mylonas, C. C. 2003. Induction of ovulation in captive-reared dusky grouper, *Epinephelus marginatus* (Lowe, 1834), with a sustained-release GnRHa implant. Aquaculture, 219: 841-858.

Mylonas, C. C., and Zohar, Y. 2000. Use of GnRHa-delivery systems for the control of reproduction in fish. Reviews in Fish Biology and Fisheries, 10: 463-491.

Sundby, S. 1997. Turbulence and ichthyoplankton: influence on vertical distributions and encounter rates. Scientia Marina, 61: 159-176.

Zohar, Y., and Mylonas, C. C. 2001. Endocrine manipulations of spawning in cultured fish: from hormones to genes. Aquaculture, 197: 99-136.
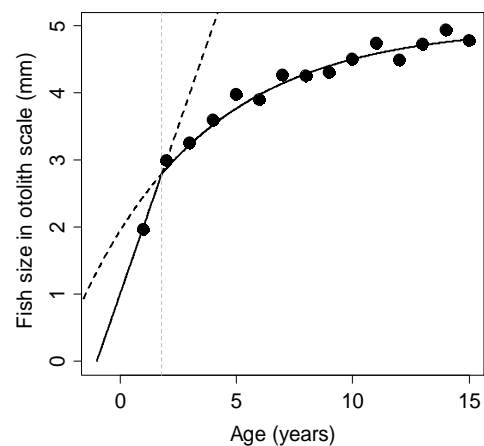
Appendix IV

Prior distributions used for individuals (i) and populations (j) used for Bayesian estimations of the individuals life-history estimations. Normal distributions are denoted as *dnorm* (mean and variance), uniform distribution as *dunif* (minimum and maximum value) and gamma distribution as *dgamma* (shape and scale). L_{max} is referred to otolith scale in mm, h is in mm year^{-1}, g and k in year $^{-1}$ and, T, t_0 and t_1 are in years.

Priors for individuals	
for (i in *1 : n fish)*	
$T[i]$	dnorm(mT[group[j]],1/sqrt(tau$t$))
$k[i]$	dnorm(mk[group[j]],1/sqrt(tau$k$))
$L_{max}[i]$	dnorm(mL_∞[group[j]],1/sqrt(tauL_∞))
$t_0[i]$	dnorm(mt_0[group[j]],1/sqrt(taut_0))
$g[i]$	3*(exp($k[i]$) - 1)
$h[i]$	$L_\infty[i]$*(exp($k[i]$) - 1)
$t_1[i]$	$T[i]$ - (1 - exp(-$k[i]$*($T[i]$ - $t_0[i]$))))/(exp($k[i]$) - 1)
Prior for groups (sampling method)	
for(j in *1 : n groups)*	
m$T[j]$	dnorm(2,1/sqrt(0.5))
m$k[j]$	dunif(0,1)
m$L_{max}[j]$	dnorm(5, 1/sqrt(0.001))
m$t_0[j]$	dunif(-2,1)
m$g[j]$	3*(exp(m$k[j]$) - 1)
m$h[j]$	m$L_\infty[j]$*(exp(m$k[j]$) - 1)
m$t_1[j]$	m$T[j]$ - (1 - exp(-m$k[j]$*(m$T[j]$ - m$t_0[j]$))))/(exp(m$k[j]$) - 1)
Prior for variances	
tau	dgamma (0.001, 0.001)
tau$T$	dgamma (0.001, 0.001)
tau$k$	dgamma (0.001, 0.001)
tauL_{max}	dgamma (0.001, 0.001)
taut_0	dgamma (0.001, 0.001)

Appendix V

The feasibility of the Bayesian approach estimating individual values of life-history traits (LH) was tested via simulation. We generated simulated data (length-at-age data) for one individual with known LHs (L_{max}, g, T and h). A Gaussian error (reasonable otolith reading error) was included to the simulated data using a distribution of mean 0 and standard deviation 0.1 (see Figure 1 of this Appendix). Then the individual values of LH traits were estimated using the model parameterization described in the text (see M&M). The distributions of the Bayesian means estimated were compared with the true values.

Figure 2 Individual trajectory of one individual growing following the somatic growth derived by Lester el al. (2004) (solid line). Grey dashed line shows the timing of maturation (in that case T = 1.8). Dashed black lines after maturation (T) is the projection considering immature lineal growth, while before T is the projection of the VB growth curve exclusively fitted with the mature length-at-age data. Solid circle are the back-calculated length-at-age data at otolith scale (mm).

Simulation exercise demonstrated high feasibility of the Bayesian framework estimating individual life-history traits L_{max}, g, h and T (Table 1 of this appendix). Values estimated trough MCMC from the simulated individual (with known parameters) were very close to the true values (Table 1 of this Appendix). Credibility intervals are relatively small and unbiased for all the parameters (Table 1 of this Appendix).

Table 1 True and estimated (MCMC) values obtained in the simulation exercise done to check the performance of the Bayesian framework used in this study (Fig 2). Estimated values are the Bayesian mean and standard deviation as well as Bayesian credibility intervals. Estimated values are very close to the true values showing the robustness of the approach.

True values		Estimated values (MCMC)				
Parameter				Bayesian credibility intervals		
	value	Mean	SD	2.5%	Median	97.5%
L_{max}	5	5.01	0.09	4.82	5.01	5.19
T	1.8	1.79	0.20	1.35	1.81	2.14
g	0.6	0.62	0.06	0.53	0.61	0.77
h	1	1.04	0.09	0.92	1.02	1.26

[Blank page]