PANAMJAS
Pan-American Journal of Aquatic Sciences

Fisheries, Ecology and Modelling: an historical perspective

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Abstract. Some time ago a physicist said that "scientists have as much interest in the history and philosophy of science as birds have in ornithology". Notwithstanding these sentiments, knowledge of the past of our subject is an important requirement to avoid repeating mistakes. This paper briefly describes models in Ecology and Fisheries from an historical perspective and tries to show how those two disciplines influence each other. Perhaps if birds could be aware of ornithology they might avoid threats to their livelihood. At present, in the face of global climate change and "over-depletion" of our fish stocks, it might be a good moment to overview the past to understand the present as well as to try and foretell the future and avoid disaster.

Key words: Malthus model; logistic model; Lotka-Volterra equations; von Bertalanffy; Beverton and Holt.

Resumo. Ecologia, pesca e modelagem: uma perspectiva histórica. Tempos atrás um físico disse que "cientistas têm tanto interesse na história e filosofia da ciência, como pássaros têm em ornitologia". Apesar disto, o conhecimento do passado de nosso assunto de pesquisa é importante para evitarmos os mesmo erros. Este trabalho descreve modelos em Ecologia e Ciência Pesqueira de uma perspectiva histórica e tenta mostrar como estas duas disciplinas influenciam-se mutuamente. Talvez se os pássaros pudessem ser conscientes da ornitologia, eles conseguiriam evitar ameaças à sua própria existência. Hoje, em face das mudanças globais e da "sobre-depleção" de nossos estoques de peixes, talvez seja um bom momento para revisar o passado, entender o presente e tentar prever o futuro para evitar o desastre.

Palavras-chave: modelo de Malthus; modelo logístico; equações de Lotka-Volterra; von Bertalanffy; Beverton e Holt.

Introduction

Recently, some historians credited Leonardo Da Vinci with the label of first scientist in the modern sense (White 2000). Da Vinci invented, or at least proposed, a large number of machines, and also thoroughly studied both anatomy and physics. Atalay (2006) showed that in each of the three portraits of women that Da Vinci painted, including Mona Lisa, a golden rectangle can be superimposed, incorporating the head and upper chest of the subject. Leonardo also knew mathematics and, more importantly, he knew how to apply it.

In the same year that Leonardo died [1564] Galileo Galilei was born, and his scientific contributions are perhaps better known. He "preached" the quantification of objects, stating that the natural world was written in mathematical symbols and it would be impossible to understand the natural world without mathematics. He created a model to describe the behavior of the planets which, among other things, provided him with an early retirement.

History repeated itself and in the year that Galileo died [1642], Isaac Newton was born in England. At that time, mathematics was reaching the status of a respected discipline. As a result, in 1664 Cambridge University nominated its first professor of mathematics, Isaac Barrow, later replaced by Newton (Gleick 2004). At the age of 24 years, Newton described the calculus, afterwards published in the Philosophical Transactions of the Royal Society; this is considered to be the first formal scientific paper (dealing with optics and light).

This brief historical review aimed to show that science (in a modern sense) and mathematics are twins; if science is constructed through hypotheses that need to be confirmed by data ("real world"), models are hypotheses, *per se*, of "quantitative" scientists. As many hypotheses are techniques to guide the natural sciences, so are models, a word derived from the Latin *modus*: the way that things are done. It makes sense.

Hilborn and Lierman (1998) have fairly defined science as an approach for learning about nature. A model can be shortly defined like "a totality of logical connections, formalized dependences, and formulas, which enables the studying of a real object without its experimental analysis" (Gertsev & Gertseva 2004) or merely "an abstraction of the reality" (Mulligan and Wainwright, 2004). The objective of this work is to describe models in Ecology and Fisheries from a historical perspective and to try to show how these disciplines influence each other. The main framework of this paper is based on Kingsland (1985) and Smith (1994).

Ecology, Fisheries and Models

The first model used in ecology was by Malthus (1759), concerning exponential population growth. Darwin and Wallace (independently) understood the basic idea of food constraints in the Malthusian model (the food base exhibits arithmetic growth) and its implication for natural selection; only more capable organisms release offspring which themselves are better adapted. This described the mechanism of evolution (the way things change). Some researchers say that Malthus' model does not work in the real world (Hall, 1988), but this ignores the essence of its scientific contribution. Population data might not fit the exponential curve, but this first and simplest model supplied the foundation of natural science. It is enough, isn't it?

In 1838, before publication of *The Origin of the Species* by Darwin in 1859, Pierre-François Verhulst added just one term to Malthus' equation: K, the maximum number of individuals that the environment supports, or its carrying capacity. Unfortunately, nobody paid any attention to it at the time (Petrere 1992). Only 80 years later would this model be renewed, as discussed below.

At the same time that Darwin was hurrying to publish "*The Origin*", the Norwegian Government hired Axel Boeck to investigate fluctuations in the herring fisheries. One year later Norway installed the first monitoring system to collect fishery statistics (number of fish caught and fishermen).

In 1863, in a speech that was given at least twice, Thomas Huxley made the famous, misunderstood statement "… and probably all the great sea-fisheries, are inexhaustible; that is to say that nothing we do seriously affects the number of fish. And any attempt to regulate these fisheries seems consequently… to be useless". However, Huxley had prefaced this statement with the qualifier "… in relation to our present mode of fishing…". The main defender of evolution did not realize the extent to which gears and boats would evolve over the coming decades.

Despite Huxley's standing in the scientific world, his assertion was not universally accepted. For instance, Ray Lankester in 1884 proposed that fishing activity had the potential to disturb prey-predator equilibria in fished populations. In 1854, before the publication of Darwin's book, Cleghorn put forward the idea of overfishing (Cleghorn 1854), which was very unpopular among fishermen. Around the same time [1865], G. O Sars showed that fish eggs float freely in the water and are therefore not directly affected by fishing operations (Russel 1932).

The late nineteenth century was noticeable for some important experiments and definitions of concepts. In Germany in 1882, Karl Möbius did an experiment to investigate the productivity of ponds that contained carp. The productivity of ponds with predators (pike, *Esox lucius*) was found to be higher than those without, because the predators decreased the competition among prey. One year later Möbius proposed the term "biocoenosis" for a community of species inhabiting a given territory, and the first analysis of food relations among species was published five years later in the classical "The lake as a microcosm" by Forbes (1887) who supported the ecosystem's concept from Tansley in 1935 (Kingsland 1991).

The earliest experiment with trawl gear was performed by Garland in 1887, showing that catch rates in areas restricted to fishing were higher than in open fishing areas. This conclusion was supported in 1900 by Garstang, who demonstrated a decrease in CPSU (Catch Per Smack Unit) in Scotland, and concluded that the fisheries there might be exhausted (Garstang 1900).

The definition of immature fish was pioneered by E. W. L. Holt in 1890 (Holt, 1895) in extensive species-specific explanations, such as "a sole which measures less than 10 inches, a turbot which measures less than 12 inches…" and so on. The initial attempt to determine fish age was based on skeletal bones and was developed by J. Reibisch (1889) in Prussia, when the First International Conference to study the sea took place in Stockholm.

Our understanding regarding maturity of fish started to be highlighted by C. G. J. Petersen (1892) through his method to determine the age of fish based upon their lengths. The technique developed by Petersen enabled him to estimate the population size/age structure through marking fish and recapturing them two years later. Meanwhile T. W. Fulton (1891), J. T. Cunningham (1895a, 1895b) and E. W. Holt (1895) were performing reproductive studies through the analysis of gonads.

At that time, understanding fish maturity, reproduction and its biological constraints had became an important issue. Pushed by this need, F. Heincke (1898) studied herring from different areas, looking for an "ideal type". He compared fish measurements using adjusted least square methods, and made a great contribution to fishery studies by establishing the theoretical basis for considering individual populations of fish.

New century, same problems, innovative approaches

The early 1900s were marked by Petersen's efforts to elucidate the effect of fisheries on fish stocks, the concept of immature fish, and the diminishing average age of the marketable size of fish in his paper "What is the overfishing?" published in 1903. Also, in 1905, H. M. Kyle (Kyle, 1905) identified two main problems in the study of fisheries. The first concerned the decrease in fish numbers, which was a soluble problem since it was a scientific issue. The second concerned irrational fishing, which was a practical and economic problem, and could negate the impacts of all scientific work. Fisheries science was proving to be much more complicated than simply comprehending the "supply of fish".

Ecological studies were also making progress at that time. In the same year that Kyle was grappling with the complexities of fisheries science, Brandt (1905) showed that chemical nutrients could control the production of marine algae. This study was improved in 1910 by G. E. Bullen (Bullen, 1910) who described the relationships among phytoplankton, zooplankton and fisheries. However these approaches did not gain popularity, and fisheries continued to be analyzed based solely on fish stocks.

Following this trend, Heincke (1913) estimated mortality rate by analyzing fish lengths, and argued that a reduction in catch upon the small fish might be lucrative to the fishery, because the fish will grow and earn more. As a consequence, for the very first time, the Plaice Committee formally recommended the establishment of a minimum size for plaice as a management strategy.

While C. H. Gilbert (Gilbert, 1913) in Stanford established a relationship between the number of scale rings and the size of fish, concluding that salmon lived for four years, J. Hjort (1914) showed that catch fluctuations in Northern Europe were due to natural variability and depended on just one age-class. This paper was acclaimed by some people, but D. W. Thompson (1914a, 1914b) strongly disagreed with the conclusions, because for him there was no evidence that each ring in a scale could correspond exactly to one year.

A. G. Huntsman (1918) was the pioneer in using a pyramidal diagram to represent fish populations, and he concluded that many years would be necessary for fishing to fully impact on fish stocks. However, independently of the magnitude of this impact, fisheries should decrease the average length of fish. Unfortunately this paper had no scientific impact.

Then the First Great Experiment, i.e., the lack of fishing activities during the outbreak years of the World War I, happened and after the war the length of fish was greater than at its beginning. This was clear evidence that fishing had an effect on the fished populations, but for some researchers the evidence was flawed for being based on just one species (Petersen 1922), and because the increase of a fish population could produce a decrease in its individual growth rates, through competition (Garstang 1926).

These two processes (fishing impact and decreasing of individual growth rate) were quantified by Fëdor I. Baranov (1926), in which it was argued "that the effects of reducing the fish populations might be the release of food, food that the population itself could use". Another Russian scientist Knipowitsch objected: "it is completely unacceptable to me, as a biologist, to reach a conclusion on the basis of formulae" (Smith 1994, p.196).

Ecology, the crucial collaboration

Knipowitsch's objection came in the face of increasing use of mathematics in ecology. In 1920, Raymond Pearl discovered Verhulst's equation about carrying capacity, and suggested that it be transformed into an "ecological law", changing ecology into a *hard* science (Kingsland 1985). If we keep in mind that Einstein published his paper about relativity 15 years before, we can agree with Cohen's statement "Physics-envy is the curse of ecology" (Cohen 1970).

Vito Volterra (1926) trying to help his son-in-law D'Ancona to understand the fluctuations in fisheries in the Adriatic Sea, described the "predator-prey" model and published it in Nature. Lotka reclaimed priority, showing his "Elements of physical biology" of 1925. The model is now commonly known as the "Lotka - Volterra equations" and even today is very useful (Enlem *et al.* 2003), despite the fact that it usually does not fit with real data. Hall (1988) points out that the data collected by Charles Elton in 1924 from the Hudson Bay Company for hare and lynx, and frequently quoted (until today) to validate the predator-prey equations, were not suitable because they were from populations that lived in different regions, and the changes in the lynx populations sometimes preceded those of the hare populations.

The 1920s to 1940s are called the "golden age of theoretical ecology" (Scudo & Zeigler 1978). Following Pearl and Lotka's approximations, Elton, for example, created the term food cycle and the pyramid of numbers, i e., there are more plants than herbivores, more herbivores than carnivores and so on (Summerhyes & Elton 1923, Elton 1927, 1930). In 1934, Gause published *The struggle for existence* and showed the competitive exclusion principle. One year later, Tansley coined the term ecosystem (Tansley 1935), based on the "super-organism" concept of Clements (1916), who stressed the phenomenon of succession in plant communities. Thus, the concept of the ecosystem was born, with development as an important theme, a subject that was later improved by the brother's Odum in the 1950s to 1960s.

Parallel to these developments in ecology, a number of methods to understand fisheries were available in 1930, including "age determination; research vessel sampling of adult fish and their eggs and larvae; mark and recapture; actuarial statistics; mathematical statistics; and commercial catch, effort and fish length statistics. The biology was understood: fish grow and die, but reproduce large numbers of young only in certain years. The effects of fishing, at least some of them, were known: fishermen could catch a large proportion of a population in a year, and periods of reduced fishing were followed by periods of increased catches" (Smith 1994, p. 196).

In 1931, stimulated by ecological ideas and especially Lotka's work, which emphasized ecological interactions, Edward Russel (Russel 1931) recognized that it would be essential to look for "general principles about which there can be no reasonable doubt", and wrote an equation (similar to Baranov 1926) predicting the weight of a fish population based on its initial weight plus population growth and recruitment (to describe the population increasing) minus fishing and natural mortality (which represented the population decreasing).

In his revision of the contribution of fisheries research to ecology, Russel (1932) said that fishing is "auto-ecology in a big scale" and he recognized that fluctuations are an ecological problem, overfishing is extremely complex, and environmental causes could explain many unanswered questions about fisheries. He quoted Petersen (1918) as being the source of a pyramid of weights with the general assumption that 10 kg of producers were required to make 1 kg of consumers! Unfortunately we could not obtain the original Petersen paper, but when developing Elton's (1930) pyramid of numbers through the second thermodynamic law, Lindeman (1942) proposed the trophic level concept and the pyramid of energy with a trophic efficiency around…10%! Neither Elton (Summerhyes & Elton 1923, Elton 1927, 1930) nor Lindeman (1942) quoted Petersen's (1918) paper. We think that this might be an intriguing line of investigation for historians of science.

The life table for a fish (Atlantic mackerel) was carried out for the first time by Sette in 1932, using the example of Pearl & Parker (1921). Sette concluded that, for replacement, just one fish is required to survive from one million spawned. He also showed that larvae might be transported far away over the great depths by adverse currents, and that their survival could also diminish in areas where plankton abundance is low. Sette only published these results in 1943 (Sette 1943).

The origin of Maximum Sustainable Yield

One year after [1933] Sette constructed the Atlantic mackerel life table, the logistic equation was given adequate treatment in a paper with the suggestive name: "The optimum catch" (published just in 1943). Hjort, Ottestad and Jahn (Hjort *et al.* 1933) focused on the inflexion point of the curve (midway to the size of the population at carrying capacity) where growth was fastest. At this population size, exploitation can be at a maximum without causing the population to decrease. Smith (1994) believes that this paper reoriented the thinking of a generation of fishery biologists. Two years later, Graham (1935) used Hjort's theory of optimum yield, with some simplifications and aggregation of data from several species, and argued that a reduction in fishing rate would not harm the yield, and it would allow the populations to increase.

At this point, we would like to remind the reader that Malthus' model provided the original insight into natural history. After being enhanced by Verhulst's ideas, this model inspired the concept of "optimum catch", which is a foundation of much of fisheries science. As Graham said in 1943 "after a certain point the total yield of a fishery fails to increase any more, whatever the fishermen do. This is the key to the history of fishing, all over the world (…) that the benefit of efficient exploitation lies more in economy of effort than in increase of yield" (Smith 1994, p.231). In fact, Schaefer (1954) developed a model plotting CPUE against net productivity, and answered the question "What is overfishing?" by stating that it is "fishing so hard that the total sustainable yield begins to decline" (Smith, 1994, p.254-257).

Joseph Louis Lagrange (1736−1813), one of the most important mathematicians and physicist of the 18th century, provided a proverb which represents a good advice to researchers: "Search for simplicity, but suspect it". In 1938, Ludwig von Bertalanffy described his growth equation for fish, although its final form was developed in 1947 by Raymond Beverton & Sidney Holt. These latter two researchers would make history in following years. While they were still studying under the supervision of Hulme, mortality rates were described by Ricker (1940, 1944), inspired by the *enfant terrible* Baranov, who in 1918 had described natural and fishing mortalities, but in a paper that was written in Russian.

In 1947 Hulme, Beverton and Holt published the yield equation in Nature, and five years after that Beverton and Holt further developed it by linking into a single equation four cornerstone concepts in fisheries science: Russel's conceptual approach, Graham's and Ricker's instantaneous rates, Baranov's catch equation, and von Bertalanffy's growth equation. Elementary! My dear Watson!

The systemic paradigm: interactions between fisheries science and ecology

The IATTC (Inter-American Tropical Tuna Commission) was created in 1951 under the administration of Schaefer. The fundamental research paradigm of the commission was influenced by Schaefer's (1956) diagram concerning the main levels of investigation in fisheries. In this diagram, ecological research is presented as an ideal rather than a priority, because "the need to take action [in fisheries] tends to override the necessarily slow pace of science" (Smith 1994, p.331).

Not by chance, diagrams were becoming popular, since von Bertalanffy (1950) developed the general system theory (published in *Science*) based on his own "organismic system theory" of 1930. His starting point was to deduce the phenomena of life from a spontaneous grouping of system forces to the developmental biology of the system. He postulated two biological principles, namely, maintenance of organisms in non-equilibrium, and hierarchical organization of a systemic structure. Later, he developed his theory of open systems from a thermodynamic view to a general system view, which describes its models in a qualitative and non-formalized language (diagrams). This approach was first adopted by Lotka (1925), who was aware of the strong relevance of connections and interrelationships among the parts of a system.

Howard Odum, using this approach and under the supervision of Hutchinson (who had supervised R. Lindeman), created a compartmental model to explain the strontium cycle (Odum 1951). In 1960 he represented the system using an electronic analogy, emphasizing the potential of this analogy for ecology. In 1969, his brother Eugene published the "development of ecosystems" with emphasis on succession, where he described the attributes of 24 ecosystems in order to understand the systems and their resilience under aging.

The Odum brother's energetic language contrasted with that of Robert MacArthur (who was also supervised by Hutchinson) and his theories about island biogeography, optimal diet, competition and diversity (Brown 1991). The perspective of the Odum brothers had the advantage of trying to understand human impacts on the environment, and the Odum brothers supported this objective all their life, especially when they proposed the concept of emergent properties, a measure to understand the whole system.

In 1952 the FAO (Food and Agriculture Organization) published the Report of the First International Meeting on Fishery Statistics (Gerhardsen 1952). This was followed by the publications of many FAO manuals for research or monitoring of landings to support fisheries around the world. These manuals contributed to comparisons of fisheries dynamics and improved knowledge over a broad sphere. However, at the same time, it is impossible to know if these manuals forced and/or imprisoned the scientists' mind, preventing the creation of new and better models (Miguel Petrere Jr., personal com. for R. Angelini).

In 1957, Beverton and Holt used general system theory to describe a system that "feeds back into itself" and allied it with specific mathematical methods ("research operations"). They were able to combine surplus production theory (Schaefer 1954), yield per recruit theory (Beverton 1954) and spawner - recruit theory (Ricker 1954). Their description emphasizes the last of these, but the yield per recruit theory was more applied.

Beverton (1998) quoted the 1945−1965 period as the "carefree age" since he and Holt felt they were in the right track to do something good and valuable. He affirmed that such a period had ended with the discoveries of techniques for estimating biomass and fishing mortality, which came to be known as Virtual Population Analysis (VPA).

In fact, Gulland (1977) confirmed "Derzhavin (1922), based on age structure, conceiving the idea of estimate the contribution of each year-class to each year's catch. By adding the catches removed in the future years to the existing the year-classes alive in a given year, he estimated the minimum number of sturgeon alive in the reference year. This was named *utilized stock* by Voevdoin (1938) and *virtual population* by Fry (1949)". The equations of VPA were lately formalized by Gulland (1965). Afterwards, with the collaborations from Andersen and Ursin (1977), Helgason and Gislason (1979) and Pope (1979) the Multi-Species Virtual Population Analysis or MSVPA emerged. However, recently Xiao (2007) derived its fundamental equations and pointed logical inconsistency which demands a revision in all past work based on MSVPA and its variants.

Cushing (1981) wrote that the models used in fisheries management were mainly those of Graham (1935), Schaefer (1954) and Beverton and Holt (1957).

The ecosystem approach

Fish landings in the world increased greatly after the Second World War, from 20 million tones until they reached maximum levels in the 1990s at 85 million tones (FAO 2003). Throughout this period many huge fisheries collapsed, despite the proliferation of surveys using echo sounders, a new technique at the time (it started in 1935; Cushing 1973) that allowed the estimation of "how many fish there are in the sea", which should have resulted in improved advice for decision-making. This was not the case. Despite the collapse of some stocks around the world, total landings remained stable because the variety of species being exploited increased (*portfolio* theory). This resulted in new approaches for fisheries management, including multi-species models.

From the 1960s to 1990s ecology moved towards problems of biodiversity, and the question of whether higher biodiversity increases resilience of a system. Robert M. May (1973) showed that single species models might have chaotic behavior. On the other hand, multispecific models, i.e., more complex would "tend to beget instability rather than stability". Recently Tilman *et al.* (2006) found experimental evidence (in terrestrial ecosystem) that higher plant diversity increases temporal stability of ecosystem. Ecology was also driven by the recognized abyss between the approaches of the Odums and MacArthur (Brown 1991), which is smaller nowadays, but is still important.

At the end of twentieth century Fisheries Science was deeply improved by the publication of a series of papers that described simple and empirical regressions to quantify, for example, mortalities (Pauly 1980) and consumption (Palomares & Pauly 1989). Another "central" improvement was the development of the Elefan software (Pauly & David 1981), which allows the estimation of population parameters such as growth and mortality (including VPA), which supported many essential studies and nowadays aid to develop the ecosystem approach, supplying information about species.

Currently, Ecosystem Based Fisheries Management (EBFM) or the Ecosystem Approach to Fisheries (EAF) is developing as an important approach (Pikitch *et al.* 2004), building on the theory developed by the Odums, and synthesized to some extent by the Ecopath approach. This approach was first used by Polovina (1984), and subsequently developed in a software package by Pauly *et al.* (1987) and Christensen & Pauly (1992a, 1992b), who added Ulanowicz's phenomenology (Ulanowicz 1986). It was later adapted by Walters *et al.* (1997) to perform simulations (Ecopath with Ecosim). Walters & Martell (2004) recognize that the ecosystem approach is a result of scientific advances as well as of a strong public demand for sustainable fisheries and conservation of non-target and charismatic species (especially aquatic mammals).

Conservation biology and fisheries science are both disciplines that have focused on single species or single populations, and that have developed strong quantitative and theoretical bases. The combination of their modeling approaches is an intriguing disciplinary mix that warrants further attention. Conservation biology is concerned with the effect of small population size on the persistence of populations, and the factors that cause populations to decrease (Caughley 1994). Both these issues can be attributed to fished populations, but the perspectives of the scientists and their models differ, with fisheries models focusing on human-fish interactions (catches), whereas conservation models focus on individual-environment interactions.

Additional important and useful approaches have been individual based models (IBMs), which were first proposed in Huston et al. (1988, see also the review of Grimm 1999), and can be used for one species (Miller 2006) or for multiple trophic levels (Hermann *et al.* 2001). Some classical statistical techniques have been employed with success to understand fisheries dynamics, including Bayesian inference (Askey *et al.* 2007), generalized models (Duarte *et al.* 2005) and trophic indicators such as the FIB index (Pauly *et al.* 1998, Cury *et al.* 2005, Milessi *et al.* 2005). In this proceeding, there are examples of these approaches.

Regardless of these advances, the main concern in fisheries science continues to be the MSY – Maximum Sustainable Yield (Mace 2001, Mueter & Megrey 2006). Given the evidence of depletion in many stocks (Pauly *et al.* 1998, Worm *et al.* 2006), we believe that social problems (Symes 2006) especially in small-scale fisheries (Berkes *et al.* 2001, Hauck & Sowman 2003), and approaches that link social and biological fishing problems, as in Chuenpagdee *et al.* (2006), with her *Public Sentiment Index*, or a fuzzy-logic approach to facilitate decision-makers (Paterson *et al.* 2006) must be considered and evaluated in the next meetings.

Concluding remarks

Since 1859, governments and their scientists have been trying to understand what causes fluctuations in fish catches. Nowadays, almost 150 years later, we are looking to identify "fisheries and environmental dynamics" using the ecosystem approach. It seems that, in general, scientists agree with Cohen's statement "Physics-envy is the curse of ecology". Newtonian physics did not work in all dimensions, and physics has become a highly probabilistic science. Similarly, modern fisheries modeling approaches have developed to embrace complex statistical methods, and many species (and stocks) in a unique model. In addition, there is a need to consider a social approach. No more simple models? Suspect this.

Acknowledgements

Thanks for Adriana R. Carvalho for the improvement on the first draft. The authors are grateful to Miguel Petrere Jr and Simone Libralato by the historical review and valuable suggestions. The first author was supported by CNPq (Research Brazilian Agency) scholarship during his Post-Doc. program at University of Cape Town (South Africa).

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Received April 2007
Accepted May 2007