# Sixteen lessons from a 40-year quest to understand the mysterious life of the grey triggerfish

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## Food for Thought

# Sixteen lessons from a 40-year quest to understand the mysterious life of the grey triggerfish

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Fish stock assessments based solely on energy flow through the ecosystem are not good predictors of population dynamics. To accurately forecast the response of populations within one or more ecological regimes, consideration must be given to non-trophic mechanisms allowing interactions inside the system, and fish behaviour in response to changes in their habitats. The example of the grey triggerfish (*Balistes capriscus*) in West Africa shows that fisheries biology is unable to model satisfactorily the life of a fish population. The Ecosystem Approach to Fisheries improves the models but does not overcome this fundamental limitation. Data from direct observations of fish biology and behaviour must be added to the catch and environmental data to help to design energetic-cybernetic models in order to anticipate non-linear and chaotic dynamics. This requires adding data collected by fishers (e.g. underwater acoustics) to scientific data bases, conceiving environmental indicators (e.g. habitat), and using scenarios to anticipate the reactions of populations to regime shifts. It also requires a good understanding of the population structures and strategies. We developed the concept of "pelagic metapopulation" which, through comparative analysis with the jack mackerel (*Trachurus murphyi*), allowed us to propose a hypothesis explaining the history of the grey triggerfish population.

**Keywords:** fish behaviour, fisheries acoustics, habitat, metapopulation, stock assessment.

## Introduction

Naïve question from the audience: if fisheries biology did not exist, would the present status of the world's fisheries be different? Most likely the answer is, "not substantially". We must take two points into consideration: (i) as stated by Zwolinski and Demer (2012) "It is widely recognized that many fish stocks worldwide have collapsed because of overexploitation, [and also] perhaps because of cyclical environmental factors, anthropogenic factors, or both" (Pauly *et al.*, 2003; Myers and Worms, 2005a; Hilborn *et al.*, 2005; Coll *et al.*, 2008; Hilborn, 2011); (ii) almost all the large pelagic stocks worldwide have suffered big changes (collapses and/or recoveries) at least once in their history (Hutchings and Reynolds, 2004), which were not foreseen by the assessment experts (Myers and Worms, 2005b; Worm *et al.*, 2009). The story that I present here is the result of a long series of personal experiences which slowly opened my mind to these questions and allowed me to formalize some hypotheses that I tested, with both successes and failures. Analysing such a long process accumulated during one's career may help to understand how hypotheses, which cannot be considered as spontaneously created by the mind, arise: personal history plays an important role in their conception. This was my [Lesson 1]: if science may be pure logic, research is more likely a craftsman's trade. It essentially works through empirical feed-backs between what the scientist knows and what he/she experiments on, observes and measures.

## Back to the beginning

As a student I attended the University of Paris-Sud. My first experience in fisheries came from a student job on side trawlers in Brittany—several 2-week fishing trips collecting data. At that point of my career, fishers taught me a series of important lessons. [Lesson 2]: data quality depends on many things, not necessarily linked to the fishery itself (seasickness being one of them!); [Lesson 3]: catch data alone do not adequately represent what happens during a fishing operation; [Lesson 4]: being on the deck every 4 h during 15 days of landing, sorting, discarding, cleaning, and storing fish is a unique experience for learning what a fishery is all about; [Lesson 5]: fishers, who are at sea most of the time, are an extraordinary albeit—until recently—largely underexploited source of knowledge (Hind, 2015) and data (Karp, 2007; Melvin *et al.*, 2016a,b; Stephenson *et al.*, 2016); [Lesson 6]: fish behaviour represents a major issue in fisheries research, but at this time was completely ignored by the assessment studies.

When I was recruited in 1973 by ORSTOM (*Office de la Recherche Scientifique et Technique Outre-Mer*, then IRD—*Institut de Recherche pour le Développement*—since 2001: www.ird.fr), my background was of a zoologist with some limited skills in fish population dynamics and marine ecology. In November, 1973, ORSTOM took me to Ivory Coast to a work part-time in a project studying the fisheries resources and exploitation of the large lagoons surrounding Abidjan; and part-time under Emile Marchal's direction to evaluate the marine stocks along the West African coast with a new technique: fisheries acoustics (Forbes and Nakken, 1972; Stéquert and Gerlotto, 1977). The priority in the 1970s in West Africa was "exploration", for two reasons. First, in the 1960s, the French colonial empire was being dismantled. African countries became independent and began to evaluate their own economically important assets, including their marine resources. Second, the idea of creating "Exclusive Economic Zones" (formalized in 1982 with the UN Convention on the Law of the Sea) arose, and evaluating these still largely underexploited, if not completely unknown, offshore resources allowed these young countries to negotiate treaties to either sell fishing rights or develop their own fisheries.

Once in Abidjan, I had the unique opportunity to undertake pioneer activities in the Ebrié lagoon, as it was the first time fisheries research was conducted there, although a few studies on natural history and ecology had been performed some years or even decades earlier (Monod, 1950; Fernandes *et al.*, 1951; Daget and Durand, 1968). Ebrié lagoon is 150 km long and 10–20 km wide, with a yearly catch around 10 000 tonnes (Gerlotto *et al.*, 1976a, b). The only other important research in the lagoon at this time was Serge Garcia's on *Penaeus duorarum* (Garcia, 1977). The project allowed me to practice, on a small scale, all the steps usually performed separately by big teams in fisheries research: counting canoes and fishing gear; preparing a catalogue of fishing methods and techniques; evaluating the potential fishing effort; embarking with fishers; defining the catch per unit effort (CPUE) and the fishing seasons; studying the commercialization systems (Gerlotto *et al.*, 1976a,b). I established a network of data collectors, prepared data bases for statistics, and data processing. I also had to obtain the biological information needed for fisheries research: ecological stratification in the lagoon, and growth curves, fecundity, distribution, spawning periods, spawning grounds, migrations and behaviour for the most important species. I eventually worked up the data and published the results (Albaret and Gerlotto, 1976; Gerlotto, 1976, 1979; Durand *et al.*, 1978; Gerlotto and Stéquert, 1978). This rather short (1973–1978) but exhaustive experience allowed me to discover in detail all of the elements collected and calculated for an assessment analysis of a stock. I received there my second series of lessons. [Lesson 7] taught me that even sound decisions could have unexpected ecological consequences. The lagoon is a complex ecosystem within which the fishery is one actor among others, and changing one single compartment of this system was likely to induce a cascade of many other unexpected (and often not desirable) changes. Let me describe a personal (unpublished) observation. Fishers around the lagoon were also farmers. Reducing fishing effort for conservation reasons implied that they had to increase their effort in agriculture to maintain their activity, which they did by burning the forest to get more cultivable lands, with negative impact on the terrestrial ecosystem. Here, a conservative decision for the lagoon led to an ecological concern in a completely different area. One thing is to define the recommendation of a model in your office; another one is to measure its actual effects on the field.

[Lesson 8] was that you should not accept the "obvious" if you don't check it by yourself. I discovered that the artisanal fishery, usually considered a small and traditional activity in tiny villages, was quite different from this "obvious" view in West Africa. On the contrary, it was probably the most effective fishing activity, even more international, modern and profitable than the national fishing industry in Ivory Coast at this time (Gerlotto *et al.*, 1980). Fishing gear and outboard engines were imported from Japan, huge dugout canoes were purchased in Ghana, some of the fishers used to come seasonally from Benin, part of the fishery migrated seasonally to Senegal, etc. (Gerlotto *et al.*, 1979, 1980). Part of the catch (frozen shrimp) was sold in Europe and the smoked fish was exported over long distances in Africa, from Abidjan up to Ouagadougou or Niamey, i.e. thousands of km from the fishing grounds. The fish market was probably as important (in volume and costs), international, reactive, complex, speculative, and sophisticated as any other in the world. That made me extremely reluctant to accept the "obvious" idea that artisanal fishery is always the "good guy" and industrial fishery the "bad guy".

[Lesson 9] was that data are not "the truth", but are built according to preliminary, often implicit, hypotheses. Just think about this: by convention, a fishing activity is almost always inferred by the catch. This means that anything else is ignored (fishing conditions, market, weather, fishers' experience, fish behaviour, competition, predation, fish learning, precision of measurements, vessel noise, hydrological conditions, multi-specific structure of the catch, etc.). The "catch-data-only" approach implicitly assumes that fishing activity can be correctly described through the local abundance of fish and the fishing effort, which can be measured using the weight of the catch. Why the weight and not any other information? Most likely because catches in weight were already collected by the fisheries administrations (for their own needs) and the scientist just took the data and continued the series, following the rule "if it works, don't fix it". I will detail later what strong hypothesis is hidden behind the catch data. This is often forgotten in a world where, thanks to the internet, databases become independent from their sources. Forgetting this link may produce silly results; data become absolute truth, and this can be disastrous. A good example is given by Pauly (2016) on how such faith in international catch data bases led to incorrect interpretation of the history of global fisheries.

My other activity was in fisheries acoustics. ORSTOM received a research vessel in June 1972, the RV "Capricorne", equipped with SIMRAD analogue instruments: an EKS echo sounder and a QM echo integrator. After a series of preliminary surveys from Congo to Senegal, my first usable results were obtained in July 1974 on the pelagic distribution of micronekton density inside the mid-Atlantic "Deep Scattering Layer" (Gerlotto, 1975; Marchal *et al.*, 1993). It was a revelation. I could provide relative abundance indices and dynamic distribution of the biomass in relation to 3-D hydrodynamic characteristics of the ocean environment. Fisheries acoustics was opening large perspectives, not yet explored. Later, from 1976 to 1980, we were able to obtain biomass estimates in Senegal (Gerlotto *et al*., 1976a,b), Guinea Bissau (Stéquert *et al*., 1977), Ivory Coast (Marchal and Picault, 1977), and Guinea (Marchal *et al*., 1979, 1980).

## The mysterious history of the grey triggerfish in West Africa

Being fortuitously in the right place at the right time I was among the first scientists to explore these ecosystems using modern methods and techniques, and to make a series of (modest) discoveries, among which, one in particular influenced the trajectory of my scientific career: the expansion of the grey triggerfish (*Balistes capriscus*) population of West Africa during the 1970s.

Before 1972, the major stock on the Ghanaian-Ivorian continental shelf was the round sardine *Sardinella aurita*. It was principally exploited by artisanal fisheries using big dugout canoes with large purse seines (Gerlotto and Stéquert, 1978; Gerlotto *et al*. 1979a,b). The average catch was around 25 000 tonnes per year (mean 1963–1971). In 1972, the catch increased substantially and reached 72 000 tonnes (close to 95 000 tonnes when including the small industrial fishery operating in the area). Then it dropped dramatically to 4700 tonnes in 1973 and 1400 tonnes in 1974, and for a few years it remained at this order of magnitude. In parallel, the formerly scattered and insignificant population of grey triggerfish increased enormously after 1972, expanding eventually to the entire West African shelf from Nigeria to Senegal. We estimated its biomass peaked at around one million tonnes, making this species the most abundant in West Africa (Caverivière *et al*., 1981; Caverivière, 1982; Binet *et al*., 1991). This expansion took approximately 5–6 years and several generations of fish: we captured schools of juvenile triggerfish in 1978 in Guinea (Marchal *et al*., 1979, 1980), which were too young to be born elsewhere. Moreover, the biology of this fish changed. The grey triggerfish is usually known as a solitary sedentary demersal fish, displaying territorial behaviour around its nest during the spawning season (Simmons and Szedlmayer, 2012). After the explosion, the fish became pelagic, gregarious, migratory (Caverivière *et al*., 1980, 1981; Caverivière, 1982), living in big schools: the biggest catch we performed on a single school weighted 27 tonnes (Robertson, 1977). Then, the stock dropped off and although not exploited except in Ghana, triggerfish abundance returned to its original level, i.e. sporadic distribution of a few individuals all along the shelf. Since the 1990s, the global situation has been as it was before 1972 (Figure 1).

How did scientists explain this story? A dedicated international workshop was held in 1976 (Ansa-Emmin and Marcille, 1976). It concluded that the round sardine would likely take decades to recover from such a collapse, because the stock suffered a combination of strong overfishing, occupation of its niche by *B. capriscus*, and changes in the ecosystem (Binet, 1982; Binet *et al*., 1991).

Actually, the recovery was much faster; from 1978 to 2000, the average catch was around 59 000 tonnes, i.e. twofold higher than before 1972 (Binet *et al*., 1991). Obviously the conclusions were not accurate. In 1991, the synthesis of a series of workshops in West Africa was published (Cury and Roy, 1991), which included new keywords: instability, variability, and environmental changes. Climatic or environmental variables began to be included in the models (Fréon, 1989; Cury and Roy, 1989). This effort eventually led to the "Ecosystem Approach to Fisheries" (Garcia, 1996). This new approach was particularly welcome in tropical ecosystems which presented a high sensitivity to climatic changes, strong behavioural reactions of fish to external stimuli, a rather low pressure (at that time) from fisheries, displaying clearly the impact of environment on stock dynamics. But even this series of improvements did not explain the variations in triggerfish biomass and behaviour; changes did not have anything to do with human activities and environment could explain the beginning of the story, but not the full story. Why? Such questions oriented assessment scientists' activities towards more sophisticated models, adding environmental hypotheses and metrics, but always using mostly fisheries data; they oriented mine towards a rather different domain: fish behavioural ecology.

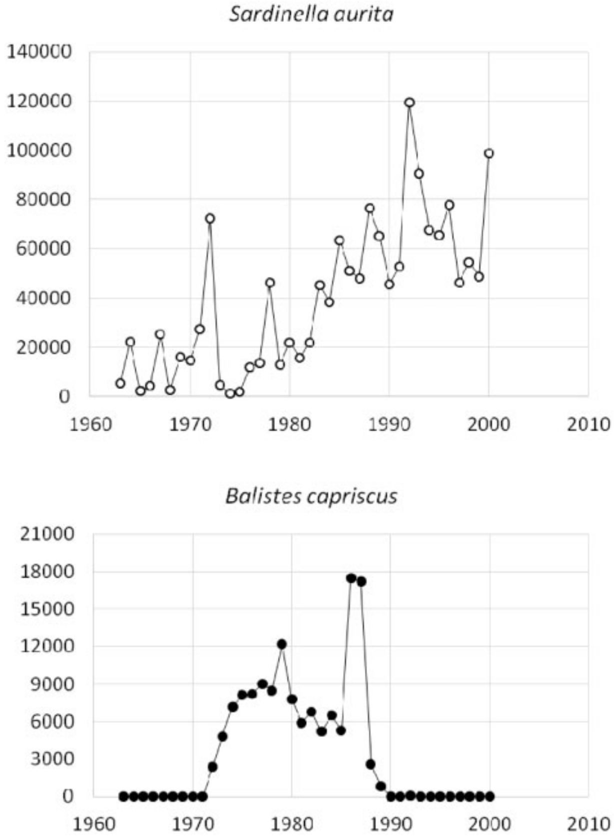

**Figure 1.** Catches of the Ghanaian artisanal fishery (from Aggrey-Fynn, 2007; Binet et al., 1991; Caverivière, 1991, for *B. capriscus* data before 1972).

## Contributions to fisheries acoustics and fish biology

My activities took two different but complementary routes. The first was to develop tools and methods able to provide good and abundant pieces of information. The second was to build some conceptual models based on these biological and behavioural questions. But this kind of activity cannot be performed alone, and there was a need to discuss the results, the questions and the hypotheses with the international community. From 1986 to 1991 my colleagues Fréon, Soria and myself developed an ORSTOM project (EICHOANT) devoted to studying the effect of fish behaviour on fish stock assessment, by way of experiments and surveys in Martinique (FWI) and Venezuela. We submitted the important series of results obtained between 1985 and 1990 (Anonymous, 1990a,b) to the international community and became active members of the ICES groups, and more specifically the ICES Working Group on Fisheries Acoustics Science and Technology (FAST), which was (and still is) the most important world forum in this discipline. Belonging to this community was especially critical for us who were somehow outsiders. First of all, at this time, the English language was not considered indispensable for doing good science in France, making the contacts (and the literature) limited. Second, our work area and major objectives were apparently different from those of the "northern" community. Anderson (2015) describes ICES very clearly and how critical its role is for the fisheries research community. After 10 years of membership in the FAST, I received from Peter Stewart, the then chair of the Fisheries Technology Committee (FTC), the parent Committee of FAST, the following suggestion: "François, in life there is a time to be young and a time to be old; a time to be a son and a time to be a father; a time to be a student and a time to be a teacher; it is time for you now to consider being chairman of FAST". I complied, applied for the job and was elected the fourth chair (1997–2000) following Kjell Olsen, Jim Traynor and John Simmonds in that capacity (Fernandes *et al.*, 2002). Fréon and Misund (1999) summarized our research results in a book which is still a reference. I later was elected chair of the Fisheries Technology Committee (2005–2007), which gave us even greater access to the ICES forum where our hypotheses could be discussed.

I included this story because it is linked with [Lesson 10]: full integration in the international community is essential in a scientist's life, especially for those who are not from English-speaking countries. Most of my career was in Africa (Ivory Coast, Senegal), the Caribbean (Martinique, Cuba, Venezuela) and South America (Chile, Peru). I discovered that one of the strongest limitations in these countries, as far as research was concerned, was the timidity of their young scientists, handicapped by their poor practice of English. Scientists from English-speaking countries can hardly realize how difficult it is to belong to the international community when one is not fluent in English, and how thoughts expressed in one's mother language, whatever their quality, lose their strength when they have to be translated into (poor) English. Institutions like ICES, with their long practice of international exchanges, play a critical role, and I strongly recommend that these "non-English-speaking" scientists should become involved in such groups.

Echo-integration was progressing quickly. A history of fisheries acoustics in ICES was published by Fernandes *et al.* (2002), who related all of this collective adventure. In the 1990s, technique was no longer a real issue: evidently, many improvements were still needed, but because the electronics, computer facilities, and theoretical concepts already existed and were rapidly progressing, their development was just a matter of time and money. Methodology was another story. It still presented theoretical and fundamental limitations and prevented acoustic results from describing the stock structure and absolute abundance estimates with the degree of accuracy required by assessment models. In particular, two types of scientific studies were needed to which I could contribute: statistics and fish behaviour.

## Statistical meaning of acoustic data

Before the 1980s, statistical methods applied to echo-integration results were very poor. Apart from the works of Bazigos (1975, 1981) and Shotton and Bazigos (1984), no reference work had been published on this topic. Scientists simply applied conventional statistics, violating various conditions for their application. Acoustic samplings present a series of characteristics that theoretically forbid the application of standard variance estimates. Samplings in transects are systematic, auto-correlated, continuous in time and space, and much more detailed in the direction of transects than perpendicular to them (anisotropy). Under these conditions, standard confidence intervals have no meaning (Aglen, 1983; Gerlotto and Stequert, 1983). Some studies intended to find solutions (Johannesson and Mitson, 1983) but the result was often worse, as these solutions actually added more violations to the list, such as post-stratification using the data themselves. Jolly and Hampton (1991) published the only effective method that introduced stochasticity in the data by determining randomly the starting point of the survey and the inter-transect distances. They produced more acceptable variance measurements. But these methods, and especially the random inter-transect distance, did not improve the estimate of the biomass value, as wide inter-transect spaces may become unexplored (Fernandes *et al.*, 2002). Knowing that distribution laws of fish concentrations are highly asymmetric (Fréon *et al.*, 1991; Mullon and Pichon, 1991), the risk of missing during a single survey the small spaces where the bulk of the biomass was concentrated was higher. The cost of statistical acceptability was an increased risk of bias in the abundance estimate. FAST formed a group of scientists to work on this question and publish a Cooperative Research Report (Simmonds *et al.*, 1992) which was probably the first document describing the state-of-the-art and recommendations on acoustic sampling methods.

In the early 1980s, Marchal suggested the use of geostatistics in fisheries acoustics. A first paper introducing this method was presented (in French) at the ICES/FAO Symposium on Fisheries Acoustics held in Bergen, Norway (Norway, 1982; Laloë, 1985), but remained completely ignored. Then, we submitted some very preliminary results at the FAST (Gerlotto and Marchal, 1985; Marchal and Gerlotto, 1985), but again with very poor success. The fact that we had a very low level of English, that geostatistics was a French concept developed by the École des Mines de Paris (Matheron, 1970), that the acoustic community was not really interested in statistics, and that we were not geostatisticians, did not help our case. We had to write stronger papers in better English (Gerlotto and Marchal, 1987; Anonymous, 1990a, Petitgas, 1990; Gerlotto, 1993), and to plead almost 10 years before to becoming convincing. Incidentally, I learned [Lesson 11] that could be named the "10 year law", i.e. the usual time needed for a new concept to be accepted by society. As far as science is concerned, we could define this law as: "Between the moment a new (and potentially fruitful) hypothesis is proposed and the moment it has impact on research, whatever the supporting evidence, a precautionary delay of ten years is implicitly applied by the scientific community". Although this is highly frustrating when we know that our hypothesis is good because it is supported by serious scientific work, we could consider this delay as a precautionary adaptation of human society; there is need for a 10-year delay to be sure that a new rule is pertinent. How many apparently strong research studies and hypotheses did not survive 10 years, just because they were fundamentally weak or wrong, despite their convincing descriptions (Davenas *et al.*, 1988)? After this long lobbying, ICES organized a workshop in Reykjavik in 1990 which analysed the use of geostatistics and concluded that this method was likely to resolve most of the statistical problems of acoustic surveys (Anonymous, 1990b). Later, a reference book was published by Rivoirard *et al.* (2008). Nowadays, confidence intervals are meaningful and geostatistics has become a standard method for statistical analysis of acoustic surveys.

## Exploring school behaviour: the multibeam systems

The second source of uncertainty in fisheries acoustics was the existence of biases at many levels, as was detailed early (Simmonds *et al.*, 1992) and confirmed many times (see Fréon and Misund, 1999, for a summary). The most important among them was fish avoidance, first observed by Olsen (1969, 1990).

During the 1980s, the capacity to observe schools was very limited. Schools were only recorded as black spots on the echogram. Due to this weak knowledge, contradictory results existed, e.g. between density evaluations by visual methods (counting on photographic or video recordings) and by acoustics (Simmonds *et al.*, 1992). Acoustics provided density values orders of magnitude below visual counting, and contradicted the universal visual observation of fish organization inside a school (individuals separated by around one to three body-length distances). I obtained the answer to this contradiction through an unexpected personal observation of small schools in Martinique. I was working on this French island at the time and used to spend week-ends with my family on a small beach called Grande-Anse. I once had the opportunity to swim during a couple of hours in shallow waters (4 m depth) over a small school of *Harengula sp.*, practically flat and observable in two dimensions. I could see that the school structure was highly heterogeneous, fish being effectively separated by around one body-length to each other, but schools presenting also large empty areas very similar to vacuoles in a cell. Here was the reason for the contradiction. Photographic or video observations usually do not record these vacuoles, while acoustics average them with the dense parts of the school (Fréon *et al.*, 1992). That was [Lesson 12], confirming what many naturalists and ecologist used to say. A discovery is not only obtained through the use of sophisticated experiments; it can come from any observation and at any moment as long as you know what you are looking for and you are prepared to receive it (Fabre, 1924). A discovery is almost always due to the particular capacity of the brain to make analogies and this can happen at any moment and for any reason. Always being open to inputs from the external world is essential in research. Anyway, this observation gave us a hypothesis on school structure that we could test once digital echo-integrators became able to process the acoustic signal received from inside the school. In the late 1980s, we produced the very first acoustic cross section of a school that confirmed its high heterogeneity, showing nuclei and vacuoles (Fréon *et al.*, 1992). Schools appeared to be more complex organizations than expected.

At the same time, a pioneering study on school avoidance using long range omnidirectional sonar was presented by Diner and Masse (1987), who described and measured the avoidance behaviour of schools in front of a vessel. Following this first experiment, we developed a series of studies (Gerlotto and Fréon 1988; Fréon and Misund 1999 for a summary). We concluded that (i) avoidance was a major source of bias for a vertical echosounding survey, and (ii) multibeam systems were likely the only tool able to evaluate it (Gerlotto *et al.*, 1999). I suggested adapting one of the new multibeam echosounders (MBE) already developed for bathymetry to fisheries research, and we submitted the project AVITIS to the EU with the objective of building an appropriate instrument (Anonymous, 2000). The project was approved and the Reson 6012 SEABAT Multibeam Echo Sounder became the first one available for fisheries research in the early 2000s (Gerlotto *et al.*, 2000).

We first used MBEs to measure school avoidance. The results showed that biases due to avoidance were much higher than expected; in some cases, up to 80% of the schools were avoiding the survey vessel (Soria *et al.*, 1996). But this avoidance reaction also appeared to be extremely variable (Brehmer *et al.*, 2000; Gerlotto *et al.*, 2004), and in some cases no avoidance was observed (Figure 2). Modeling avoidance (Soria *et al.*, 2003) and, thereby, predicting it during a given survey, remains intractable due to the huge number of factors driving avoidance.

The series of experiments we performed gave me my [Lesson 13]: beyond specific results e.g. avoidance, schooling behaviour was a key to understanding fisheries biology. For instance, contrary to the standard hypothesis in stock assessment, each individual fish may display a different catchability pattern, as they are able to learn and present individual adaptive reactions to exploitation and particular fishing pressure (Pyanov, 1993). Soria (1994) showed in tank experiments in Martinique that trained fish from one school were even able to transmit the learned knowledge to another school. *In situ* studies confirmed this fact. Heavily exploited populations of *S. aurita* in West Africa exhibited significantly higher avoidance reactions to the same trawler (RV "Antea") than populations in non-exploited Venezuelan waters (Brehmer *et al.* 2000).

With the use of MBEs we could better understand what schools were and how they behaved (Gerlotto and Paramo, 2003; Gerlotto *et al.*, 2004, 2006; Soria *et al.*, 2007; Gerlotto *et al.*, 2010). Collectively, these results allowed us to build a conceptual model, presented in Figure 3 (Bertrand *et al.*, 2008).

This model shows that schools balance two motivations: maintaining a stable social structure; and exploiting a favourable habitat. We also see that if large organizations can be explained mostly by trophic patterns, things are quite different at small scales. We can now define a school as the smallest collective and coherent structure that allows coordinated reactions to changes in fish physiology and environment.

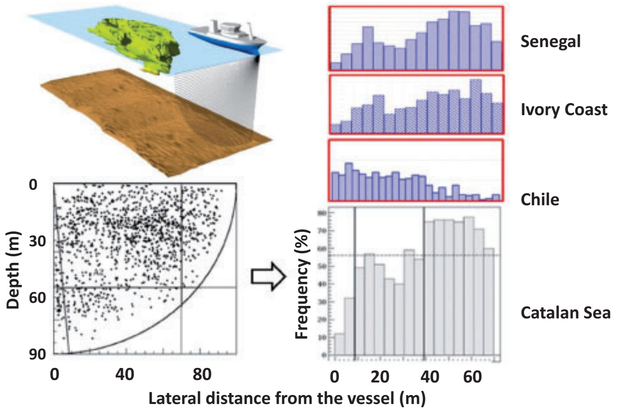

**Figure 2.** Use of multibeam echo sounder for evaluating the school avoidance. Top, left: description of the method; down, left: results from a survey in the Catalan Sea. All the schools recorded are represented by a dot located at the co-ordinates of their gravity centre. Scales in m. Right: histograms of school numbers related to their distances from the vessel (in m), for Senegal, Ivory Coast, Chile, compared to the Catalan Sea (results from left, down). All regions display a similar avoidance pattern except Chile (no avoidance).

## Towards a different approach of fisheries biology

In the mid-1990s, the knowledge of pelagic fish behavioural ecology was already sufficient to deliver useful information to the assessment people. But the bad surprise was that, except biomass estimates, our results were never used for assessment purposes. Why? My analysis was the following.

Ecology involves two processes: (i) energetic and (ii) cybernetic. Energetics is the dissipation of (mostly solar) energy through successive biochemical steps. Solar energy is stored and transported by metabolizing complex biochemical molecules through photosynthesis (phytoplankton). These high energy level molecules concentrated in phytoplankton organisms are then slowly catabolized through a succession of predators from zooplankton to apex predators, ending with bacteria which release low energy level molecules ($CO_2$, $H_2O$…) that are recycled, etc. Cybernetics (Frontier *et al.*, 2008) refers to mechanisms such as fish behaviour, spatial organization, interactions with other species, which exist in an ecosystem but do not belong to the biochemical metabolism process. Their function is to allow the (intra- and inter-specific) individuals in the ecosystem to interact with each other. Although they do not feed the ecosystem, they sustain it. Conventional fisheries biology mainly considers energetics and not cybernetics. Consequently, the data used are related to energy flows. As I said above, there are hypotheses behind data. The one behind catch data is that these data represent the energy produced by the stock. They synthesize the thermodynamic exchanges and are assumed to describe exhaustively the relationships between the stock and the ecosystem. Most models are based on food chains and productivity patterns and can only work using energy-flow data. On the contrary, direct observations, and especially acoustic data, mostly consider the interactions inside the ecosystem: organizations, adaptations, spatial structures, relationships between compartments, etc. The only exploitable information that conventional assessment can receive from acoustics is energetic: the biomass.

However, fish catches or abundance estimates are alone unable to describe the interactions between the exploited population and its habitat, as the history of *B. capriscus* told us. In this context, we decided to introduce non trophic and behavioural indicators into models, for two reasons. First we hypothesized that behaviour allows the fish to adapt to their environment (Figure 3), affecting population dynamics. And second, we highlighted the idea that forecasting capabilities are not the privilege of humans. Marchetti (1998) claimed that "Every living thing has or is a machinery for learning, remembering, and forecasting. The objective is to provide anticipatory reactions to the interactions with the external world" (Marchetti, 1998). If behavioural patterns are the adaptive answer to variations in environmental parameters, then they are integrative and may display easy-to-measure characteristics synthesizing reactions to a number of non-measured or non-measurable environmental variables.

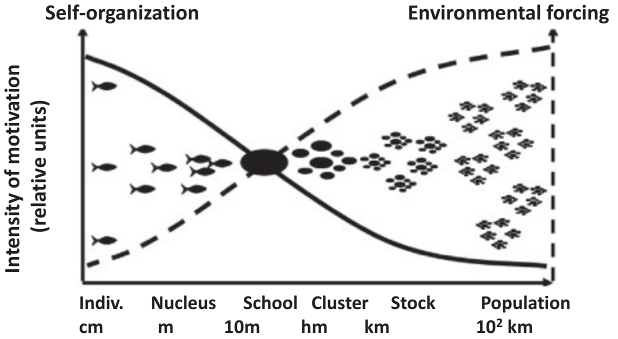

**Figure 3.** A conceptual model describing the relative importance of factors regulating aggregation of gregarious fish as a function of scale. There are two *y*-axis in relative units, one based on self-organization, the other on environmental forcing (from Bertrand *et al.*, 2008).

These analyses were shared with a few colleagues inside IRD and IFREMER in France (Massé and Gerlotto, 2003) but did not evoke any positive reaction in our Institutions in the 1990s. The objective of assembling a multidisciplinary study on stock assessment and fish behaviour was considered either useless or impossible, and the projects that I submitted to IRD or to the European Commission were rejected. Besides entering into the endless debate between "reductionist vs. holistic" concepts, we simply faced the technical difficulties of crossing borders of scientific disciplines. This was [Lesson 14]: research institutes are organized vertically by disciplines. Therefore, they don't have the administrative instruments to deal with horizontal multidisciplinary projects: where and how in the institution structure can one evaluate their proposals, methodologies, budgets, results, publications, even the scientists themselves? Things evolved in the early 2000s when climate change became a real issue and required multidisciplinary projects. In 2001, with a new generation of scientists interested in this analysis, I was able to create a research unit inside IRD (ACTIVE, see www.ird.fr) gathering scientists from France, Belgium, Chile, Peru, Hawaii, and La Réunion Island to study fish behaviour as an indicator of how climate, hydrology and the whole ecosystem, including fisheries, impact fish populations.

Once this group was formed, we began to consider the situation of "fisheries ecology". We discarded the "mostly deterministic" vision of dynamics of populations, knowing that fish populations often respond non-linearly to physical forcing (Hilborn *et al.*, 1994; Hsieh *et al* 2005). With this criterion in mind, the critical question of the predictive capacity of assessment models became an issue. We had to find a way to overcome this oxymoron: providing some anticipatory recommendations to managers on a system characterized by non-linear or chaotic dynamics (in the sense defined from Poincaré's works: small changes in the starting conditions produce outcomes of great magnitude, making the system unpredictable, e.g. Boccaro, 2010), which prevent predictions over the long term. Marchetti (1998) showed that resolving this contradiction is a major output of natural selection: "DNA is an active memory that learns through hypothesis (mutation in a broad sense) and experiment (survival value of the mutated offspring). (…) The only link to the external world can be the *survival feedback*". Survival being the only objective and reward, successful species are those that have developed by selection (through million years of evolution) strategies allowing adaptation to regime shifts, which means some capacity to predict and anticipate them. Then, studying these population strategies, we could get pieces of answers to this apparent contradiction. One possible solution was to work on scenarios. Indeed, a regime shift is not extremely frequent, and between two such events (i.e. up to decades), the dynamics of the population can be considered as reasonably deterministic, following a scenario. But at a given, unpredictable moment, due to regime shift the scenario is replaced by another one. Then we must be able to (i) describe the different scenarios a population can follow, (ii) define which scenario is currently in use according to the existing regime, and (iii) obtain indicators from the population which could inform that, due to regime shift, the system would likely soon move from one scenario to the other. Under these conditions, we could advise the managers that, as long as the scenario remains unchanged, the population is likely to respond linearly to variations in fishing effort, and its dynamics can be anticipated; but we should also be able to ring the alarm when a regime shift is likely to occur (Gerlotto, 2007).

The preceding requires obtaining much more environmental and behavioural data than is currently collected. Costs then become an issue for scientific institutes. We addressed this constraint in two ways. First, we extracted all the existing information from data already collected. For instance we could measure the precise position of the oxycline from the recorded echograms in Peru (Ballón *et al.*, 2011) and classify echoes in several groups by comparing acoustic frequencies which allowed us to evaluate zooplankton as well as fish abundance quantitatively all along transects (Ballón *et al.*, 2011). Second, we integrated and empowered the fishers as observers and actors in the management of the environment that they exploit (Melvin *et al.*, 2016a, b). This is technically possible because the instruments used on board fishing vessels are now exactly the same as those used by researchers (echosounders and sonars, underwater sensors of physical parameters, etc.). During my chairmanship of the ICES Fisheries Technology Committee I encouraged the works of a study group studying this question and a Cooperative Research Report was published in 2007 (Karp, 2007) which concluded that fishers' data could be useful for scientific purposes. Actually, this question of involving the fishers is not only a matter of data collection: they must be full "actors of science" (Massé *et al.*, 2016), for a number of obvious reasons. They have deep knowledge of fish behaviour (Hind, 2015); no improvement in the ecosystem-based monitoring (EBM) can been obtained without their active participation; their willingness to respect regulation depends on their approval of the research and its conclusions; they are part of the ecosystem and as such are both producing and suffering from the changes.

Since the early 2000s, IRD has been co-operating with the Marine Institute of Peru (IMARPE, *Instituto del Mar del Peru*). There, we discovered the richness of a long series of acoustic surveys operated by fishing vessels, the famous EUREKA operations which began in the 1960s and were conducted on a yearly basis (Villanueva, 1971; Fernandes *et al.*, 2002). This was later applied by other countries and laboratories (Chile, USA, Canada, etc. e.g. Melvin *et al.*, 2016a), but in most cases, as in Peru, fishing vessel sampling strategies were decided by scientists. The question now concerned the acoustic data collected during autonomous fishing trips. Only very few occurrences existed in the late 2000 (Barbeaux *et al.*, 2013; Niklitschek, 2016), but we may consider that fishers' data are currently exploited, as evidenced in the special issue of the journal Fisheries Research that we edited on this topic in 2016 (Melvin *et al.*, 2016b), ten years after the Karp (2007) proposal, i.e. after the already mentioned delay imposed by the "10 year law".

## Fishing vessels as scientific platforms

Another preliminary question had to be answered: can fishers be considered as "natural" predators or are they completely outside of the ecosystem mechanisms? The reason behind this question was the need to study fishers' strategies and their relationships with fish distributions. As said above, the weight of a catch is a poor descriptor of a fishing operation, and any attempt to go further requires knowledge on the fisher's behaviour. A series of important results were obtained in Lima, during the early 2000s (Bertrand *et al.*, 2005), which completely changed our vision of fishers' behaviour. Not only were the fishers similar in their hunting strategies to other predators (e.g. seabirds), but their trajectories were, as for every predator, highly sophisticated and could be formalized as a Lévi flight equation (Bertrand *et al.*, 2005, 2007). Later, this specific equation for trajectories was included in a wider system, being modelled by the Hidden Semi-Markov Models (Joo *et al.*, 2013).

These results confirmed that the fishers' trajectories could be formalized, extracted and exploited for scientific research. For instance, Joo *et al.* (2015) presented proxies of anchovy distribution maps using the fishers' trajectories: the results were comparable to acoustic estimates.

Once confirmed that fishers were a scientifically valid source of information, we could develop projects that made them partners in fisheries research, beginning with the use of their own acoustic data. At this time, a new Regional Fisheries Management Organization, the SPRFMO (South Pacific RFMO) was created to regulate and manage the exploitation of international stocks, especially the South Pacific jack mackerel, *Trachurus murphyi* (www.sprfmo.int). I worked on this species in co-operation with the National Fisheries Society of Peru (SNP, *Sociedad Nacional de Pesquerías*) and inside the EU delegation to SPRFMO (Hintzen *et al.*, 2014). Acoustic data on jack mackerel were collected on board fishing vessels, processing methods were developed, and annual workshops were organized (Gerlotto *et al.*, 2016a).

Applying that concept to anchovy, the Peruvian scientists adapted the Hilborn *et al.* (2001) recommendation and developed an "Adaptive Precautionary Management" model (Chávez *et al.*, 2008; Gutierrez, pers. comm.) which looks extremely efficient and is likely one of the first assessment models taking fish behaviour and general acoustic information (including fishers') into consideration.

## Habitat as indicator

The observation and measurement of fish behaviour helps to better understand (and anticipate) the dynamics of their populations. The next step was to find the best synthetic indicators to follow the dynamic changes of the population. A correct study of fish behaviour would require sampling such a large number of metrics that it is simply impossible, as observations on fish avoidance told us. Integrative indicators are necessary. We proposed the use of habitat as an ecological indicator, based on the following hypothesis. The fundamental motivation of fish behaviour is to guarantee the survival of the species. This means maintaining the population in a favourable environment, i.e. a given suitable habitat. This habitat is recognized by the species through the synthesis of a number of metrics, which we do not necessarily record. Then, habitat definition and evolution could be one synthetic indicator for understanding, analysing, and predicting the dynamics of the population (Zwolinski *et al.*, 2010; Bertrand *et al.*, 2016). Large stable habitats favour the development of the population; shrinking habitats are likely to reduce the population abundance. In order to test these hypotheses, IMARPE and IRD worked on habitat of the Peruvian anchovy (*Engraulis ringens*), and Bertrand *et al.* (2010, 2011) demonstrated for this species that (i) direct observations give enough pieces of information to describe, measure and map this habitat in three dimensions, and (ii) that the population dimension of the anchovy is directly linked to the habitat dimension (Bertrand *et al.*, 2014).

## End of my story: the triggerfish mystery revealed

We had now developed alternative hypotheses and instruments to propose a more realistic approach to fish population dynamics. But one element of the puzzle was lacking: we described the need to define the scenarios a species may select according to environmental conditions, but what should be included in a scenario? Information on the environment, the fishery, and fish behaviour was already available. The missing piece of information for writing a complete scenario concerned the population strategy of a species. Depending on their population strategies, species may react differently to environmental changes. For instance, existing models of reproductive strategies, e.g. the r- and K-selections (MacArthur and Wilson, 1967) consider the selection of a reproduction pattern; from them, a series of hypotheses have been drawn, e.g. the BOFFFF (Big Old Fat Fecund Female Fish, e.g. Hixon *et al.*, 2014) which have strong implications on assessment. Nevertheless, they do not take into account the dynamic strategies acquired through natural selection on the population. There was a need to define the structure of the population and to find the mechanisms explaining why a species like *B. capriscus* is able to so dramatically change its behaviour, abundance, and spatial distribution. The concept of habitat that we described gave us some potential elements of an answer. It seems logical that, if habitat drives population abundance, it also drives its structure. Unfortunately, *B. capriscus* stocks are not considered profitable enough in fisheries to justify any funding for such research. Instead, we were urged to test this hypothesis on jack mackerel. This fish represented the most important exploited stock in the world in the 1980s and 1990s, when its biomass reached almost 25 million tonnes and catch in the 1990s was close to 5 million tonnes. By the 2010s, the biomass was less than 5 million tonnes, and production was less than half a million tonnes (www.sprfmo.int).

The population structure of *T. murphyi* was studied over several years by teams from the different fishing countries, but no consensus was obtained. SPRFMO organized a dedicated workshop in 2008 (SPRFMO, 2008), and a series of hypotheses were listed, from a wide single stock to many discrete stocks all over its distribution area. I received here my [Lesson 15]: scientific results are very often influenced (or biased) by political interests. The conclusions of scientists from the different countries of the South Pacific were generally more in phase with the wishes of their respective governments than with actual scientific evidences. I fully understand that politicians decide not to take into consideration scientific recommendations. After all, this is their raison d'être: to make choices. But we cannot accept pressures on the scientists. The easiest recommendation is to say "resist", but this is often extremely difficult. At least, scientists must know that this pressure will permanently exist when economic interests are involved.

We worked on the population structure of *T. murphyi* and proposed a metapopulation hypothesis (Gerlotto *et al.*, 2012), based on the definitions listed by Kritzer and Sales (2004) for marine organisms from the model developed by Levin (1969). For this study, we used the considerable sum of biological and ecological information accumulated on jack mackerel (Gerlotto and Dioses, 2013). This hypothesis was not completely satisfactory, because some of the conditions for metapopulations found in the literature were not fully respected, and we decided to go further in this study. A project submitted in 2011 to the EU was approved and after two years of work we concluded again that metapopulation was the most likely structure (Hintzen *et al.*, 2014). In this project, we focused on jack mackerel habitat (Bertrand *et al.*, 2016). Although more convincing, some conditions were still not fulfilled.

We had to question whether the existing definition and conditions for metapopulation were applicable to large pelagic populations (McQuinn, 1997). We established a wider definition for metapopulations, making a distinction between two types according to their habitat characteristics: (i) the species living in "territory-bounded habitat" (TBH) and (ii) those living in "environment-bounded habitat" (EBH), pelagic metapopulations belonging to this last group (Gerlotto *et al.*, 2016b). Animals living in TBH are unable to cross the geographical borders of their territory (e.g. mountains, lakes, islands . . .) and extend their habitat outside of the territory, even though environmental conditions would allow it (except for a few individuals going from one TBH to the other; Cury, 1994). On the contrary, populations living in EBH, where no such geographical borders exist, can increase their area of distribution by filling a suitable habitat only limited by favourable environmental conditions. Under this definition, jack mackerel inside its EBH was organized into a pelagic metapopulation.

There are at least three selective advantages to this adaptive population strategy: (i) the fish is able to recolonize the niches that have been lost during the low abundance periods (paleoecology says on a scale of centuries, e.g. Sifeddine *et al.*, 2008); (ii) separate subpopulations are small enough to adapt rapidly to changing conditions of the environment; and (iii) when all the subpopulations merge, the favourable genetic mutations which occurred in one given subpopulation are transmitted to the whole species, which allows it to adapt more rapidly to a highly variable environment.

And now, back to the beginning: this EBH hypothesis, developed for *T. murphyi*, finally enlightens the "triggerfish mystery" when applied to *B. capriscus*. Generalizing the observations made on the jack mackerel, we can now suggest the following hypotheses: the triggerfish, although not pelagic during its period of low abundance, is not limited by territorial borders, and can be considered as an EBH metapopulation. The natural changes in triggerfish biomass could be described through an EBH metapopulation strategy for this species: a small climatic event occurred in 1972 in West Africa which favoured a successful recruitment. This high abundance induced a change in *B. capriscus* behaviour, making it possible to expand all over the new suitable pelagic habitat and to cover the entire Gulf of Guinea. This expansion lasted several generations and allowed the species to recover all of its lost niches and to homogenize its genetic pool. Eventually, the abundance decreased and the fish returned to its "natural" benthic behaviour and went back to its historical distribution and abundance.

Incidentally, if this hypothesis is correct, the natural depletion of the triggerfish could indicate that the "collapse" of jack mackerel in the South Pacific Ocean is perhaps more the result of a population strategy than overfishing (although the two effects can be additive). Moreover, it questions (among other points) the meaning of a fixed natural mortality coefficient and of a "virgin biomass" ($B_0$), which are currently used in assessment models. The distinction between natural depletion and overfishing collapse as defined by Petitgas *et al.* (2010), may also become an issue for assessment analysis.

I would like to conclude this paper with Lesson [16]: I hope my story demonstrates that scientific research is a long process depending not only on intelligence, knowledge, ability to design hypotheses etc., but also on the availability of adapted techniques, intrinsic delays, and maturation of ideas. Unfortunately, modern life favours mostly short time scales, even in science where administrations impose short-duration (1–4 years) projects and a frenetic rhythm of publication production, evaluated quantitatively regardless of their actual value. There are some visible effects, such as the increasing creation of profit-driven scientific journals, the enormous inflation of meaningless articles, the almost complete absence of references older than 5 years in the bibliographies, and many others (cf. Lawrence, 2016). I am not sure that this short memory strategy is good news for research. In any case I am convinced that today, a 40-year quest for exploring the triggerfish mystery would not be accepted. Young scientists may have to comply with the bureaucratic requirements of the modern organization of research, but they must know that doing good science is another (long) story.

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