

Theme Session H

Evolutionary effects of exploitation on living marine resources

ICES CM 2006/H :01

Evolutionary effects of exploitation on short-living marine resources: nektonic squid *Illex argentinus* and *Loligo gahi* in the Southwest Atlantic

A. I. Arkhipkin

The short-finned squid *Illex argentinus* and Patagonian squid *Loligo gahi* have been continuously exploited in the Southwest Atlantic since the 1980s. *Illex* is a temperate species with high concentrations on the shelf and slope of South America between 38°S and 54°S. It is targeted by both jiggers and bottom trawlers and catches have ranged between 200,000 and 800,000 tonnes per annum. In contrast, *Loligo gahi* spends its entire life in cold subantarctic waters and its highest densities are found to the southeast of the Falkland Islands (51–52°S). This species is exploited exclusively by bottom trawlers, with total annual catches averaging ~50,000 tonnes. Both these species have a lifespan of about one year. A detailed analysis of their biological data collected from 1988 to 2006 has not revealed any consistent interannual trends in weekly length-frequency distributions, sex ratios, maturities, or age compositions. This suggests that the heavy exploitation of these species has not been noticeably affecting their main population parameters. It is known that short-living animals have evolved adaptations to survive under drastic short-term fluctuations in abundance. They are therefore much less susceptible to prolonged periods of heavy exploitation, unlike the majority of long-living fish.

Keywords: *Illex argentinus*, *Loligo gahi*, squid, exploitation.

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ICES CM 2006/H:02 – Withdrawn

ICES CM 2006/H:03

Exploitation-induced changes in farmed stocks of Pacific oysters along the French Atlantic coast

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In addition to demographic consequences for the target species, commercial exploitation of living resources may induce adaptive changes in life history traits because of selective harvesting. Such adaptive changes may be expressed as either immediate plastic responses to environmental variation or as micro-evolution potentially

occurring within decades. Using a suitable model system, the Pacific oyster (*Crassostrea gigas*), we aim to disentangle plastic and evolutionary components of life-history changes in this commercially important species. Following the extinction of the Portuguese oyster (*C. angulata*) 35 years ago, Pacific oysters originating from Japan were introduced to the French coastlines to sustain production. Since this introduction, there has been a gradual decrease in growth rates and delay in timing of spawning.

Reduced growth rates lower economic potential of the species and although delayed spawning may ensure higher fecundity and better egg quality because of more time for energy acquisition, there is a risk that larvae miss the time window of optimal environmental conditions for development. By using time-series of environmental parameters (biotic and abiotic) to remove noise due to plastic responses in time-series of phenotypic traits, we may observe temporal trends in residuals and thereby separate the effects of plastic and evolutionary components of the observed changes in growth and reproduction.

Whereas plastic responses can be reversed within a generation, backtracking undesirable evolutionary changes generally require several generations.

Investigating the causes of life-history changes is therefore crucial for the selection of correct management strategies to obtain long-term sustainable yields of this species.

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ICES CM 2006/H:04

Management options for reversing depressed maturation-size in Baltic Cod

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The Baltic cod has been heavily exploited for several decades. Therefore there is reason to suspect that fishing may select for a smaller maturation-size, leading to earlier maturation. We develop a general model to determine the optimal maturation size and rate of evolution in fish stocks, based on size spectrum theory and quantitative genetics. The model is simple and uses only few parameters, which are well known for many fish stocks, namely von Bertalanffy growth parameters, maturity ogives, and fishing mortality. Parameters are fitted to Baltic cod, and the effect of three different management

options are explored: 1) lowering the fishing mortality; 2) fishing only on the mature individuals, and 3) reducing fishing on the large individuals only. For Baltic cod we find that the optimal maturation size is very much influenced by the fishing mortality. The only possibility for reversing this selective pressure seems to be a strong reduction of the fishing mortality. Reducing fishing on large individuals can in principle change the optimum, but incremental evolution will not be able to reach that optimum.

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Late or partial fishing moratoria can lead to irreversible changes in age and size at maturation

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Fish in exploited stocks mature earlier and usually at smaller sizes due to genetic and plastic responses. The latter occur e.g. when individual fish grow faster at lower population sizes due to reduced competition for food. Using a size-structured consumer-resource model based on a planktivorous fish life history, we show that exploitation can easily induce irreversible evolutionary changes in individual life histories and stock properties. As a result of annual spawning, early maturation at small sizes and late maturation at large sizes can become alternative, evolutionary, and ecologically stable states in the same environment. Exploitation of late-maturing populations can induce evolution to smaller maturation sizes associated with stepwise decreases in age at first reproduction. We show that complete and early fishing moratoria slowly reverse this process, but belated or partial moratoria can accelerate or even instigate further evolution to smaller sizes at maturation. We suggest that abrupt decreases in maturation age can be used as early warnings of upcoming detrimental evolutionary changes, and should inspire timely restrictions of fisheries.

Keywords: life-history evolution, ecological feedback, density-dependence, harvesting, trade-offs, reversibility, fishing moratoria, complex adaptive systems.

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ICES CM 2006/H:06

An overview of evolutionary effects of fishing on populations, and their implications for management

Marie-Joëlle Rochet

This proposed contribution is a review of the current knowledge about fishing-induced evolution in exploited populations. First, a summary of theoretical models predicting how fishing could cause evolution will be given, focusing on the three main categories of approaches to this problem, namely optimisation, adaptive dynamics, and quantitative genetics. Then, a summary of published evidence for fishing-induced evolutionary changes will be presented, including selective fishing experiments, the evidence of selection pressure due to fishing in exploited populations (mainly on growth), and evidence for evolutionary changes in exploited fish populations (recent finding about fast evolution).

Finally, the proposed implications of these effects for management advice will be examined. Current assessments and diagnostics are flawed by not taking these effects into account, but the development of efficient models including these effects will be impaired by over-parameterisation and limited knowledge. At least appropriate indicators could be useful to monitor these changes. The management objectives, tools, and strategies proposed to address this problem will be reviewed.

Keywords: evolution, population changes, fishing effects.

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ICES CM 2006/H:07

Morphological features of walleye pollock individuals from the different parts of a trawl

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Our previous investigations revealed morphological and behavioural heterogeneity in walleye pollock aggregations. For its further investigation, a trawl fishing survey was conducted in the northern part of Sea of Okhotsk, with sampling of fish from the different sections of the trawl. Sample A was taken from the terminal part of the codend (specimens caught first); sample B – from the nearer part of the codend (specimens caught last); sample C – from the catcher (along with specimens meshed in the belly part around the catcher). The number of vertebrae in the abdominal section (Va), caudal section (Vc), and the total number of vertebrae (Vert) were counted in each sample. Sample C is characterized by higher Va and Vert values in comparison with samples A and B. Modal Va value in sample A is shifted from 18 to 19. The percentage of “long-tail” fish in sample B is greater than in

sample A. Sample C is notable for its maximum diversity and increased number of vertebrae in Va. Morphological features of fish in sample A are the most similar to the characteristics of the whole catch. Based on the results of trawl fishing, the following structure of walleye pollock aggregations is seen. Some fish in the aggregation will be inevitably caught in a trawl with no chance of escape (sample A). Another part of the aggregation consists of the individuals actively getting away from the approaching trawl (sample B). The tactics of fish in group C is rather to get out of the trawl than to escape from the approaching gear. "Short-tail" fish are numerous in sample C, while the "long-tail" specimens are abundant in sample B. Fish of groups C and B having avoided capture maintains the intrapopulation variation of walleye pollock.

Keywords: walleye pollock, population structure, trawl, vertebral column.

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ICES CM 2006/H:08

Size-dependent mortality causes divergent evolutionary responses in maturation size

Anna Gårdmark and Ulf Dieckmann

The size of an individual, especially its size at maturation, influences both individual and population level characteristics. Body size is an important determinant of resource use, fecundity, and mortality risk. Maturation size affects the spawning stock biomass. Evolution of maturation size in response to size-dependent selection is thus a fundamental part of life-history theory. It is also an essential process to consider when assessing the ecosystem effects of fishing in general, and when projecting stock development in particular.

Increased mortality among small individuals has previously been predicted to cause larger maturation size, whereas increased mortality among large individuals is expected to have the opposite effect. We used a continuously size-structured model to show that, contrary to these widespread expectations, increased mortality among small individuals can have three alternative effects: maturation size may increase, decrease, or become evolutionarily bistable (i.e., the response depends on pre-exploitation maturation sizes in the population). We show that such complex responses in maturation must be reckoned with whenever mortality is size-dependent, growth is indeterminate, reproduction impairs growth, and fecundity increases with size, conditions that are particularly common in fish. Predicting adaptive responses to altered size-dependent mortality is urgently needed in fisheries. However, we demonstrate here that predicting the response to size-selective fishing is inherently difficult, since such mortality can not only reverse

the direction of adaptation, but also cause abrupt shifts in evolutionarily stable maturation sizes.

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Fishing-induced early reproduction at the cost of growth in the Baltic cod *Gadus morhua*?

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Increased adult mortality is predicted to decrease maturation age and increase reproductive effort at the cost of somatic growth. Using Swedish survey data we assessed whether the Baltic cod (*Gadus morhua*) stocks (ICES Subdivisions 21 & 23, 24 and 25–30) have undergone evolutionary changes in maturation reaction norm by age and length during the years 1989–2003. Both male and female cod from Baltic Proper showed decreasing trends in length-at-age and condition in several ages, but such changes were not detected in Subdivisions 21 & 23 and 24. Male cod from Baltic Proper showed a linear trend towards decreased length at 50% probability of maturing at age three, but there were no statistically significant trends in other ages, areas, or in females. Males had a reaction norm for earlier maturation than females and fish from the Southern Baltic tended to mature earlier and reach the equal maturation size faster than their specimens from the Baltic proper. Also good condition at small size and at young age contributed to high maturation probability. Our results suggest that fishing might affect sexes differently. Faster growth in Southern areas of the Baltic Sea did not turn into different maturation reaction norm, but environmental factors contributed to the earlier maturation of Southern fish by their faster growth rate. We suggest that some fisheries-induced evolution has occurred in the heavily exploited cod population of the Baltic Proper, but further studies are needed about factors that led to the concurrent decrease in their condition.

Keywords: evolution, human-induced, life history, reaction norm, reproduction.

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The propensity for marine reserves to slow the evolutionary effects of fishing

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Several recent theoretical and empirical studies have provided evidence that fishing is capable of inducing

evolutionary changes in key life history traits. These evolutionary changes can have unwanted consequences, such as reduced body sizes in the catch, which might lead to a deterioration of the quality of the fishery. Therefore, managers need viable options for slowing, stopping, or reversing the evolutionary consequences of fishing. In this study, we explore one potential management strategy by developing and analyzing an eco-genetic model aimed at studying the effects of marine reserves on fishing-induced evolution. Our model advances previous theoretical approaches by including features such as phenotypic plasticity, density-dependent growth, and evolution of multiple life history traits. We parameterize our model for a population of cod that undergoes an annual migration from feeding grounds to spawning grounds. Using our model, we explore the consequences of marine reserve location (either in the feeding grounds or in the spawning grounds) and proportion of area protected on the speed, direction, and magnitude of evolutionary responses. The results of our model underscore the importance of having an evolutionary perspective when implementing management strategies aimed at protecting commercially important fish stocks.

Keywords: fishing-induced adaptive change; evolution; marine reserves; life history theory; exploitation; density-dependent growth; phenotypic plasticity.

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Eco-genetic models: A new framework for understanding fisheries-induced evolution

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The majority of existing evolutionary models have not been designed to match the specific and rather complex needs of studies of fisheries-induced evolution. This is because such studies require accounting for (a) the physiological structure of fish populations in terms of age, size, and maturation status; (b) trade-offs between the fitness consequences of changes in salient life-history traits; (c) the considerable degree of phenotypic plasticity typically underlying the population dynamics of fish populations; (d) frequency-dependent selection pressures resulting, e.g., from density-dependent growth and recruitment; and (e) the amount and distribution of additive genetic variance harbored by fish populations. Earlier modeling approaches based on life-history optimization methods or on quantitative genetics theory succeeded in reflecting (a) and (b), but have rarely incorporated (c), and typically fall short of reflecting (d) and/or (e). More recent models, based on adaptive dynamics theory, can take care of (a) to (d), but fail to do justice to (e). This situation sets the stage for the development of a new generation of models of fisheries-induced evolution capable of addressing (a) to (e) simultaneously. These new models are called 'eco-genetic,' to reflect that they are

specifically geared to incorporate a sufficient amount of ecological detail, thus tackling features (a) to (d), in addition to a suitable rendering of genetic detail, thus tackling feature (e). Eco-genetic models help (1) evaluate hypotheses advanced for explaining observed data; (2) understand and quantify fisheries-induced selection pressures; (3) forecast the direction, speed, and outcome of evolutionary changes; and (4) investigate the consequences of realistic management scenarios.

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Effects of fisheries on energy- and sex-allocation in slow-growing hermaphrodites such as groupers

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Fishing is identified as a potential cause for driving evolution towards earlier maturation in many fish stocks and has been suggested to lead to earlier sex change in sex-changing species such as groupers. Many studies have focused on the ecological effects of fisheries on sex-changing fish, but little attention has been directed towards understanding the evolutionary responses to high and size-dependent fishing mortality. We have developed an individual-based model of emergent size at maturity and energy allocation under varying levels of fishing mortality. In the model, individuals differ in their age at maturation and energy allocated to reproduction in male and female phase. Our results predict that these traits are quite sensitive to even low fishing mortalities. Age and length at both maturation and sex change decrease in the population with increasing fishing mortalities. The model predicts shifts (at the population level) between a hermaphroditic and dioecious strategy with increasing fishing mortalities, as well as decreasing population size and increasing female to male sex ratios with fishing effort. Yield peaks are at low to intermediate levels of fishing mortality (about 0.08 year⁻¹). The simplest form of management of the fishery requires implementing a low fishing mortality and choosing proper size limits for the fishery.

Keywords: fisheries-induced life history change, sex allocation, energy allocation, individual-based model, grouper.

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Effects of different management regimes on harvest-induced life history evolution in Northeast Arctic cod

Christian Jørgensen, Øyvind Fiksen, and Bruno Ernande

Field and lab experiments, analyses of fisheries data, theory, and models all corroborate that harvest may induce rapid and substantial life history changes in many exploited fish stocks. Which life history trait will change and to what degree depends on the selectivity of the fishery and the ecology and life history of the species in question, making it hard to reach general conclusions about potentially successful management options. Here, we ask to what degree different management regimes may decrease or reverse the negative effects of harvest-induced life history evolution in the Northeast Arctic cod. We use a state-dependent energy-allocation life-history model for cod. A set of life history strategies are optimized by varying the mortality, and we then use quantitative genetics to describe how these strategies change in frequency in a population due to harvest-induced selection. We can thus quantify the evolutionary effect of fishing on life history change and assess evolutionary rates. We present the effects of three different management regimes: marine protected area, maximum size-limit, and minimum size-limit. Marine protected areas and minimum size-limits result in reduced evolutionary rates compared to current fishing regimes, while maximum size-limits result in little change.

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Fisheries-induced evolutionary change at the onset of maturation in North Sea sole (*Solea solea*)

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Age and size at maturation has been observed to decrease in some commercially exploited fish stocks during the last decades. According to evolutionary theory of life history traits age and size at maturation play a crucial role in optimizing lifespan fitness and a change might be consistent with increased mortality, in this case fishing mortality. However, it is not unambiguous whether the observed changes are due to other factors than mortality and if they reflect evolving allelic frequencies or phenotypic plasticity. The plastic responses to compensatory density-dependent and environmental effects such as increased food availability might be much larger and therefore overshadow the direction of life history evolution. In order to disentangle phenotypic plasticity from evolutionary change, we employ the probabilistic reaction-norm approach, which allows for estimates of probabilities of maturing independently on growth and survival. The method, which is applied to 34 female cohorts

(1963 to 1996) using market sampling data from the German Bight and Southern Bight separately, showed that the reaction norm for age and length at first maturation has significantly shifted towards younger age and smaller length. Consequences of fishery-induced evolution for the sustainability of the fishery are discussed.

Keywords: maturation, fisheries-induced change, phenotypic plasticity, evolution.

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The influence of reproductive behaviour on the direction and rate of fishery-induced evolution

Sherrylynn Rowe and Jeffrey A. Hutchings

Reproductive behaviour has the potential to influence the direction and rate of evolutionary change in exploited populations. This may be particularly evident in species for which mate choice is an integral component of the mating system. Mate preferences exerted by one sex that are non-random with respect to phenotype will generate selection pressures on heritable traits. Genetic and behavioural data on Atlantic cod (*Gadus morhua*), for example, are consistent with the hypothesis that both males and females prefer spawning with larger mates. All else being equal, this has the potential to generate selection against early-, small-maturing genotypes. Fisheries for cod, by contrast, have significant potential to select against late-, large-maturing genotypes. Should such a selection dichotomy exist, it has the potential to influence the direction and, perhaps more interestingly, the rate of evolutionary change in life history traits. Using data on temporal changes in Atlantic cod life history traits, we explore the potential consequences of interactions among mate choice, fishery-induced selection, and rates of evolutionary change in commercially exploited marine fishes.

Keywords: mating system, mate choice, exploitation, selection, evolution, life history.

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ICES CM 2006/H:16

A bio-economic model on fisheries-induced evolution in Northeast Arctic cod

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High fishing pressures may cause evolution towards maturation at earlier ages and smaller sizes, and therefore decrease the profit of the corresponding fishery. For example, the world's largest stock of Atlantic cod, the Northeast Arctic cod population of the Barents Sea, has experienced a considerable reduction in its mean age at maturation from 10 to around 6 to 7 years during the second half of the twentieth century. There is a price premium of about 70% on fish above 3 kg compared with fish below 1 kg, and this premium will in all likelihood increase when the abundance of large fish in the stock is diminished.

Considering that the total value of Norwegian cod fisheries was 3 billion Norwegian Kroners (approximately 400 M€) in 2005, it is clear that fisheries-induced evolution can lead to considerable economic losses.

In this study, we aim to integrate and strengthen the interface between ecological, evolutionary, and economic modeling, in order to contribute to an improved understanding of the long-term effects of fishing. We will analyze how the economic returns from fish stocks are affected by this interplay and examine what harvest strategies are optimal, both economically and ecologically. The biological component of this approach is based on an individual-based eco-genetic model for the Northeast Arctic cod.

The primary management objective to be analyzed will be to maximize the long-term profitability of the fisheries as measured by the present net value of the fisheries-generated cash flow. Making the economic and ecological costs of fisheries-induced evolution explicit in this way will serve as an important step forward in the development and implementation of improved management practices.

Keywords: fisheries-induced adaptive change, economy, life-history evolution, individual-based model, *Gadus morhua*.

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ICES CM 2006/H:17

Evolutionary consequences of harvesting in ecosystems

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Short-term population dynamical consequences from exploitation of commercial fish stocks have been studied for a long time, but it is only recently that the evolutionary dimension has started to receive attention.

Most of the studies of fisheries-induced evolution up till now have focused on a single or a few species in isolation, leaving important co-evolutionary interactions relatively unexplored. In this study, I present a model for the origin and evolution of size-structured food webs which is based on the Lotka-Volterra equations, where size-dependent interactions and small mutations in body size over time leads to food webs with three to four trophic levels. The resulting ecological communities are then subjected to various harvesting regimes, after which the consequences for population dynamics and evolutionary dynamics are analysed.

Keywords: multi-species communities, harvesting, evolution, food web.

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ICES CM 2006/H:18

Ecological and evolutionary recovery of exploited fish stocks

Katja Enberg, Erin S. Dunlop, and Ulf Dieckmann

As a result of the current, declining trends in the abundance of many exploited fish stocks, fisheries management is compelled to deal also with stocks that have collapsed and are in the phase of recovery. There is a growing concern of the possibility and potential for recovery of such stocks. Evolutionary changes caused by fisheries are known to affect the genetic and phenotypic structure of the exploited fish stocks. These changes have been most visible in the life history characteristics, influencing age and size at maturation. Important questions still remain unanswered: is the recovery potential of fished stocks also influenced by such changes? Moreover, are such adaptive changes in, for example, maturity schedule, restorable? In our paper we study, by means of an eco-genetic model with multiple evolving traits, how fisheries-induced evolution affects and is affected by the collapse and recovery of fish stocks. We further present the outcome of introducing environmental uncertainties into the population dynamical component of this model, and investigate whether it is possible to facilitate the recovery process. Our results elucidate the different levels of stock recovery, including its ecological (population

size and biomass) and evolutionary (genetic composition and adaptability) components.

Keywords: Fisheries-induced change, eco-genetic model, recovery, life history, environmental fluctuations.

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ICES CM 2006/H:19

Body condition and evolution of maturation of Atlantic cod in Newfoundland

Loïc Baulier, Mikko Heino, George R. Lilly, and Ulf Dieckmann

Atlantic cod (*Gadus morhua*, L.) stocks off Newfoundland and Labrador underwent severe depletions that started in the late 1980s and led to moratoria in the early 1990s. Fisheries closures are still applied in most of the areas where cod is found. A very low stock level, probably resulting from the combined effects of overfishing and bad environmental conditions, has been accompanied by modifications of life history traits of the fish. Among the reproductive traits, a decrease in both age and size at first reproduction has been observed. A partial genetical determinism of these shifts is supported by earlier analyses of probabilistic maturation reaction norms, revealing a consistent trend towards earlier maturation but also strong short-term fluctuations. In this study, we elucidate the effect of changes in individual body condition on short- and long-term changes in maturation of cod. The condition of individuals has already been shown to influence the number and quality of offspring in cod. Here we use maturation reaction norms with three explanatory dimensions (age, size, and condition) to set out to know if the changes in age and size at maturation are linked to changes in condition, measured by the hepato-somatic index.

Keywords: maturation, condition, reaction norm, cod, hepato-somatic index

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ICES CM 2006/H:20 – Poster

Effects of a trawling ban on the life-history patterns of exploited fishes. The case of red mullet (*Mullus barbatus*, L. 1758) in the Gulf of Castellammare (north-western Sicily – Mediterranean)

Fabio Fiorentino, F. Badalamenti, G. D'Anna, T. Fortibuoni, G. Garofalo, M. Gristina, and C. Pipitone

Red mullet (*Mullus barbatus* L., 1758) is one of the main target species in Mediterranean demersal fisheries. Reproduction is reported to occur from May to July, when the bulk of the spawning stock is 1 year old (mean total length (TL) range: 120–150 mm for females, 110–135 for males), followed by a discrete recruitment in August–October. The remarkable increase in red mullet biomass that occurred in the Gulf of Castellammare after a trawling ban prompted us to examine the size structure and sexual maturity of the population over time (i.e. within seasons and in the years before and after the ban) to better understand this recovery success.

Only one discrete period of recruitment in summer was observed in the years before the ban. Conversely, a diffuse recruitment all year round was recorded after the ban, when the bulk of mature individuals (median TL range: 140–150 mm in females, 130–140 mm in males) was found in spring-summer, although large-size spawners (median TL range: 160–215 mm for females, 135–160 mm for males) were also recorded in other seasons. Spawners were distributed over a wide bathymetric range and size was positively correlated with depth. Indeed, larger mature individuals were found deeper than 100 m (median TL range: 165–180 mm in females, 145–155 mm in males).

The observed differences—with respect to the known recruitment pattern—may be related to the major presence of larger and older specimens with potentially different reproductive strategy. Results are discussed on the basis of the reduction of fishing mortality in the area.

Keywords: trawling ban, red mullet, recruitment, spawning stock, Mediterranean.

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