ISSN 1198-6727

Fisheries Centre Research Reports

2006 Volume 14 Number 4

Fishes in
Databases and Ecosystems

Proceedings of the 2006
FishBase Symposium

Fisheries Centre, University of British Columbia, Canada

Fishes in Databases and Ecosystems

edited by
Maria Lourdes D. Palomares, Konstantinos I. Stergiou and Daniel Pauly

Fisheries Centre Research Reports 14(4)
95 pages

The Fisheries Centre,
University of British Columbia

2202 Main Mall
Vancouver, B.C., Canada, V6T 1Z4

ISSN 1198-6727

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DIRECTOR'S FOREWORD

This report was assembled for the 4th Annual FishBase Symposium, and also celebrates the 7th meeting of the FishBase Consortium, gathered for the second time outside of Europe (the first being at Los Baños, Philippines in 2003). Last year, the Consortium met at the Aristotle University of Thessaloniki, Greece, hosted by Consortium member K.I. Stergiou and his team, and the proceedings of that symposium were published two days before it was over. Here we tried to emulate this, but failed: this report was published two weeks after the event.

This report consists of 6 papers that were presented at the Symposium and 8 'relict' papers, i.e., papers which, for various reasons, did not find their way into print right after they were originally written.

Typically, these papers, which here contain facts on the life history of fishes (growth, size at maturity, etc.) and/or parameter estimates that would be useful for FishBase and its user community, languish in the drawers of middle-aged scientists after rejection from a prestigious journal ("we don't publish local studies"), or because they were just about, but never completely, finished. Such unpublished manuscripts, turned into 'relict papers' and published, are useful not only because they make available to the community a body of knowledge, acquired at great cost, which otherwise would be lost, but also because this knowledge refers to historical states of fish population or ecosystems, and thus can serve as baseline. Thus, relict papers can help counter the effects of shifting baselines.

Also, relict papers represent much of the personal knowledge of authors, a type of knowledge that is often lost upon their retirement. This loss has been identified in connection with taxonomists. It also happens, however, with other students of applied ichthyology, e.g., with stock assessment scientists, who usually know much more field biology than may be inferred from their equation-ridden papers.

Conventional peer-reviewed journals often have problems with the subject matter that would be typical of relict paper: they often cover topics viewed as pedestrian, such as age and growth studies of fish. Such studies, however, are the motor that drives comparative studies, meta-analysis and biodiversity studies, and evaluation of the impact of global change. Hence, this compilation of relict papers, if the first, is not the last to be published as a Fisheries Centre Research Reports.

Daniel Pauly
Director Fisheries Centre, UBC
02 September 2006

SCIENTIFIC IMPACT OF FISHBASE: A CITATION ANALYSIS[1]

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ABSTRACT

Since its creation in the late 1980s FishBase has evolved into a highly dynamic and versatile ecological tool. A citation analysis based on Scopus, mainly for citations in journals, and Google Books, for citations in books, revealed that it has penetrated into the primary aquatic and general literature, review literature, and aquatic and general books and textbooks. With a cumulative number of citations of 653 during 1995-2006, it belongs to the 0.11 % of the highly-cited items published during 1900-2005, irrespective of discipline.

INTRODUCTION

FishBase (www.fishbase.org) is a global information system on fishes useful for research, for education at all levels, as an information source, and for the sensitization of the public at large (Froese and Pauly, 2000; Stergiou, 2004, 2005; Nauen, 2006). It includes a plethora of data, covering all levels of biological organization, for the known 29,400 fish species (as of August 2006). These data are derived from over 37,000 published sources (gray literature, books, journals, symposia proceedings, reports, etc.). FishBase, which was developed in the late 1980s (Froese and Pauly, 2000), and another ecological tool, Ecopath (www.ecopath.org; Christensen *et al.*, 2000), which was also developed during the same period, widened the scope of fisheries science. This is because these two tools, in a synergetic fashion, led to global studies (e.g., Pauly, 1998; Pauly *et al.*, 1998; Froese and Pauly, 2000; Froese and Binohlan, 2001, 2003; Christensen *et al.*, 2003; Froese *et al.*, 2005; Froese, 2006) in which previously-reported pieces of information on local knowledge were transformed into global knowledge, thus providing the framework for answering 'mega-questions' (i.e., questions pertinent to large spatial and temporal scales, and many species; see Stergiou and Karpouzi, 2002; CIESM, 2003; Stergiou, 2003, 2004).

The success of the FishBase website is demonstrated by the large number of 'hits' (about 30 million hits per month, with number of hits/month increasing exponentially with time), coming from all continents and from a variety of users (i.e., individuals, universities, museums, research institutes, NGOs) (Nauen, 2006; Froese, unpubl. data). In this report, we show that this success is also true in terms of the scientific impact of FishBase, when impact is evaluated based on 'traditional' bibliometric indices (i.e., citation analysis).

SCIENTIFIC IMPACT: ESTABLISHING CRITERIA

Visualizing the scientific impact of a work requires the establishment of measures of impact. "Science employs a knowledge filter that slowly separates the wheat from the chaft" (see Chapter 3 of Bauer, 1992). Such a filter acts at different steps (Bauer, 1992):

- A scientific finding is subjected to peer-review;
- If peers find it useful then it gets published in the primary literature;
- If other scientists also find it useful, it is cited;

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[1] Cite as: Stergiou, K.I., Tsikliras, A.C. 2006. Scientific impact of FishBase: a citation analysis. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 2-6. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

- If it is cited a lot it gets into review articles/monographs/books; and eventually
- It is cited into university textbooks.

In addition, there is a strong gap between terrestrial and aquatic ecologists (Stergiou and Browman, 2005): they read, cite, and publish in different journals. Thus, two other indices of the impact of an ecological work, which measure the exchange of ideas between ecologists and the education of ecologists, are (Stergiou and Browman, 2005):

- Its penetration into the primary 'general ecological' literature; and
- Its penetration into 'general ecology' textbooks (in which the percentage of aquatic references is less than 15%).

SCIENTIFIC IMPACT: THE CITATION SOURCE

Until recently, Thomson's ISI Web of Science was the only citation source available. However, in recent years other bibliographic services have become available, such as the Google Scholar (scholar.google.com) (Butler, 2005) and Scopus (www.scopus.com). These alternative tools perform as well as ISI (e.g., Google Scholar: Pauly and Stergiou, 2005), and moreover they are more flexible in terms of options for analyses that they provide (Scopus). In addition, these alternatives do not distort the scientific output of countries and institutions as ISI does through its limited use of sources, because they cover a much wider range of sources (*sensu* Stergiou and Tsikliras, 2006). For our analysis we selected Scopus for citations in scientific journals and Google Books (http://books.google.com) for locating citations in books.

Scopus is an abstract and citation database covering more than 15,000 peer-reviewed series from more than 4,000 international publishers, including coverage of 500 Open Access journals, 700 Conference Proceedings, 600 Trade Publications, 125 Book Series, 28 million abstract records, and 245 million references (going back to 1996), added to all abstracts, and 200 million quality web sources, with more than 60% of the titles covered being from countries other than the US (copied from http://www.info.scopus.com/detail/what/).

FISHBASE: CITATION ANALYSIS

FishBase was not subjected to formal peer-review in the sense that journal articles do. However, since its development in the late 1980s, it has undergone several reviews by experts and in response is constantly adapted to meet suggestions and new needs (Froese and Pauly, 2000).

A citation analysis with Scopus (on 5 July 2006) using 'FishBase' as the keyword in all fields revealed 580 citations for 1995-2006, whereas a search in Google Books revealed citations in 73 books. This adds up to 653 citations and implies an annual mean rate of about 57. A cumulative citation rate of 653 puts FishBase into a very small group of highly-cited published items. This is because from the *ca* 38 million items that have been published since 1900, half have not been cited at all. From the remaining half that has been cited at least once, only 21,200 items (0.11%) have been cited more than 500 times (Garfield, 2005).

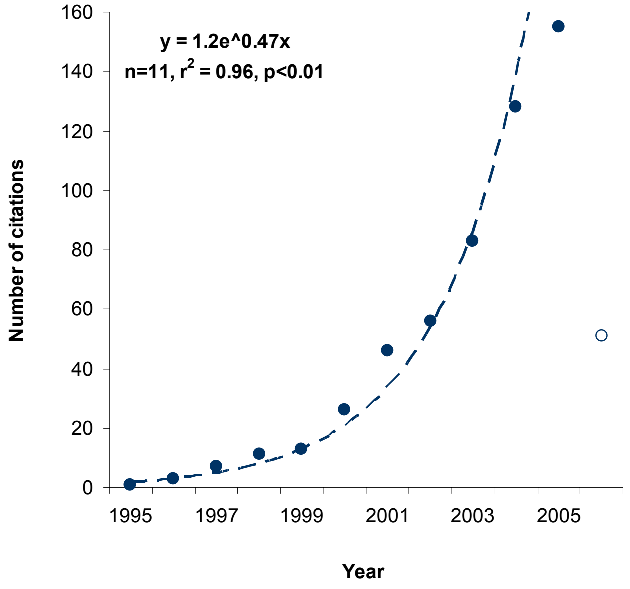

Figure 1 Annual number of citations to FishBase (source: Scopus, www.scopus.com, accessed on 5 July 2006).

The number of Scopus citations per year increased exponentially during this period from 1 in 1995 to 155 citations in 2005 and 51 for the first half of 2006 (Figure 1). The 580 Scopus citations occurred in 199 different journals. Fourteen out of the 199 journals (i.e., *Systematic Parasitology*, *Journal of Fish Biology*, *Folia Parasitologica*, *Marine Ecology Progress Series*, *Fisheries Research*, *Acta Parasitologica*, *Journal of Parasitology*, *Journal of Applied Ichthyology*, *ICES Journal of Marine Science*, *Reviews in Fish Biology and Fisheries, Canadian Journal of Fisheries and Aquatic Sciences, Aquatic Living Resources*, *Bulletin of Marine Science*, and *Ecological Modelling*), covering parasitology, fish and fisheries, and aquatic ecology, each cited FishBase more than 9 times and cumulatively accounted for 223 citations (38.4%). The 199 journals covered different fields, from agricultural and biological sciences to energy, business management and accounting (Figure 2).

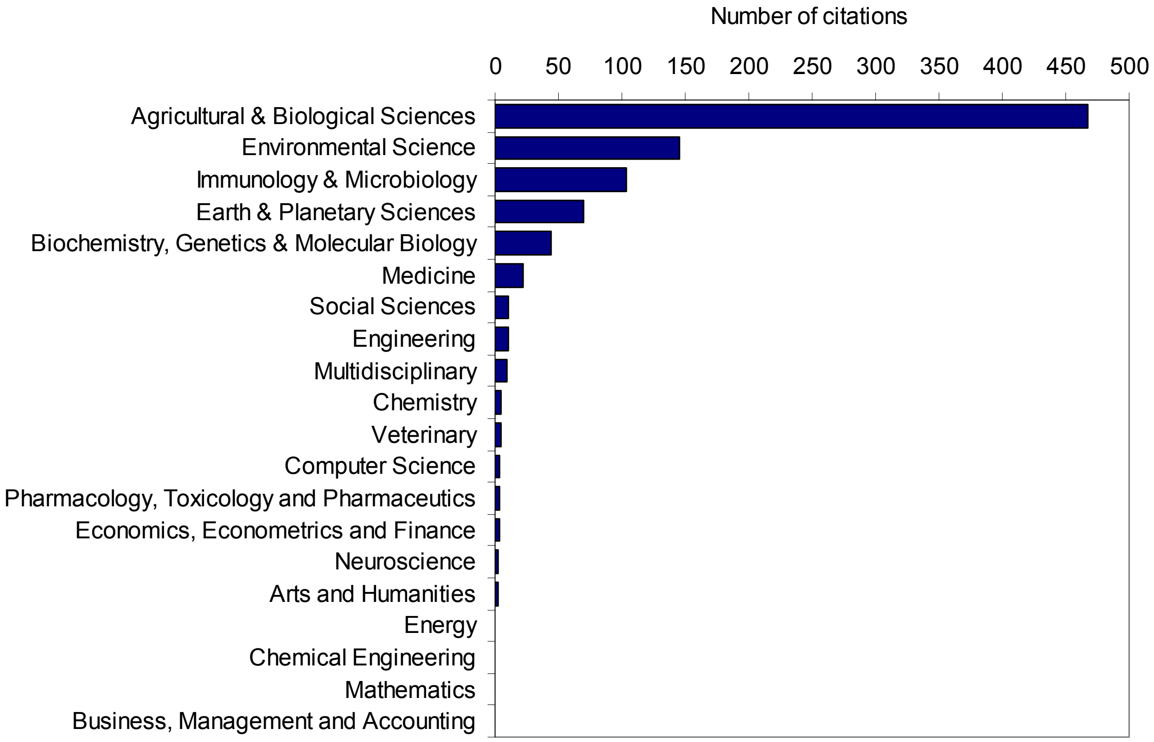

Figure 2 Number of citations to FishBase per field of journals (many journals cover more than one field) (source: Scopus, www.scopus.com, accessed on the 5 July 2006).

In total, 121 (60.8%) out of the 199 journals were general journals and 74 (37.2%) were aquatic journals (there were also 4, 2%, conference proceedings). In terms of citations, 299 (51.6%) out of the 580 citations occurred in general journals and 276 citations (47.6%) in aquatic journals (there were also 5 citations in conference proceedings). Thus, more than half of the citations to FishBase and of the sources of such citations were in 'general' journals. This clearly indicates that FishBase had a very good penetration into the primary 'ecological' (and other general) literature. FishBase also had a good penetration into the review literature: 46 (8%) out of the 580 citations were in journals specializing in reviews.

FishBase was also cited in 48 aquatic and 18 general books as well as in three general (e.g., Lévêque and Mounolou, 2003) and four aquatic textbooks (e.g., Jennings *et al.*, 2001; Walters and Martell, 2003) (Figure 3). However, it is not yet cited in recent general ecology textbooks (e.g., Smith and Smith, 2003; Townsend *et al.*, 2003; Odum and Barrett, 2005; Begon *et al.*, 2006).

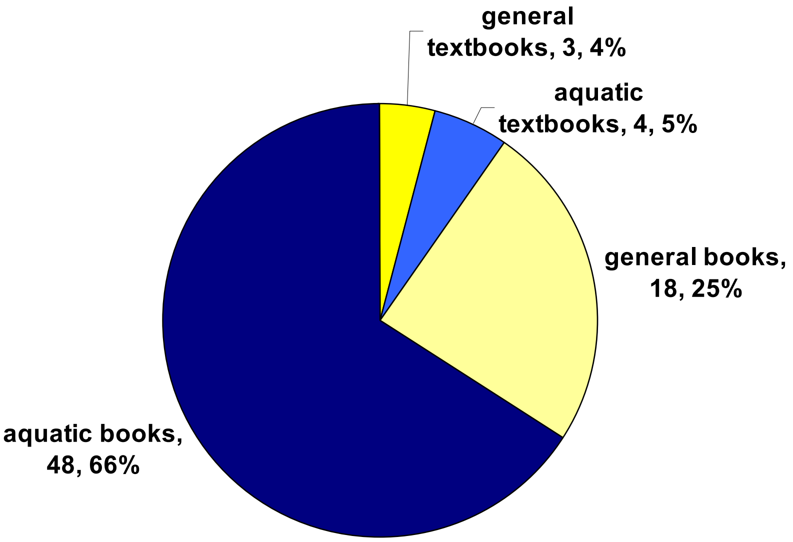

Figure 3 Number of citations (left) and percentages (right) of citations in books (source: Google Books, accessed 7 July 2006).

To sum up, the analysis presented here shows that FishBase is also very successful in terms of scientific impact, when the latter is evaluated based on 'traditional' bibliometric indices. Naturally, the number of citations to FishBase is much larger than the one presented here, since it is most probably cited in many other scholarly publication types not covered by Scopus, some of which are covered by Google Scholar (e.g., theses, technical reports, and technical papers, if online). In addition, the analyses of citations especially in non-peer reviewed, 'popular' items (e.g., general public publications, newsletters, newspaper articles, thematic maps, websites) will also be useful for measuring whether FishBase has become such a part of the public knowledge infrastructure that people from all walks of life refer to it (Cornelia Nauen, European Commission, Brussels, pers. comm.).

Acknowledgement

The authors would like to thank Dr Rainer Froese (University of Kiel, Germany) for his comments and suggestions.

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ANALYSIS OF COMMON NAMES OF BRAZILIAN FRESHWATER FISHES[1]

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ABSTRACT

A database of 2230 common names for 769 Brazilian freshwater fishes was compiled based on fifteen sources. An average of three names per species was found, with 361 species associated with only one common name. However, each of these names may be associated with other species. This is the case for *cascudo*, which is associated with 46 species. This does not cause much problem for analysis of catch statistics as *cascudo* catches are very small (408 tonnes·year^{-1}). On the other hand, *curimatã* catches are the highest for Brazilian freshwaters (28,700 tonnes·year^{-1}) and the correspondence between common and scientific name is not well-understood. Most of the common names originated from Ameridian languages, followed by Latin names. These names represent mainly primary lexemes and mostly describe the morphology or colour pattern of each species.

INTRODUCTION

There is a growing concern with the biodiversity loss caused by different factors, particularly anthropogenic ones. Fishing is one of these factors. Fishing causes differential mortalities for different segments of a population, depending on its sex, age, and size, besides the total removal. Depending on the effect on these different segments, the impact may be more or less serious. In some countries, e.g., the USA and Canada, catch statistics are recorded by common name. In some cases, there is enough knowledge about the correspondence between common and scientific names for each species based on extensive work that has been done since the late 1940s and has culminated in the most recent volume, authored by Nelson *et al.* (2005). In other countries, this correspondence is far from well-understood. In Brazil, for example, Freire and Pauly (2005) analyzed the diversity of marine and brackish fishes, and found that each species is associated with six names in average, and that each name may be used for different species, even from different families. Such a large scale analysis was lacking for Brazilian freshwater fishes and is presented here.

MATERIALS AND METHODS

A total of 2230 common names referring to 769 freshwater species from Brazil, representing about 35% of the species recorded for Brazil in FishBase (www.fishbase.org), were compiled in this study. Fifteen references were included in this compilation: Mutti (1971), Santos (1981), Nomura (1984), FUEM-NUPÉLIA (1987), Godoy (1987), Komissarov (1988), Begossi and Garavello (1990), Begossi *et al.* (1999), Ferreira *et al.* (1999), Toledo-Piza (2002), Godinho and Godinho (2003), CBPDS(2004), IBAMA (2004a), PNDPA (2006), and Becker *et al.* (2006). The states associated with the occurrence of each name were recorded.

Each name was translated from Portuguese to English and the origin of the name was identified. The core of the name and its modifiers were classified according to Palomares and Pauly (2000) as associated with behaviour, color pattern, habitat/ecology, inanimate object, locality/area, abundance, size, morphology, non-fish animal, other, person (generic), person (specific), plant, primary lexeme, or taste/smell.

Catch data were obtained from the national statistics provided by the Brazilian Institute for the Environment and Renewable Resources (www.ibama.gov.br): IBAMA (2001, 2003, 2004b, 2005).

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[1] Cite as: Freire, K., 2006. Analysis of common names of Brazilian freshwater fishes. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 7-11. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

RESULTS AND DISCUSSION

A total of 361 species are associated with only one common name, 147 species with two common names, 78 with three names and 183 with four or more names (Figure 1). *Trachelyopterus galeatus* is an extreme case, associated with 30 common names, some of them representing only different spellings of the same word: *Anduiá, Anojado, Anuiá, Anujá, Cabeça de ferro, Cachorro, Cachorrinho, Cachorrinho de padre, Cachorro de padre, Cangatá, Cangatí, Cangati, Capadinho, Carataí, Chorão, Chorãozinho, Cumbá, Cumbáca, Cumbaca, Jauzinho, Mandi, Mandí cumbá, Mandi cumbá, Mandí sapo, Mandizinho, Pacamão, Pacu, Peixe cachorro, Pocomão,* and *Ronaca ronca* (Figure 1). On the average, each species was associated with three common names. For marine fishes, Freire and Pauly (2005) found an average of six common names per species, with an analysis based on a more extended database.

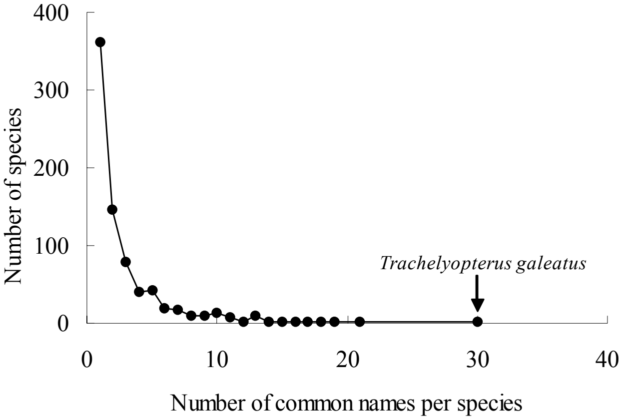

Figure 1 Richness of names of Brazilian freshwater fishes represented by the frequency of scientific species that have one to thirty common names.

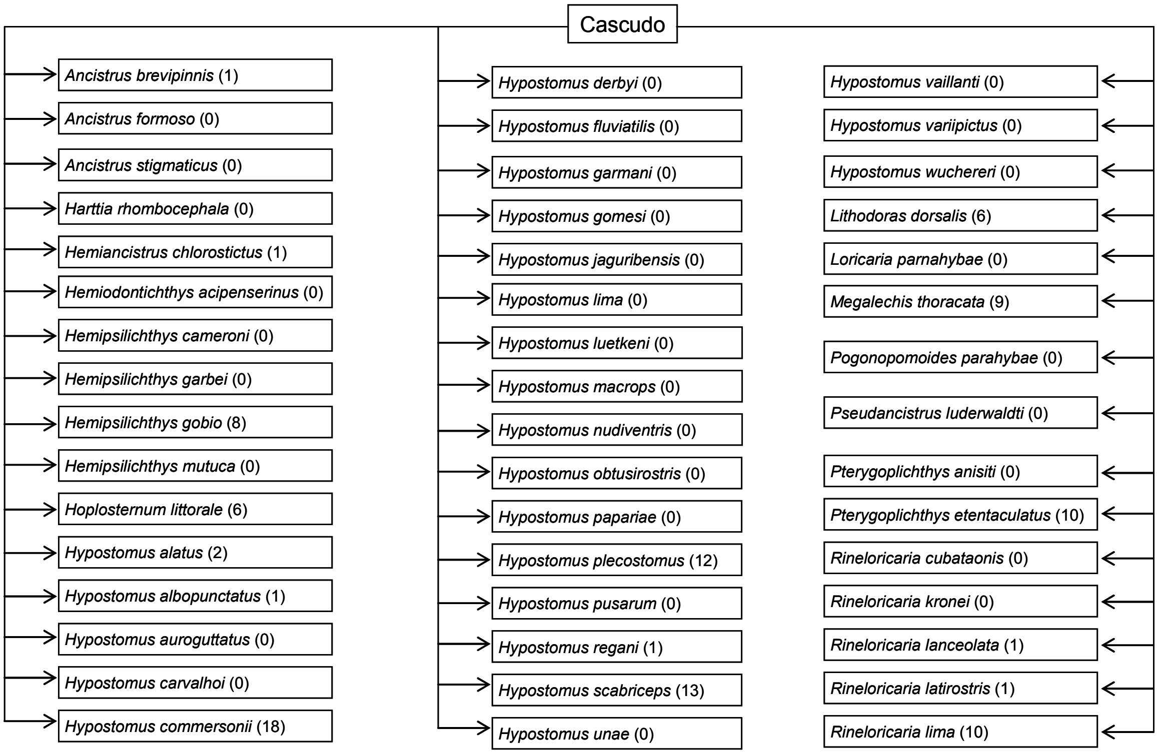

Figure 2 Scientific names associated with the common name *cascudo*. Numbers in parentheses represent other names besides *cascudo* that each species is associated with.

Even though almost 50% of these species are associated with only one common name, that name may be associated with one or more species. *Cascudo*, for example, is a common name used in association with 46 species (Figure 2). Thirty-one of these species are not associated with any other common name, seven are associated with one more name besides *cascudo*, one with 2 names, two with 6 or 10 names, one with 8, 9, 12, 13, and 18 other common names. Most of these species belong to the family Loricariidae, but two belong to the family Calichthydae (*Hoplosternum littorale* and *Megalechis thoracata)* and one to the family Doradidae (*Lithodoras dorsalis*). In order to better understand the intricate naming system, all the additional names (besides *cascudo*) for each species were presented together with the number of additional species the names are associated with (Figure 3). Thus, *Hypostomus scabriceps* is associated with the names *bacu puá, cascudo, cascudo cachichô, cascudo prêto, iarú urá, jaru itaquara, jaruitacoara, pirá tatu, uacarí, uará urá,* and *yaru itacura*, all exclusively used for the species presented in Figure 3. *Acarí, cascudo comum,* and *guacarí* are associated with *H. scabriceps* as well, but also with four, one and one other not shown species, respectively. Catches for cascudo are low in Brazil corresponding to only 408 tonnes on average for the period 2001-2004 (in Maranhão, Paraná, Santa Catarina, Rio Grande do Sul and, more recently, in Minas Gerais states).

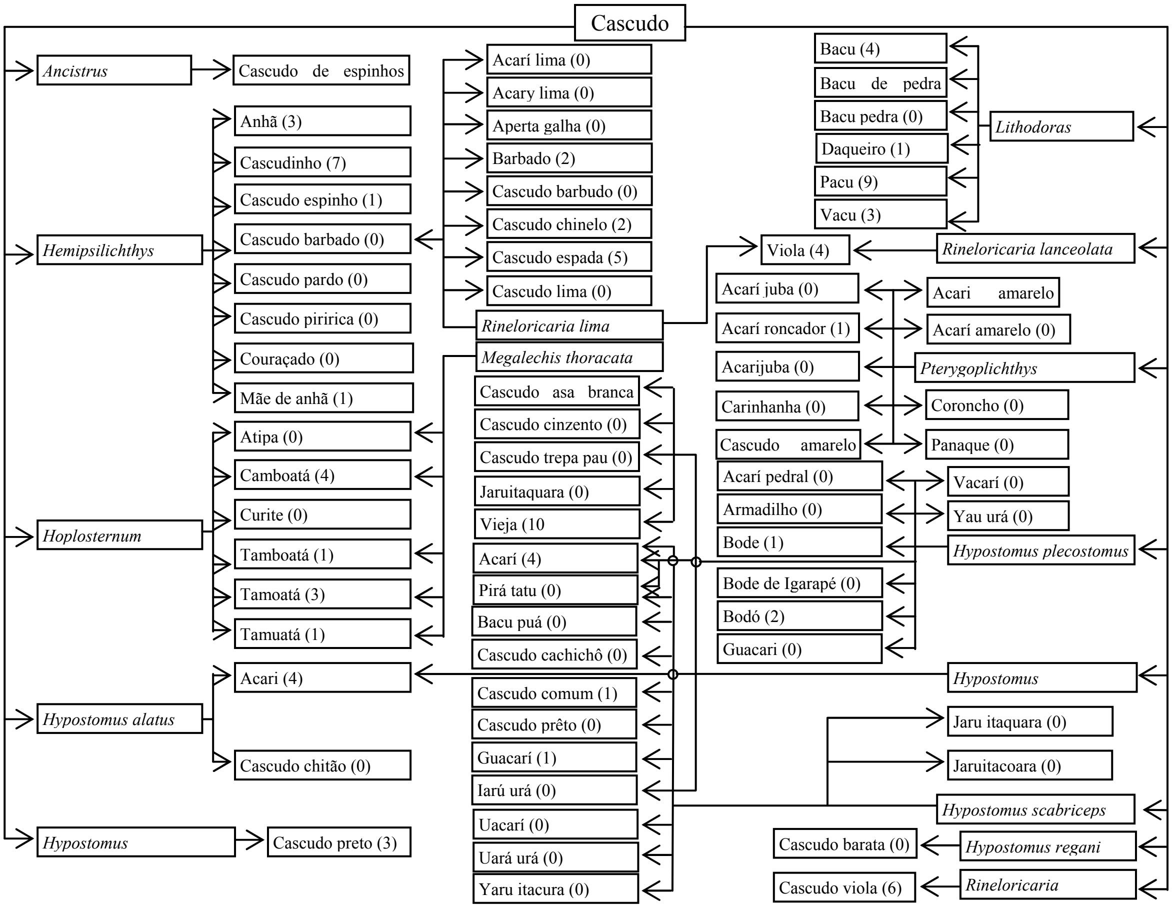

Figure 3 Scientific names associated with the common name *cascudo* and additional names for each species. Numbers in parentheses represent other species associated with each name.

The highest catches originating from Brazilian continental waters are for *curimatã, dourada* and *piramutaba*, which account, together, for about 30% of the total catch of freshwater fishes (Figure 4). IBAMA does not mention in the national bulletins the species associated with the name *curimatã*, which alone is responsible for annual catches of about 28,700 tonnes (2000-2004). According to the database compiled here, this name is associated with five species: *Prochilodus brevis, P. costatus, P. lacustris, P. nigricans,* and *P. vimboides*. As this name is associated with catches in all 26 Brazilian states, where they may represent different species, it is critical to establish the correct correspondence. With the exception of a small catch in Espírito Santo and Goiás states, all *dourada* catches originate from northern Brazil as is the case for *piramutaba*. IBAMA associates *dourada* to *Brachyplatystoma flavicans*, but two other species are also associated with this name (*Brachyplatystoma rousseauxii* and *Pellona castelnaeana*) according to the National Plan for the Development of Recreational Fisheries in Brazil (PNDPA, 2006). If one is to compare catches originating from commercial and recreational fisheries, this difference should be considered. *Piramutaba* represents *Brachyplatystoma vaillantii* according to IBAMA (2005) and is considered an overexploited resource (Anonymous, 1999; Ruffino, 2005). Even though this is not a unique association (as this common name was also related to *Platysilurus mucosus* in Acre state; Begossi *et al.*, 1999), it does not cause any problem to catch statistics due to the inexistence of catch records for *piramutaba* in this state.

The origin of several names could not be identified using Tibiriçá (1984), Bueno (1998) and Ferreira (1999). Among those that could be identified, 61 % originated from Ameridian languages, represented mainly by Tupi and Guarani; these were followed by Latin names (26.3%), Brazilianisms (3.5%), African names (0.9%), and others (8.1%), including French, Greek, Spanish, Italian, German, English, and Arabic. For marine fishes, Freire and Pauly (2003) found the opposite, with most of the names originating from Latin through Portuguese (40%) and less influence from Ameridian languages (24%). This may be due to Amerindian influence being stronger in the interior of the country.

Table 1 Descriptors used in the core, and in the first and second modifiers of the common names of Brazilian freshwater and marine fishes.

Descriptor	Freshwater	Marine
Primary lexeme	857	1793
Morphology	461	557
Color pattern	408	444
Inanimate object	297	314
Non-fish animal	206	419
Behaviour	202	158
Modification for size	199	232
Plant	124	162
Other	106	228
Person (generic)	92	143
Habitat/ecology	74	138
Locality/area	24	32
Modification for abundance	21	5
Person (specific)	19	46
Taste/smell	8	21

Most of the descriptors used in the names of Brazilian freshwater and marine fishes represent primary lexemes or are associated with the morphology or color pattern of the species (Table 1). A test of independence between the descriptor and the environment (fresh and marine water) was performed and the null hypothesis of independence was rejected ($\chi^2 = 212.8$; df = 14). Descriptors related to inanimate objects were more frequently used to describe freshwater than marine species. For the latter, the use of descriptors associated with non-fish animals was more common.

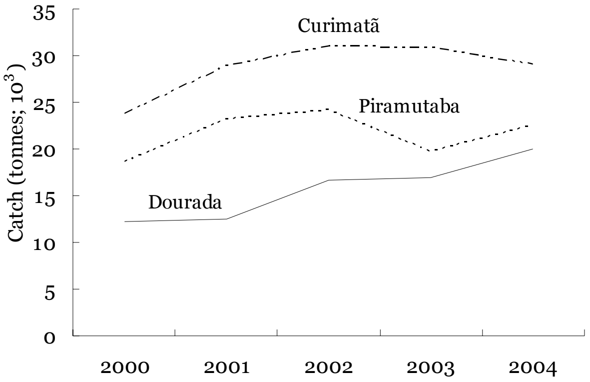

Figure 4 Catches from Brazilian continental waters for the three main species (2000-2004).

The spatial coverage of the name database for freshwater species is rather small as only seven states are associated with more than 50 names each: Amazonas, Acre, Tocantins, Minas Gerais, Paraná, Santa Catarina, and Rio Grande do Sul. For the remaining 19 states, there are less than 50 names and none were recorded for Amapá, Roraima, Rondônia, Mato Grosso do Sul, and Espírito Santo. This is the first database of names ever compiled for the analysis of Brazilian freshwater species. Ten other sources have been selected to be included in the database in the next future.

ACKNOWLEDGEMENTS

I would like to thank Juarez Rodrigues for encoding part of the common names compiled here; Carolina Minte-Vera, Fernando Becker, Juarez Rodrigues, Maurício Cetra, Paulo Chaves, and Projeto PróVárzea/IBAMA for providing lists of names and books, including unpublished materials.

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PROMINENCE TREND IN MAXIMUM LENGTHS RECORDED FOR FISHES: A PRELIMINARY ANALYSIS[1]

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ABSTRACT

FishBase, an information system on all finfishes of the world, records observed maximum lengths needed for growth studies and ecosystem modelling, among others. A plot of the number of species and subspecies against the maximum length by each centimetre from 1 cm to 20 m showed a bias related to Albers' theory on prominence in the decimal system which defines the most prominent numbers as 'spontaneous numbers'. The explanation lies in the origin of the data (mainly synthetic documents like FAO catalogues, regional faunas and check-lists), where maximum lengths are often rounded to the highest ten or hundred. Further analyses are suggested to check the impact of this bias in global trend analysis as well as possible methods to overcome this impact.

INTRODUCTION

The form of living organisms as the combination of shape and size (Thompson, 1917; Rohlf and Marcus, 1993) tells us about their position/place in ecosystems and is thus a powerful synthetic indicator of their life history traits. But we lack simple mathematical estimators to describe the form. The size is expressed as numbers which allows all mathematic operations when the shape is expressed as textual items ('elongated', 'compressed', etc.), hence the use of size alone as a form estimator. Volume is the best measure of the size in our three-dimensional world, but is difficult to measure. The centroid size used in multivariate morphometrics (see various papers in Rohlf and Bookstein, 1990) is a better estimate, but requires several measurements along three perpendicular axes for a good approximation.

For the finfishes of the five classes of Craniata (Myxini, Cephalaspidomorphi, Elasmobranchii, Actinopterygii, Sarcopterygii), body length measured from the tip of the snout to the end of the caudal fin (TL: total length), or to the end of caudal peduncle (SL: standard length), is the most currently applied among various size estimators; the width of the disc (WD) is used for Rajoidei (skates and rays), head length (HL) for Macrouridae (grenadiers), etc. They all require only one measurement and are the size estimators used in fisheries management for growth and ecosystem models, yield per recruit assessment, and various relationships being used to link the length to the volume (Beverton and Holt, 1957; von Bertalanffy, 1960).

Maximum length is an important parameter to record for these models. That is why FishBase, the major information system on finfishes in the world, available freely on the web (www.fishbase.org), gathers this information for the about 30,000 species and subspecies already described (see fishbase.sinica.edu.tw/report/MissingDataList.cfm?what = maxlength) for a list of species and subspecies with no maximum length recorded yet; we are looking for references for these species and calling on the community to send us references to complete the dataset.

Plotting the number of species and subspecies against the maximum length for each centimetre rounded to the nearest centimetre (Figures 1-3) showed that there is a general bias in the data. We explore why this bias occurs, and if it can affect inferences built on correlations with classes of maximum lengths. Also, methods are suggested for further testing to overcome this bias when performing global trend analyses or creating size classes.

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[1] Cite as: Bailly, N. 2006. Prominence trend in maximum lengths recorded for fishes: a preliminary assessment. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 12-17. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

MATERIALS AND METHODS

The maximum lengths were extracted from FishBase, version of 18 Aug. 2006 (see Binohlan and Pauly, 2000).

FishBase records information at species and subspecies levels; when subspecies are recognized as valid, information is recorded at subspecies level but not at species level. In the text below, the word 'taxa' is used for 'species and subspecies'. In the version used, there were 29,497 taxa; 281 subspecies (i.e., not the nominal subspecies) were recognized for 193 species (i.e., information recorded for the nominal subspecies) making 29,216 species in total (Table 1).

Five major types of length are used in FishBase: Total length, Standard length, Fork length, Disk length, Width of Disk; some rarely used (like head length) are noted 'other'; it may be 'not given'. Maximum lengths are recorded for adults 'male/unsexed' and/or 'female'.

Table 1 Number of taxa (species and subspecies) with information in FishBase (as of 18 Aug. 2006).

Category	Number
Species (excl. species with subspecies)	29,023
Nominal subspecies	193
Subspecies	281

The maximum lengths used here are computed as the maximum between 'male/unsexed' and 'female', whatever the length type is. For instance, in the case of dwarf parasitic males in the family Oneirodidae, the maximum length for female is selected.

RESULTS

The numbers of taxa are computed for each centimetre rounded to the nearest centimetre.

On the total of 29,497 taxa, 4,693 had no maximum length recorded for adults (see Table 2 for a gap analysis and other statistics). The minimum length is 0.84 cm TL (Perciformes: Schindleriidae: *Schindleria brevipinguis*, Watson and Walker, 2004) and the maximum 20 m (Orectolobiformes: Rhincodontidae: *Rhincodon typus*, Smith, 1828). The maximum number of taxa is 1,334 for 5 cm maximum length.

Table 2 Statistics on maximum lengths (L_{max}) in FishBase (as of 18 Aug. 2006).

Taxa with L_{max}	Number	All taxa n = 29,497 %	With L_{max} n = 24,804 %
For one of or both sexes	24,804	84.1	100.0
For both sexes	1,082	3.7	4.4
For one of sexes	23,722	80.4	95.6
For male/unsexed only	23,395	79.3	94.3
For female only	327	1.1	1.3
Missing for both sexes	4,693	15.9	18.9
Missing for male/unsexed	5,020	17.0	20.2
Missing for female	28,088	95.2	113.2
Where Female > Male/unsexed	544	1.8	2.2
>= 100 cm	1,136	3.9	4.6
< 100 cm	23,668	80.2	95.4
>= 80 cm	1,568	5.3	6.3
< 80 cm	23,236	78.8	93.7

Figures 1 to 3 present the following characteristics:

- up to 80 cm, there are more species with maximum length expressed primarily as tens of centimetres; and secondarily as fives of centimetres;

- from 80 cm to 500 cm, there are more species with maximum length expressed in tens of centimetres except for 190, 290, 460, 480, and 490 cm; fives of centimetres are more frequently between 80 and 100 cm, 160 and 180 cm, and 300 and 320 cm, but not as much as below 80 cm; beyond this, there are more tens or fives but they pertain only to one taxon;

- from 100 cm up to 500 cm, there are more species with maximum length expressed primarily for hundreds of centimetres; and secondarily for 250, 320 (higher than for 350 cm), and 430 cm (higher than for 450 cm);

- beyond 500 cm, there are only 18 species, 13 measured in tens of centimetres, 3 in hundreds (800, 1,100, and 2,000 cm, the latter maybe as thousand), and 2 with other final digits (549 and 656 cm).

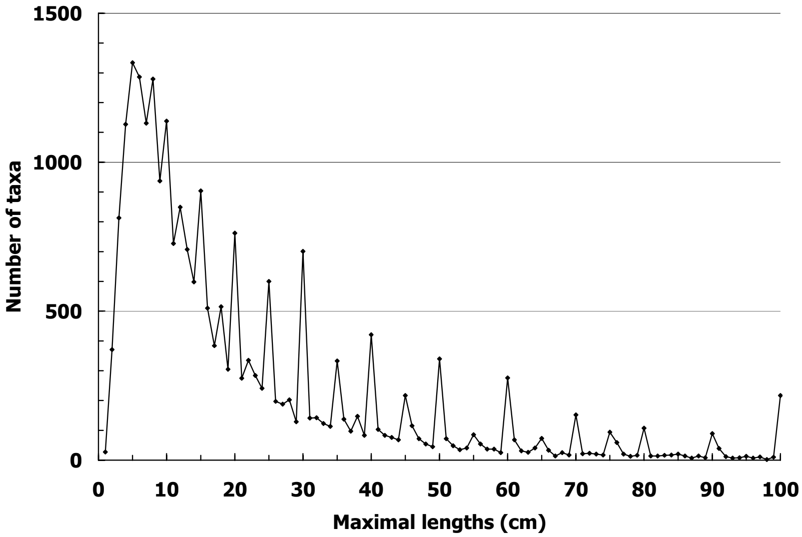

Figure 1 Number of taxa (species and subspecies) for each centimetre of maximum length from 0 to 100 cm.

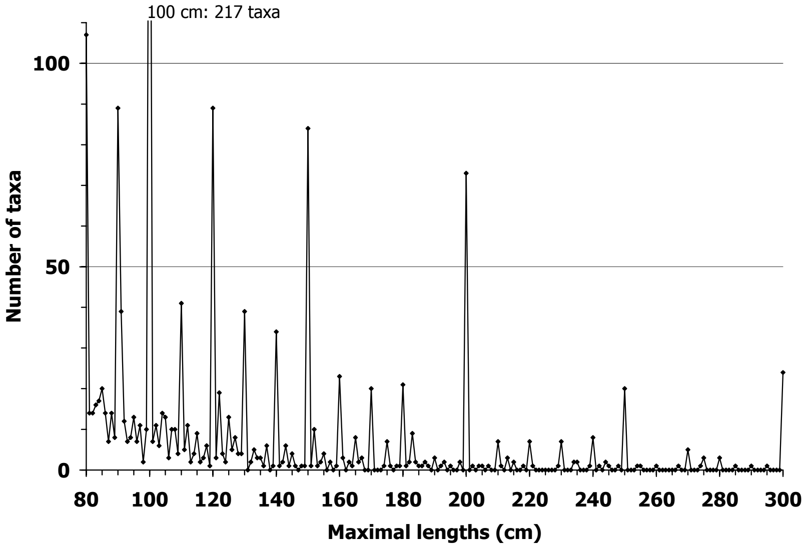

Figure 2 Number of taxa (species and subspecies) per each centimetre of maximum length from 80 to 300 cm.

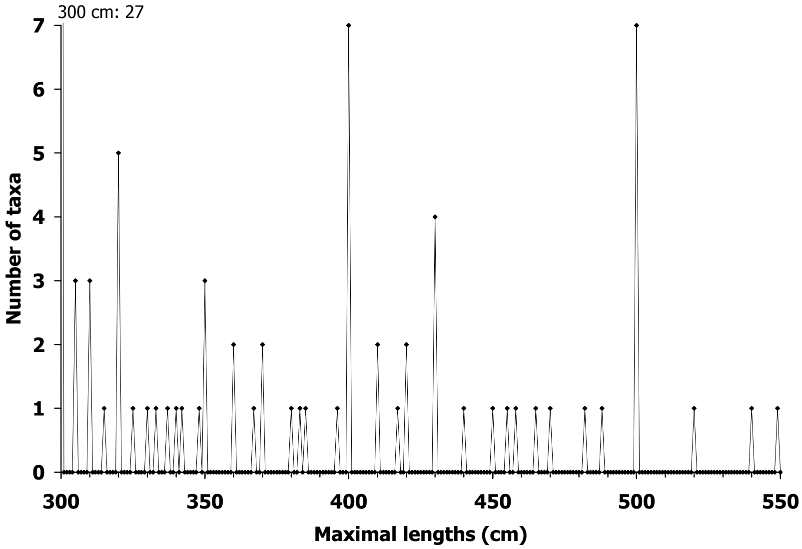

Figure 3 Number of taxa (species and subspecies) per each centimetre of maximum length from 300 to 550 cm.

We have also ranked the unit digits 0-9 from 1 to 10 in each group of ten according to the decreasing number of species with the same unit digit of maximum length. Table 3 presents the mean position between 1 to 10 in each tenth between 11 and 79. If the rank was equiprobable for each digit, the mean position should not be significantly different from 5.5 for all. As evidenced by Table 3, this is not the case. Tens are dominant followed by digits 5, 1 and 2, and digit 9 is definitely the least-represented digit. The signal fades progressively when moving towards the upper tens but the same tendency remains strong for tens, digits 5 and 9, and to a lesser degree for digits 1 and 2; digits 6, 3, 4, 8 and 7 are more variable.

Table 3 Mean rank of digits 0-9 among tens 10-70 when ordered down by number of species with the same unit digit of maximum length. SE = standard error.

Digit	Rank			
	Mean	SE	Min	Max
0	1.0	0.0	1	1
5	2.0	0.0	2	2
1	4.1	0.8	3	5
2	4.3	1.0	3	6
6	5.3	1.8	3	8
3	6.3	1.4	4	9
4	6.6	1.3	4	8
8	7.3	1.9	3	10
7	8.4	1.0	7	10
9	9.7	0.4	9	10

DISCUSSION

Fitting laws

Albers and Albers (1983): Prominence in the decimal system

The results shown in Figures 1 to 3 are consistent with the theory of prominence in the decimal system where Albers (1997) proposes that a set S called 'spontaneous numbers,' defined as $\{s*10^i \mid s \in \{1, 1.5, 2, 3, 5, 7\} \mid i \in \aleph\}$ [the notation is ours] (Hertwig *et al.*, 1999), for numbers preferentially chosen by persons for estimations (of prices in Albers' work). Indeed 5, 10, 15, 20, 30, 50, 100, 150, 200, 300, 500 are prominent in our results (Figure 4). Nevertheless, 1 and 2, and 7 and 70, are not prominent. Two complementary explanations can be suggested: the theory is about estimations without measurements, and does not completely apply to the latter case (for 7 and 70); and the maximum length distribution among fishes (approximately a Poisson distribution) strongly constrains the results (in particular 1 and 2).

A series including 8, 40, 60, 120, 250, 400, 430 constitutes a second line of prominent numbers, but non-spontaneous numbers (Figure 4), more or less mixed with the first one up to 150. This indicates a strong tendency of authors to round to the highest ten or hundred, which confirms the strong constraint of the data distribution.

For the second digit, the results are similar: digits 0, 5, 1, and 2 between 11 and 99; and 120, 250, 310, 320, 350, 430, 450 beyond (not all shown on Figure 4). Again digit 7 is not prominent in our results.

Consistently, the 9 digit is under-represented at all levels, showing again the strong tendency of authors to round to the highest ten or hundred.

Table 4 Taxa numbers by ranges of maximum lengths in tens from 0 to 99 cm, and by hundreds from 100 to 999 cm.

Range by tens	Number of taxa	Range by hundreds	Number of taxa
0-9	8,305	0-99	23,668
10-19	6,637	100-199	868
20-29	3,213	200-299	164
30-39	2,017	300-399	55
40-49	1,254	400-499	24
50-59	774	500-599	11
60-69	604	600-699	6
70-79	435	700-799	4
80-89	231	800-899	1
90-99	198	900-999	1

Benford (1938): first digit law

The distributions of the first digit between 0 and 99, and 100 and 999, follow Benford's law (1938), which predicts a decreasing number of species grouped by tens, and by hundreds (Table 4), as a logarithmic distribution $p(i) = \log_{10}(1+1/i)$ for $i = 1$ to 9 (our number fits the logarithmic tendency, but not exactly the values computed from the equation). The Poisson distribution of our data explains why the distribution of the first digit fits with Benford's law. A more rigorous demonstration can be found in Hill (1996).

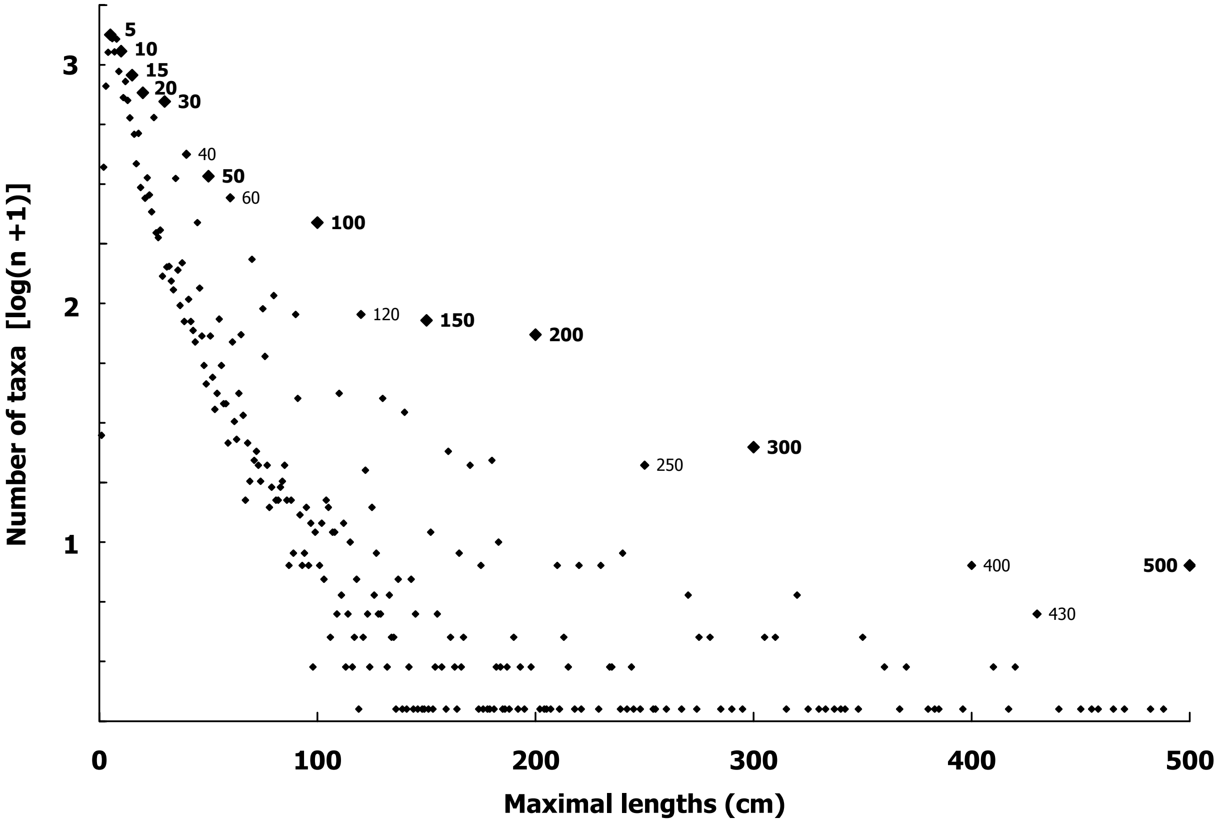

Figure 4 Logarithm of number of taxa (species and subspecies) as $\log_{10}(n+1)$ per each centimetre of maximum length from 0 to 500 cm.

It could be suggested that the full step numbers F, defined as $\{f*10^i \mid s' \in \{1, 2, 5\} \mid i \in \aleph\}$ (Albers, 2001) fit both Albers' theory and Benford's law. This is consistent for instance with the choice of coins and notes for the European currency (1, 2, 5, 10, 20, 50 Cents, and 1, 2 Euros for coins; 10, 20, 50, 100, 200, 500 Euros for notes).

When and how the bias occurs

We can reject the hypothesis that the bias is generated during data encoding in FishBase. Data are encoded as published. However, values with tenth of millimetres for lengths beyond 50 cm are rounded to the nearest millimetre.

As mentioned above, authors tend to round at the highest tens or hundreds. In which publications?

In general, in publications that first describe a species, the length is not rounded because only few specimens are usually measured, and the maximum length is extracted by the FishBase encoders and entered as such. This is confirmed by a plot (not shown) similar to Figure 4 for the taxa described from 2000 onwards that were encoded mainly from the original description (1,780 taxa of which 1,348 have a maximum length reported in FishBase). In this case, the prominent numbers are 6, 19, 25, 30, 41, 58, 69, 78 (for species described from 1996 onwards, 13, 25, 30, 44, 50, 58, 80. The spontaneous number signal starts to appear for species described from 1990 onwards: 25, 30, 40, 50, 70, 80, and 120, although 6 is still the highest value).

For species described before 2000, the FishBase Team used mainly large syntheses, such as the FAO catalogues, regional accounts, identification sheets, regional faunas and checklists and revisions to a lesser degree (about 89% on 23,238 taxa before 2000 with maximum length; 90% on 21,205 taxa before 1990 with maximum length). It is in these publications that authors round maximum lengths. Others few cases involved unit conversion (inches in cm, for instance).

Conclusions

We demonstrated that, overall, FishBase may over-estimate maximum lengths. In synthetic works, it is usually not possible to track back the origin of the information used by authors. Unfortunately, with overexploitation of natural resources, the lengths recorded in nature tend to decrease, and the reported maximum lengths cannot be validated in the field. Species, museum collection, and document databases, associated within information system networks like GBIF, should help to reappraise and re-evidence the maximum lengths from specimens and primary literature. They should not be rounded then.

Pending this, one simple solution is to compute a moving average on 4 values of number of taxa: n-2, n-1, n, n+1 for a given maximum length. This however generates other biases. Another more complex solution is to fit a distribution analytically, either a Poisson distribution, or by ignoring lengths below 5 cm or by summing them (i.e., power or logarithmic fit).

These solutions are to be tested thoroughly and eventually mathematical solutions proposed to avoid biasing global trend analyses by an over-estimation of maximum lengths.

ACKNOWLEDGEMENTS

I thank D. Pauly, Fisheries Centre, University of British Columbia, who pointed out the prominence theory and spontaneous numbers, and without whom this matter would have remained ‘une aimable curiosité’.

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AGE AND GROWTH OF MEDITERRANEAN MARINE FISHES[1]

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ABSTRACT

Age and growth data have been so far collected from the literature on 383 Mediterranean marine fish stocks, most of which (77 %) are at present not included in FishBase. The most intensively studied species were highly commercial species. Maximum length ranged between 4.2 cm (*Aphia minuta*) to 225 cm (*Xiphias gladius*), and maximum lifespans between 0.66 year (*A. minuta*) and 30 years (*Helicolenus dactylopterus*).

INTRODUCTION

Age and growth, including maximum length, which is related to many other biological, ecological and population dynamic parameters, are the cornerstones of fish biology, ecology and fisheries management (Campana, 2001; Froese and Pauly, 2000). The longevity and the maximum size which the individuals of a given species are capable of reaching, as well as the growth rate (i.e., change in size with time) are determined mainly by the environment and the genotype. Under the most favourable conditions, the individuals of a population may reach a characteristic maximum length, which is specific for each species, i.e., there are no sardine which reach 1 m (Bond, 1996). The interaction of growth with food availability and reproduction determines other crucial parameters of a species (e.g., size at first maturity, fecundity, mortality) and hence its biomass and stock composition in space and time.

The present work was motivated by the need to update FishBase (Froese and Pauly, 2000; www.fishbase.org) with information on the age, growth and maximum length of Mediterranean marine fishes, and expands on earlier compilations of such data on Greek fishes (Stergiou *et al*., 1997). This will allow us to identify patterns and propensities (*sensu* Pauly, 1998) in the age and growth of fishes in this semi-enclosed basin, which has been subjected to fishing for thousands of years, and eventually to test various hypotheses (e.g., nanism in the eastern Mediterranean, see Stergiou *et al*., 1997).

MATERIALS AND METHODS

We collected data on: (i) maximum length (L_{max}, cm; mainly total length) and age (t_{max}, year); (ii) growth parameters, i.e., asymptotic length L_∞ (cm), the rate at which L_∞ is approached, K (year^{-1}), and the theoretical age at zero length, t_o, (year). We also tabulated auxiliary information such as study area and year, frequency of sampling, sampling gear, sample size, method used for the estimation of growth parameters, and skeletal structure used for age determination. All sources as well as the data collected will shortly be incorporated into FishBase.

RESULTS AND DISCUSSION

Overall, we collected to date data for 383 records (or stocks: species-sex-area-year combinations) belonging to 86 Mediterranean fish species (Figure 1). From these records only 88 (23 %) are at present included in FishBase. We point out that so far all our records are derived from journals listed in the Science Citation Index and from other international or local journals, whereas we have not yet included records appearing in the grey literature (i.e., technical reports, conference proceedings and theses, with the exception of the CIESM proceedings), which accounts for more than 35 % of all published items on

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[1] Cite as: Stergiou, K.I., Tsikliras, A.C., Apostolidis, C.A., 2006. Age and growth of Mediterranean marine fishes. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 18-21. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

Mediterranean ecological research (Stergiou and Tsikliras, 2006). These items will be also covered during the next six months.

The most intensively-studied species were all highly commercial species: the common pandora (*Pagellus erythrinus*), European anchovy (*Engraulis encrasicolus*), European hake (*Merluccius merluccius*), red mullet (*Mullus barbatus*), picarel (*Spicara smaris*), annular seabream (*Diplodus annularis*) and bogue (*Boops boops*), each represented by more than ten stocks (Figure 2). The vast majority of the stocks belonged to families Sparidae (59 stocks), Mullidae (23), Clupeidae (22), and Gadidae, Scophthalmidae and Scorpaenidae (20).

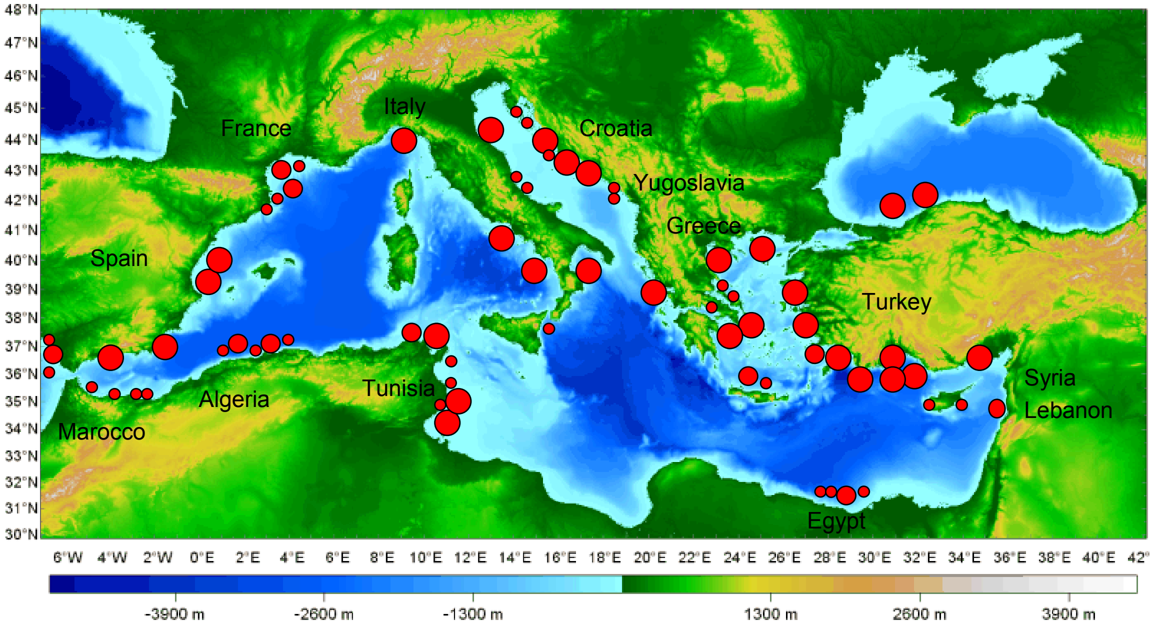

Figure 1 Map of the Mediterranean Sea showing approximate locations where data on at least one aspect of fish age and growth are available (total: 383 stocks). The red-bubble size is proportional to the number of stocks (small = 1, medium = 5, large = 10 stocks). The bottom bar indicates depth and altitude (in m). Map from Università degli Studi di Pavia (Centro Interdisciplinare di Bioacustica e Ricerche Ambientali; downloadable at http://www.unipv.it/webcib/edu-Mediterraneo-uk.html).

Age and growth data were available for the waters of Turkey (105 stocks), Greece (58), Italy (53), Spain (40), Tunisia (38), Croatia (33), Algeria (13), France (13), Egypt (8), Portugal (7) Lebanon (4), Morocco (4), Cyprus (2) and Yugoslavia (2). Our preliminary analysis showed that the eastern (179) and western (201) Mediterranean studies are so far relatively balanced (Figure 1). However, this is not true for southern when compared to northern Mediterranean (Figure 1).

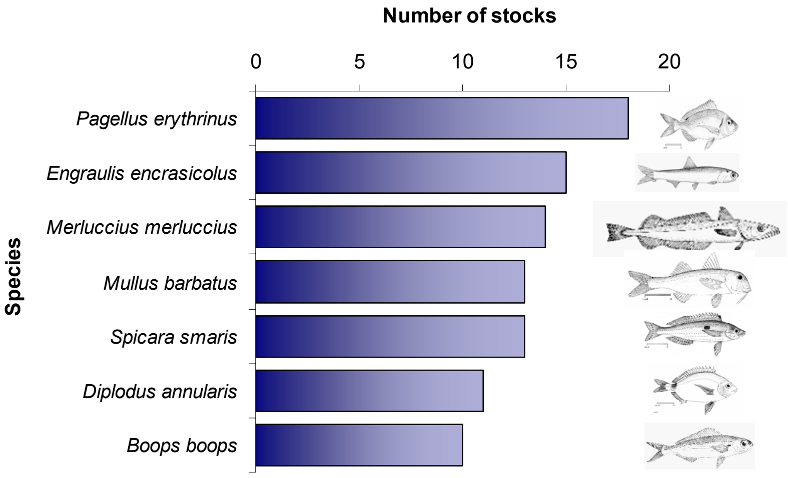

Figure 2 The most intensively-studied species in the Mediterranean Sea.

Overall, t_{max} was available for 285 stocks and L_{max} for 266 stocks. L_∞ and K were provided by the original authors for 340 stocks, and t_0 for 330 stocks. In 40 (11.5 %) out of the 340 stocks, the growth parameters were estimated from length frequency distributions using ELEFAN/FiSAT and other length-based methods. For the remaining 300 stocks (88.5 %), the growth parameters were estimated using age-at-length data derived from skeletal structures (otoliths: 204 stocks, 68 %; scales: 75 stocks, 25 %; otoliths and scales: 4 stocks, 1.3 %; spines: 8 stocks, 2.7 %; vertebrae: 9 stocks, 3 %).

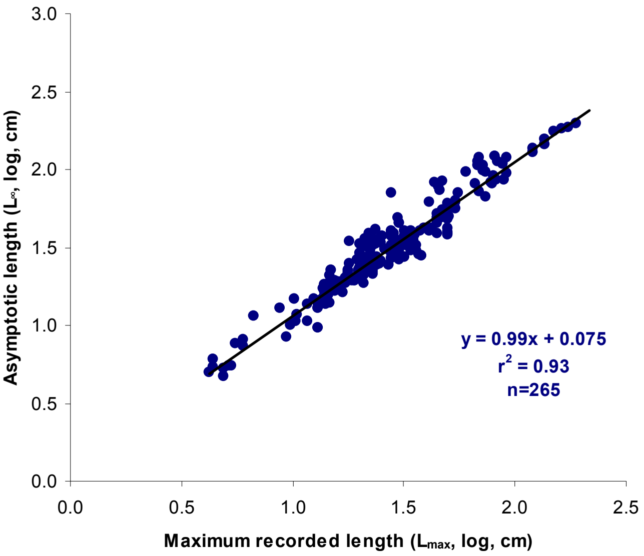

Figure 3 The relationship between asymptotic length (L_∞, log, cm) and maximum recorded length (L_{max}, log, cm) for 265 Mediterranean marine fish stocks.

Maximum length ranged between 4.2 cm (*Aphia minuta*, Balearic Islands, Spain) and 215 cm (*Xiphias gladius*, southern Aegean Sea, Greece) and had a mean value of 37.6 cm, while L_∞ ranged between 4.7 and 220.1 cm for the same species (mean = 42.8 cm). The dimensionless L_{max}/L_∞ ratio ranged between 0.40 (*Helicolenus dactylopterus*, eastern Ligurian Sea, Italy) and 1.37 (*Diplodus vulgaris*, Algarve coast, Portugal), with a mean value of 0.89. The relationship between $\log L_\infty$ and log L_{max} (Figure 3) had a slope (0.984) similar to that reported by Froese and Binohlan (2001), which was based on 551 data pairs.

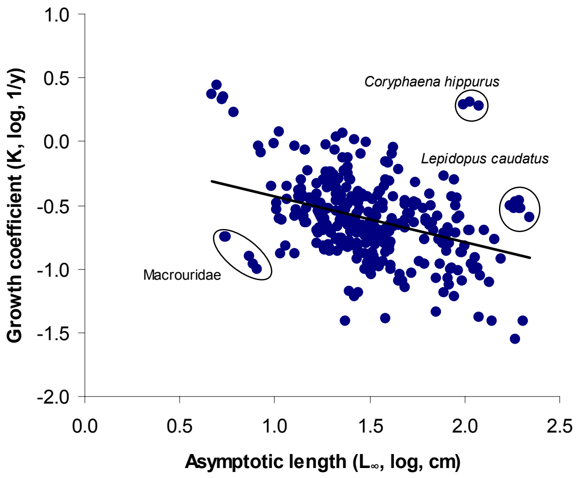

Figure 4 The relationship between the growth coefficient (K, log, year^{-1}) and asymptotic length (L_∞, log, cm) for 340 Mediterranean marine fish stocks. The outliers are circled.

The maximum lifespan recorded was 30 years (*Helicolenus dactylopterus*, Alboran Sea, Spain) and the minimum one 0.66 year (*Aphia minuta*, Balearic Islands, Spain). The von Bertalanffy K coefficient ranged between 0.028 year^{-1} (*Epinephelus guaza*, Gulf of Gabes, Tunisia) and 2.76 year^{-1} (*Aphia minuta*, Balearic Islands, Spain), with a mean value of 0.32 year^{-1}. The double logarithmic relationship between K and L_∞ (Figure 4) is described by the following equation: $\log K = -0.36 \cdot \log L_\infty + 0.07$ ($r^2 = 0.13$, n = 340). The 'outlier' stocks noted on this graph are Macrouridae, *Coryphaena hippurus* and *Lepidopus caudatus*. Finally, the theoretical age at zero length, t_0, ranged from -5.36 year to 0.96 year (mean = -1.12 year), with very large negative values most probably indicating unreliable estimates.

The relationship between K and L_∞ (as well as other life-history relationships) will be examined separately for the main families as well as for the eastern and western Mediterranean.

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TROPHIC LEVELS OF NORTH AEGEAN SEA FISHES AND COMPARISONS WITH THOSE FROM FISHBASE[1]

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ABSTRACT

We estimated trophic levels (TROPHs) for 76 species from the north Aegean Sea using diet composition, and compared the estimated TROPHs with those reported in FishBase ($\mathrm{TROPH_{FB}}$). For 41 and 14 out of the 76 species, there is no such information from the Aegean and the Mediterranean Seas, respectively. North Aegean TROPHs were linearly related to $\mathrm{TROPH_{FB}}$ ($\mathrm{TROPH} = 1.24+0.65\mathrm{TROPH_{FB}}$, $R^2 = 0.54$, $p<0.01$).

INTRODUCTION

Although food composition and feeding habits of fishes have been a favored research field for more than a century (e.g., Gerking, 1994), it was only in the early 1940s that the trophic level concept was introduced in ecology (Pauly *et al.*, 2000a). Lindeman (1942) introduced quantitative food webs as a tool in understanding temporal change in aquatic ecosystems in a paper that was initially rejected by two reviewers of the journal *Ecology* (Sobczak, 2005). Nowadays, the concept of the fractional trophic level (TROPH) is widely used, being of high importance to ecological research (e.g., for estimating 'primary production required' to support fisheries, see Pauly and Christensen, 1995; Tudela, 2000; for identifying the 'fishing down the food webs' process, see Pauly *et al.*, 1998; for comparative community analysis and construction of trophic signatures, see Pauly *et al.*, 2000b, Froese *et al.*, 2005; and for constructing trophic signatures for fishing gears, see Stergiou *et al.*, 2006; see also CIESM, 2000; Stergiou and Karpouzi, 2002 and references therein).

The success of the application of TROPH in ecological research is also demonstrated by the fact that the Marine Trophic Index (MTI), which actually refers to the mean TROPH of the landings for fish with TROPH higher than a cut-off value, has been selected by the Convention of Biological Diversity as one of the eight indices to be tested for use as an indicator of biodiversity changes (Pauly and Watson, 2005). In order for this to be realized, accurate area-specific TROPH estimates for all or most important fish species in the ecosystem must be readily available. However, this is not always the case, as diet composition data are rarely available for the area under study. Thus, one has to use general TROPH values (e.g., for the same species from different areas or from another species of the same genus). Such general values are extracted from various sources, among which FishBase (www.fishbase.org; Froese and Pauly, 2005), the largest electronic encyclopedia for fish, is the most important (see Stergiou *et al.*, 2006).

In this report, we estimated TROPH for 76 species from the north Aegean Sea using diet composition. Data were collected within the framework of a project on the feeding habits and TROPHs of fishes in the north Aegean Sea. These data were then compared to those reported in FishBase ($\mathrm{TROPH_{FB}}$).

MATERIALS AND METHODS

Samples were collected on a seasonal basis, from spring 2001 to winter 2006, using commercial fishing vessels (i.e., trawlers, purse-seiners, and gill-netters), and preserved in 10% formalin. At the laboratory, stomach contents were identified to the lowest possible taxonomic level and weighted (wet weight) to the

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[1] Cite as: Karachle, P.K., Stergiou, K.I., 2006. Trophic levels of north Aegean Sea fishes and comparisons with those from FishBase. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 22-26. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

nearest 0.01 g (expressed as a percentage of the total stomach content weight) (Hyslop, 1980). For stomachless species, the anterior half of the digestive tract was used for the analysis (e.g., Bell and Harmelin-Vivien, 1983). From the diet content, we estimated TROPH values per species, using the routine for quantitative data of TrophLab (Pauly *et al.*, 2000c), a stand-alone application for the estimation of TROPHs from the contribution to the diet and the TROPH of the prey organisms. When a prey item was an 'identified fish' species, then the TROPH of this species (as estimated in this study) was used for the estimation of predator's TROPH. The diet composition data will be incoporated into FishBase.

RESULTS

Overall, we studied and estimated feeding habits and TROPHs for 76 fish species (7,124 individuals; Table 1). No information on feeding habits existed for 41 out of the 76 species for the Aegean Sea and for 14 out of the 76 species for the Mediterranean Sea. Finally, no information on the feeding habits of *Monochirus hispidus* is included in FishBase (date: 4/7/2006; Table 1). The number of individuals examined ranged from 1 for very rare species (*Chelidonichthys lastoviza*, *Dasyatis pastinaca*, *Dipturus oxyrinchus*, *Fistularia commersonii* and *Labrus viridis*) to 759 (*Engraulis encrasicolus*) (Table 1).

Table 1 Fractional trophic levels (TROPH) and their standard error (SE) for 76 fishes, north Aegean Sea, Greece. N: number of individuals; TROPH_{FB}: TROPH reported in FishBase (www.fishbase.org; Froese and Pauly, 2005).

Species	N	Length range	TROPH	TROPH_{FB}
Alosa fallax[1,2]	27	15.0-46.8	4.32±0.48	3.60±0.60
Anthias anthias[1,2]	9	12.7-16.6	3.54±0.52	3.80±0.58
Apogon imberbis	37	8.0-11.5	3.54±0.56	3.90±0.64
Arnoglossus laterna[1]	212	4.5-16.9	4.35±0.74	3.60±0.54
Arnoglossus thori[1]	3	9.1-11.2	3.61±0.57	3.30±0.53
Belone belone[1,2]	69	27.2-53.5	3.48±0.45	4.20±0.74
Blennius ocellaris[1,2]	23	7.0-13.7	3.26±0.46	3.50±0.43
Boops boops	106	11.2-19.9	3.52±0.52	3.00±0.12
Bothus podas[1]	22	11.3-17.2	3.39±0.53	3.40±0.49
Caranx rhonchus[1,2]	16	18.0-19.8	4.50±0.80	3.60±0.59
Cepola macrophthalma	195	13.2-54.9	3.13±0.31	3.20±0.30
Chelidonichthys lastoviza	1	16.9	3.32±0.49	3.40±0.50
Chelidonichthys lucernus[1]	15	6.0-21.6	3.64±0.63	3.70±0.61
Chromis chromis[1]	97	8.6-13.3	3.25±0.37	4.10±0.70
Citharus linguatula	170	3.9-24.3	4.34±0.69	4.00±0.65
Conger conger[1]	31	34.1-99.8	4.18±0.58	4.30±0.75
Coris julis	78	11.3-18.2	3.42±0.53	3.20±0.45
Dalatias licha[1]	2	38.0-40.2	4.50±0.39	4.20±0.66
Dasyatis pastinaca[1]	1	50.1	3.46±0.53	4.10±0.63
Dentex dentex	10	11.7-15.3	4.49±0.80	4.50±0.70
Diplodus annularis	427	6.1-17.5	3.20±0.43	3.40±0.44
Diplodus vulgaris[1]	50	9.0-16.7	3.08±0.28	3.20±0.37
Dipturus oxyrinchus[1,2]	1	81.2	3.60±0.59	3.50±0.37
Engraulis encrasicolus[1]	759	5.8-14.0	3.38±0.44	3.10±0.51
Eutrigla gurnardus[1]	10	6.3-14.8	3.58±0.58	3.60±0.57
Fistularia commersonii	1	92	4.50±0.80	4.30±0.74
Gaidropsarus biscayensis[1]	65	9.0-15.3	3.93±0.67	3.60±0.54
Gaidropsarus mediterraneus[1]	15	8.5-14.5	3.95±0.61	3.40±0.53
Galeus melastomus[1]	3	23.3-54.0	4.50±0.41	4.20±0.58
Labrus viridis[1]	1	19.5	3.29±0.51	3.80±0.64
Lepidotrigla cavillone	4	8.8-11.7	3.50±0.50	3.20±0.43
Lesueurigobius suerii[1,2]	141	5.8-9.4	3.35±0.43	3.60±0.50
Lophius budegassa	45	5.0-38.4	4.54±0.60	4.50±0.76
Lophius piscatorius	6	7.7-12.7	4.48±0.54	4.50±0.76
Merlangius merlangus[1,2]	41	14.1-29.1	4.38±0.73	4.40±0.77
Merluccius merluccius	21	11.7-37.0	4.45±0.74	4.40±0.78
Microchirus variegatus[1,2]	3	9.1-10.6	3.06±0.26	3.30±0.45
Micromesistius poutassou	77	9.2-24.0	4.18±0.66	4.00±0.68

(Continued on next page)

Table 1 (continued)

Species	N	Length range	TROPH	TROPH$_{FB}$
Monochirus hispidus [1,2,3]	24	9.2-12.8	3.19±0.32	-
Mullus surmuletus	55	9.1-23.1	3.19±0.37	3.40±0.51
Oblada melanura [1]	56	12.6-22.7	3.11±0.42	3.00±0.12
Pagellus acarne	63	10.5-19.2	3.84±0.55	3.50±0.45
Pagellus bogaraveo	72	9.3-23.1	4.43±0.76	3.50±0.46
Pagellus erythrinus	59	8.4-16.4	3.30±0.39	3.40±0.47
Pagrus pagrus	10	10.2-15.5	3.36±0.34	3.70±0.61
Parablennius gattorugine	4	13.4-17.9	2.11±0.09	2.90±0.29
Phycis blennoides [1]	20	8.1-37.4	3.55±0.59	3.70±0.58
Pomatomus saltatrix [1,2]	6	13.1-18.5	4.50±0.80	4.50±0.55
Raja clavata [1,2]	7	25.6-46.5	3.90±0.67	3.80±0.59
Raja miraletus [1]	3	22.6-33.9	3.82±0.54	3.80±0.74
Raja radula	3	21.8-32.0	3.97±0.69	3.70±0.54
Sardina pilchardus	752	7.6-16.7	3.14±0.29	2.80±0.23
Sardinella aurita	230	8.4-23.9	3.20±0.32	3.00±0.00
Sarpa salpa [1]	25	11.7-19.5	2.00±0.00	2.00±0.00
Sciaena umbra [1]	11	12.2-16.0	3.53±0.54	3.70±0.65
Scomber japonicus [1,2]	371	8.8-26.8	3.99±0.57	3.10±0.43
Scomber scombrus	204	13.3-27.4	4.37±0.54	3.70±0.56
Scorpaena notata[1]	42	8.3-17.8	3.60±0.62	3.50±0.50
Scorpaena porcus	96	8.2-26.4	3.90±0.69	3.90±0.65
Scyliorhinus canicula [1]	34	24.1-45.1	4.41±0.58	3.70±0.55
Serranus cabrilla	34	9.5-23.1	3.90±0.67	3.40±0.47
Serranus hepatus	99	5.7-13.1	3.77±0.63	3.50±0.56
Serranus scriba	81	10.6-23.6	3.94±0.66	3.80±0. 62
Sphyraena sphyraena [1,2]	104	21.6-45.1	4.30±0.46	4.00±0.51
Spicara maena	282	9.0-20.2	3.24±0.34	4.20±0.70
Spicara smaris	118	7.0-18.5	3.49±0.46	3.00±0.04
Spondyliosoma cantharus [1]	82	9.7-14.0	3.41±0.46	3.30±0.43
Symphodus tinca	221	11.1-22.0	2.95±0.25	3.10±0.45
Symphurus nigrescens [1]	10	6.4-11.9	3.35±0.51	3.30±0.43
Torpedo marmorata [1]	118	8.8-37.3	4.39±0.67	4.50±0.80
Trachinus draco [1]	25	15.0-30.5	4.19±0.66	4.20±0.71
Trachurus mediterraneus	627	7.0-25.8	4.01±0.64	3.60±0.58
Trachurus trachurus	133	6.3-3.9	3.58±0.50	3.60±0.58
Trisopterus minutes	167	5.7-24.5	4.13±0.64	3.80±0.53
Uranoscopus scaber	70	8.7-26.9	4.43±0.75	4.40±0.70
Xyrichtys novacula [1]	12	12.3-17.1	3.37±0.51	3.10±0.32

[1] no TROPH estimates available from the Aegean Sea;
[2] no TROPH estimates available from the Mediterranean;
[3] no TROPH estimates available in FishBase (date: 4/7/2005).

TROPH values ranged from 2.00 (±0.00) for *Sarpa salpa*, which feeds exclusively on algae, to 4.54 (±0.60) for *Lophius budegassa*, which preys on fish (Table 1). Differences between TROPHs and TROPH$_{FB}$ (Table 1; Figure 1a) ranged from 0.00 (for *Pomatomus saltatrix*, *Sarpa salpa* and *Scorpaena porcus*) to 0.96 (for *Spicara maena*), with the mean difference being 0.29±0.03 units. In addition, the difference for more than 75% of the species was smaller than 0.40 (Figure 1a). According to the functional trophic groups identified by Stergiou and Karpouzi (2002) for the Mediterranean, approximately one-third of the TROPHs estimated in this study classified the corresponding species in a different functional group than using TROPH$_{FB}$.

Our TROPHs were linearly related to TROPH$_{FB}$ ($R^2 = 0.54$, $p<0.01$; Figure 1b). However, no relationship was found ($p = 0.16$) between the number of stomachs examined and the TROPH-TROPH$_{FB}$ difference for the studied species (Figure 2).

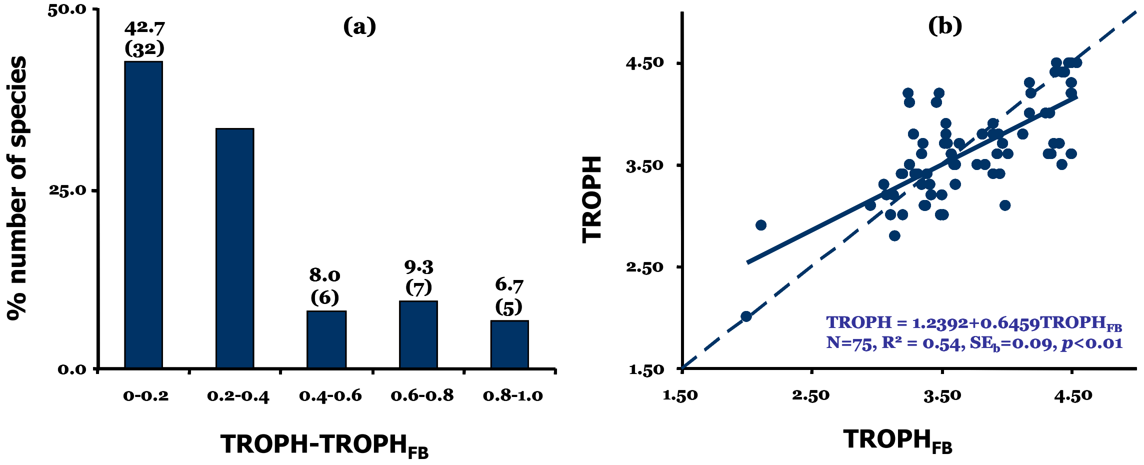

Figure 1 Troph of north Aegean Sea fishes: **(a)** Frequency distribution of the differences between the fractional trophic levels (TROPHs) estimated in this study for 75 fishes compared with TROPH values reported in FishBase (TROPHFB; www.fishbase.org). The percentages and the number of species (in parentheses) are also shown. **(b)** Relationship between TROPH and TROPHFB for 75 species (the dashed line indicates the 1:1 relationship).

DISCUSSION

Our results indicate that differences between area-specific TROPHs from the general ones reported in FishBase are generally small, with a mean difference of only 0.29 units; for more than 40% of the species studied the difference was smaller than 0.2 units (Figure 1a). Yet, in a few cases the difference can be as high as one full trophic level. Still, this indicates that in the absence of regional estimates, those from FishBase are the best estimates available. Observed differences between our TROPHs and TROPHFB could be attributed mainly to: (a) spatio-temporal differences in feeding habits, reflecting variations of prey abundance in different ecosystems (e.g., *Scomber japonicus*, *Scyliorhinus canicula*); (b) different length ranges studied (e.g., *Pagrus pagrus*); and/or (c) different methods of estimating prey contribution (e.g., qualitative: numerical, frequency of occurrence; quantitative: gravimetric, volumetric) (e.g., *Arnoglossus laterna*, *Scomber scombrus*). Although small sample size might also be responsible, the fact that there was no relationship between TROPH-TROPHFB and number of stomachs examined indicates that this is not probable. In addition, the absence of such a relationship (Figure 2) also indicates that small stomach number is not an important impediment for a preliminary TROPH estimation.

The high difference for *Spicara maena* should be attributed to the fact that the species in the Mediterranean, and hence in the Aegean, feeds mainly on copepods (54.2% present study; 6-100%, Stergiou and Karpouzi, 2002). For this species the reported diet in FishBase, from which TROPH is estimated, is composed mainly of zooplankton (Pinnegar and Polunin, 2000) and bony fish (Khoury, 1984).

The relationship between TROPH and TROPHFB for species for which regional TROPH values are available could be used to refine the general TROPHFB values for species for which no regional estimates are available (e.g., rare species). To generate more accurate predictions, the number of species for which regional TROPHs are available should be increased.

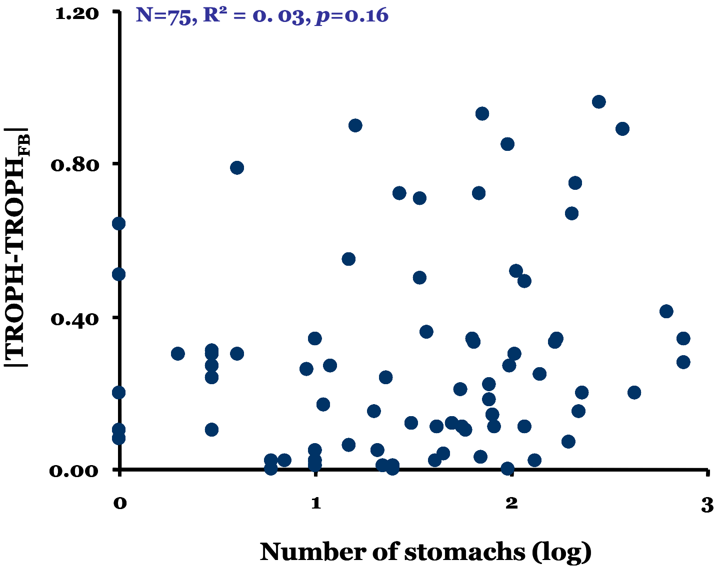

Figure 2 Relationship between the number of stomachs examined and the difference of fractional trophic levels (TROPH) estimated in this study from the FishBase ones (TROPHFB).

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DISTRIBUTION RANGES OF COMMERCIAL FISHES AND INVERTEBRATES[1]

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ABSTRACT

Distribution ranges of commercial fish and invertebrates are required by the *Sea Around Us* Project for mapping of global fisheries catches. However, published ranges exist for only a small fraction of the 1231 taxa, composed of 923 species, 161 genera and 147 higher groups used in the latest version of the mapping process (Version 3.1, representative of catches from 1950 to 2003).

This paper summarizes the methods employed by the *Sea Around Us* Project to reduce potentially global distributions to realistic ranges by identifying key ecological information for each of the 1231 commercial taxa, specifically: (i) presence in FAO area(s); (ii) latitudinal range; (iii) range-limiting polygons; (iv) depth range; and (v) habitat preferences. Furthermore, this paper presents an additional filter that outlines how (ii) and (iv) are used to correct the depth range for the effect of 'equatorial submergence.' Several examples are used to illustrate this process, notably the Florida pompano (*Trachinotus carolinus*) and the Silver hake (*Merluccius bilinearis*).

Throughout this paper, the data sources emphasized include FishBase, other fish and invertebrate databases, and online information where applicable. In addition, simple heuristics are used to replace ecological information that is unavailable or missing.

It should be noted that the *Sea Around Us* Project does not explicitly use temperature and primary production for any of the procedures discussed in this paper. The purpose of this is to allow for subsequent analyses of distribution ranges using these variables.

INTRODUCTION

The *Sea Around Us* Project, hosted at the Fisheries Centre, University of British Columbia, is a research initiative devoted to documenting the effects of fisheries on marine ecosystems worldwide and to propose methods to mitigate these impacts. One of the key elements of this work is mapping of marine fisheries catches onto the ecosystems from which they were extracted. The approach used therein is documented in Watson *et al*. (2004) and its results, regularly updated, are available on the project website (www.seaaroundus.org). This mapping approach depends crucially on the availability of distribution ranges for all taxa (species, genera, etc) reported in marine fisheries catch statistics. Previous mapping of catches relied on distributions constructed from a mixed set of ecological information that resulted in varying degrees of accuracy.

This paper, therefore, documents a major revision of all commercial distribution ranges (totaling 1231 for the time period 1950 – 2003) using a set of rigorously applied filters that markedly improved the accuracy and appearance of the *Sea Around Us* Project maps and other products. These filters include: (i) presence in FAO area(s); (ii) latitudinal range; (iii) range-limiting polygons; (iv) depth range; (v) habitat preferences; and (vi) accounting for the effect of 'equatorial submergence' (Ekman, 1967) Two sample taxa are used to illustrate the results of the filter process, the Florida pompano (*Trachinotus carolinus*) and the Silver hake (*Merluccius bilinearis*), each representing pelagic and demersal species, respectively. Other species are used to illustrate specific aspects of this filter process, and are referred to in the appropriate section.

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[1] Cite as: Close, C., Cheung, W., Hodgson, S., Lam, V., Watson, R., Pauly, D., 2006. Distribution ranges of commercial fishes and invertebrates. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 27-37. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

The procedures presented here avoid use of temperature and primary production to define or refine distribution ranges for any of the taxa. This was done in order to allow for subsequent analyses of distribution ranges to be legitimately performed using these variables. This differs from previous construction methods of distribution maps that used primary production to distinguish area of low *vs.* high abundance within a taxon's distribution range (Watson *et al.*, 2004).

MATERIAL AND METHODS

The 'filters' used here are listed in the order that they are applied; each filter is documented with a figure and a short description of major sources for the information required at that level.

Prior to the 'filter' approach presented below, the identity and nomenclature of each taxon was verified using FishBase (www.fishbase.org) and other sources, and the English common names and scientific names were updated.

Filter 1: FAO Area

The United Nations Food and Agriculture Organization (FAO) has divided the world's oceans into 18 areas for statistical reporting purposes (Figure 1). Information on the occurrence of commercial taxa within these areas is available primarily through: (a) FAO publications and the FAO website (www.fao.org) and (b) FishBase. Figures 2a and 3a illustrate FAO area occurrence of Silver hake and Florida pompano respectively.

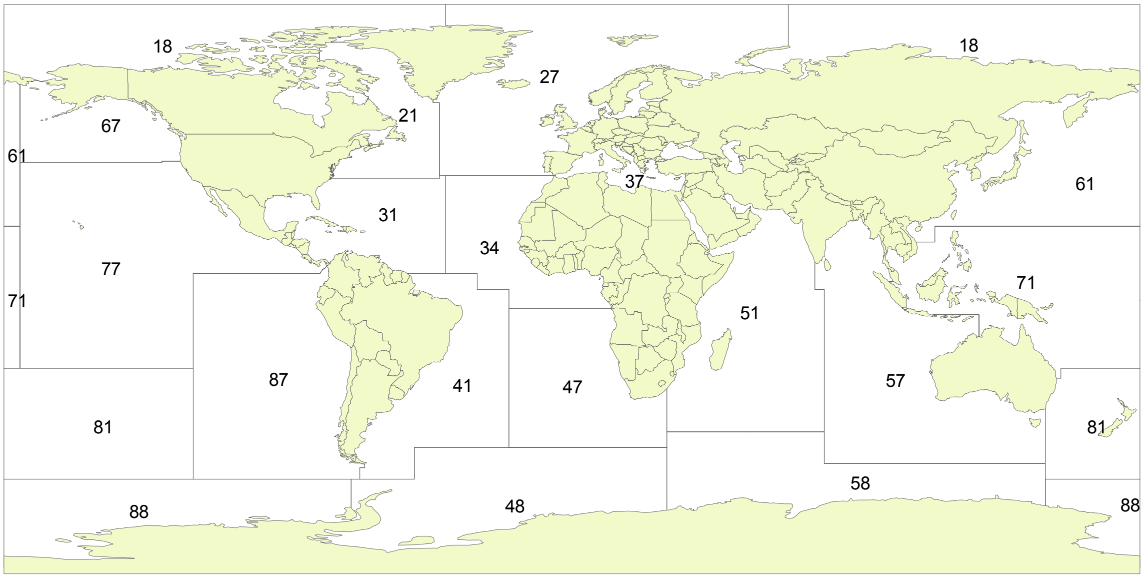
Filter 2: Latitudinal range

The second filter applied in this process is latitudinal ranges. Charles Darwin, after reviewing literature on the distribution of marine organisms, concluded that "latitude is a more important element than longitude" (see Pauly 2004, p. 125, for the sources of this and the quote below).

This does not mean, however, that longitude and other factors do not play a role in determining a taxon's distribution. Still, in the following quote, Darwin illustrates how latitude provides the key to understanding the composition of certain fauna: "Sir J. Richardson says the Fish of the cooler temperate parts of the S. Hemisphere present a much stronger analogy to the fish of the same latitudes in the North, than do the strictly Arctic forms to the Antarctic."

Latitudinal range is defined as a taxon's northernmost and southernmost latitudes of what is considered their 'normal' distribution range and can be found in FishBase for most fishes. For other fishes and invertebrates, latitudes were inferred from the latitudinal range of countries that reported them, and/or from occurrence records in the Ocean Biogeographic Information System website (OBIS; www.iobis.org).

A further refinement of a taxon's latitude range can be defined by its relative occurrence throughout its latitudinal range. From first principles, a taxon can be assumed to be most abundant at the center of its range (McCall, 1990). In cases of distributions confined to either of the two hemispheres, this is approximated by a symmetrical triangular distribution peaking at the mean of the northernmost and southernmost latitudes. For distributions that straddle the equator, it is assumed that a taxon's range can be broken into three parts – the outer two thirds and the inner or middle third. If the equator falls within one of the outer thirds of the latitudinal range, then the abundance is assumed to be the same as above, and thus the symmetrical triangular distribution can be applied. If, however, the equator falls in the middle third of the range, then the abundance distribution is assumed to be flat in the middle third and decreasing to the poles for the remainder of the distributions range. Figures 2b and 3b illustrate the result of the FAO and Latitudinal filter combined. Both the Silver hake and the Florida pompano follow the symmetrical triangular distribution as noted above.



FAO #	FAO Name	FAO #	FAO Name	FAO #	FAO Name
21	Atlantic, North West	48	Antarctic (South Atlantic)	87	Pacific, South East
27	Atlantic, North East	51	Indian, West	18	Arctic Sea
31	Atlantic, West Central	57	Indian, East	61	Pacific, North West
34	Atlantic, East Central	58	Antarctic (South Indian)	71	Pacific, West Central
37	Mediterranean & Black Sea	67	Pacific, North East	81	Pacific, South West
41	Atlantic, South West	77	Pacific, East Central	88	Antarctic (South Pacific)
47	Atlantic, South East				

Figure 1 The 18 areas of the world's oceans that the United Nations Food and Agriculture Organization (FAO) uses for statistical reporting purposes.

Filter 3: Range-limiting polygons

The third filter in the distribution process is the use of range-limiting polygons. Range-limiting polygons help to confine species in areas where they are known to occur and also to prevent occurrence in semi-enclosed seas (e.g., of low salinity) where the taxon does not occur, but which are otherwise located within its FAO areas, latitude and depth ranges.

Polygonal distributions for a vast number of species of commercial fish and invertebrates can be found in various publications, most notably those of FAO (species catalogues, species identification sheets, guides to the commercial species of various countries or regions), and in various online sources.

For taxon without published polygons, the filters described in this paper were used to generate range maps from which polygons were then drawn. In the case of many invertebrates, however, this procedure was reversed, whereby the countries that reported the taxon are used as the taxon's occurrence. In these instances, particular emphasis was given to the FAO statistics, where countries that reported the taxon in their catch were used as occurrence. However this method was not used if the taxon was caught by the country's distant water fleet.

In addition to the above polygonal methods, faunistic works that cover the high-latitude end of continents and/or semi-enclosed coastal seas with depauperate faunas (e.g., Hudson Bay, or the Baltic) were used to avoid, where appropriate, distributions reaching into these extreme habitats. Polygons were then drawn resembling those published for similar species, i.e., at similar distances from coastlines.[2]

All available polygons, whether available from a publication or newly drawn, were digitized used ESRI's ArcGIS and stored in the *Sea Around Us* Project's database, along with the latitude ranges derived from them, which were then used for inferences on equatorial submergence (see below).

Figures 2c and 3c illustrate the result of the combination of the first three filters, i.e., FAO, latitude and range-limiting polygons. These parameters and polygons will be revised periodically, as our knowledge of the species in question increases.

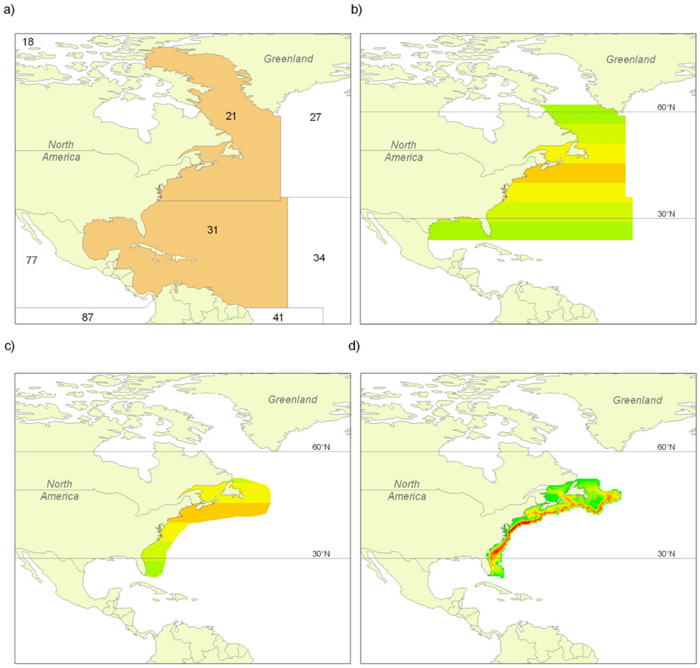


Figure 2 Sequence of filters used for deriving the species distribution range of the Silver hake (*Merluccius bilinearis*): (a) illustrates the Silver hake's presence in FAO areas 21 and 31; (b) illustrates the result of applying the FAO and latitudinal range (24°S to 62°N); (c) shows the result of applying the FAO, latitudinal, and the range-limiting polygon; and (d) illustrates the final result after the application of the four filters.

Habitat parameters for higher taxa

It should be noted that, because the *Sea Around Us* Project mapping process only deals with commercially-caught species, the distribution ranges for higher level taxa (genera, families, etc) were generated using the combination of range polygons from the taxa level below it. Thus, the range polygons for genera were built using the range polygons of the commercial species that fall within them. Similarly, family-level polygons were generated from genus-level polygons, and so on. Latitude ranges, depth ranges and habitat preferences were expanded in the same manner.

While this procedure does not mimic the true distribution of the genera in question, which usually consists of more species than are reported in catch statistics, it is likely that the generic names in the catch statistics refer to the very commercial species that are used to generate the distribution ranges, as these taxa are frequently more abundant.

However, to avoid misunderstandings, the number of species used in generating such generic distribution ranges will be made visible where appropriate, and the maps will be referred to as catch distributions, rather than taxon range distributions.

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[2] Some of these polygons were obtained by making our GIS system (see below) 'buffer' the distribution ranges resulting from Filter 1, 2 and 4. This yielded polygons slightly different in appearance from the others, but which met our needs, nevertheless.

Filter 4: Depth range

Similar to the latitudinal range, the 'depth range', i.e., "[t]he depth (in m) reported for juveniles and adults (but not larvae), from the most shallow to the deepest [water]", is available from FishBase for most fish species, along with the common depth, defined as "[t]he depth range (in m) where juveniles and adults are most often found. This range may be calculated as the range within which approximately 95% of the biomass occurs" (Froese *et al.*, 2000).

When the depth range for a taxon was not available, it was obtained from FAO (species catalogues, species identification sheets, and guides to the commercial species of various countries or regions), or online sources. One of these sources was OBIS where, in some cases, the deepest record was taken to estimate a taxon's maximum depth. Where no information was available, the depth range of a similar species was applied.

A further refinement of a taxon's depth range is its relative abundance within the water column. Based on Alverson *et al.* (1964), Pauly and Chua (1988), Zeller and Pauly (2001) and other sources, it was assumed that the abundance of a taxon within the water column follows a triangular distribution, whereby a taxon's maximum abundance, approximated by a scalene triangle, occurs in the top one-third of its depth range.

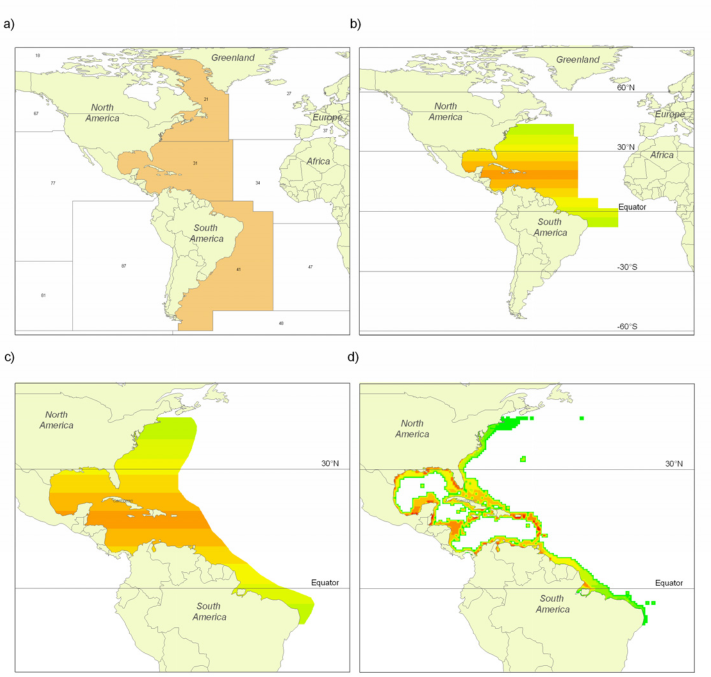

Figure 3 Sequence of filters used for deriving the species distribution range of the Florida pompano (*Trachinotus carolinus*): (a) illustrates the Florida pompano's presence in FAO areas 21, 31, and 41; (b) illustrates the result of applying the FAO and latitudinal range (43°S to -9°N); (c) shows the result of applying the FAO, latitudinal, and the range-limiting polygon; and (d) illustrates the final result after the application of the four filters.

Note that with full implementation of 'equatorial submergence' (described below as 'Filter 6'), the depth of maximum abundance will vary with latitude.

Filter 5: Habitat preference

Habitat preference is an important factor affecting the distribution of marine taxa. Thus the aim of this filter is to enhance the predictions of a taxon's distribution based on its association with different habitats.

In this context, it is assumed that the relative abundance of a taxon in a spatial cell is, in part, determined by the fraction derived from the number of habitats that a taxon associates with in that same cell, and by how far the association effect will extend from that habitat. The latter is assumed to be a function of the taxon's body size (maximum length) and its habitat 'versatility'. Thus a large species that inhabits a wide range of habitats is more likely to occur far from the habitat(s) with which it is associated, than a small species of low habitat versatility (Kramer and Chapman, 1999).

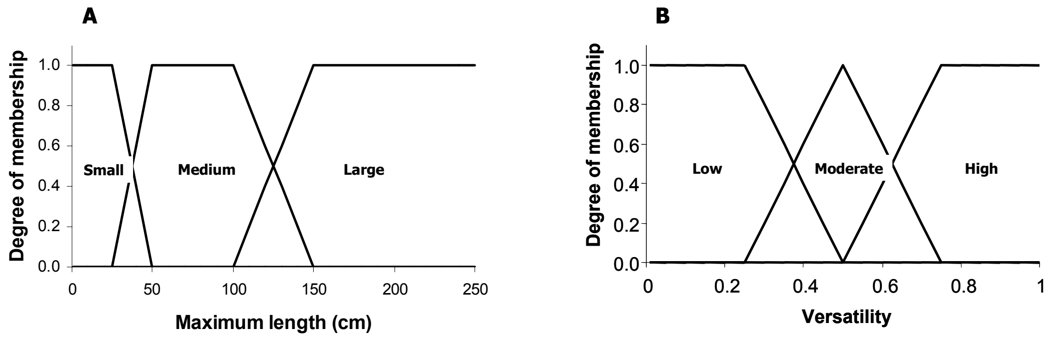

Figure 4 Fuzzy membership functions for the three categories of (**A**) maximum length and (**B**) taxon's versatility. Habitat versatility is defined as ratio of number of habitat types in which a taxon occurs to the total number of defined habitat types.

Table 1 Habitat categories used here, and for which global maps are available in the *Sea Around Us* Project, with some of the terms typically associated with them (in FishBase and other sources).

Categories	Specifications of global map	Terms often used
Estuary	Alder (2003)	Estuaries, mangroves, river mouth
Coral	UNEP World Cons. Monit. Cent. (2005)	Coral reef, coral, atoll, reef slope
Seagrass	Not yet available*	Seagrass bed
Seamounts	Kitchingman and Lai (2004)	Seamounts
Other habitats	–	Muddy/sandy/rocky bottom
Continental shelf	NOAA (2004)	Continental shelf, shelf
Continental slope	NOAA (2004)	Continental slope, upper/lower slope
Abyssal	NOAA (2004)	Away from shelf and slope
Inshore	NOAA (2004)	Shore, inshore, coastal, along shoreline
Offshore	NOAA (2004)	Offshore, oceanic

* The *Sea Around Us* Project is currently developing a global map of seagrass which will be applied when available.

The maximum length and versatility of a taxon are classified into three categories (Figure 4), and it is assumed that a taxon can associate with one or more categories with different degrees of membership (0 to 1). A higher membership value means a higher 'probability' that the taxon is associated with that particularly category. The membership values are defined by a pre-specified membership function for each of the length and versatility categories (Figure 4). For example, the Striped bass (*Morone saxatilis*) has a maximum length of 200 cm (TL). Thus, based on the defined membership functions (Figure 4A, left), Striped bass has a large body size with a membership of 1 (membership ranges from 0 to 1). There are maximum length estimates for all of the 1231 exploited taxa in the *Sea Around Us* Project database, obtained from FishBase and other published literature for invertebrates.

In this paper, versatility refers to the taxon's ability to inhabit different habitat types and is defined as the ratio between the number of associated habitats to the total number of defined habitats (Table 1). For instance, based on descriptions in the SPECIES Table of FishBase, Striped bass is associated with estuaries and 'other habitats'. Given that the total number of defined physical habitats is five (coral reef, estuary, seagrass, seamount, other habitats, while excluding shelf/slope/abyssal and inshore/offshore), the versatility of Striped bass is estimated to be 0.4. Based on the defined membership functions (Figure 4B, right), the versatility of Striped bass is classified as low to medium, with a membership of approximately 0.48 and 0.52 respectively.

Determining habitat association

Based on qualitative descriptions from the published sources, databases such as FishBase and/or through personal communications from experts, each taxon's degree of association with different habitats (Table 1) for all exploited taxa in the database was determined. The taxon's degree of association to each habitat is determined from the qualitative descriptions relating to its density or commonness in the particular habitat (Table 2). As noted above, Striped bass prefers estuaries and also occurs in 'other habitats'. Thus, the Striped bass received a score of 0.75 for estuaries and 0.5 for 'other habitats'.

Maximum distance of habitat effect

Maximum distance of habitat effect (maximum effective distance) refers to the maximum distance from the nearest perimeter of the habitat within which the 'attraction' effect to their associated taxa exists. This is defined as the maximum effective distance by the maximum length and habitat versatility of the taxa using a heuristic rule matrix (Table 3). For example: IF maximum length is large (1) AND versatility is moderate (0.52), THEN maximum occurrence distance from the associated habitat is high (0.52). Here, the number in parentheses represents the degree of membership to the categories. In this example, the degree of membership is the minimum memberships of the two predicates. When the same conclusion is reached from different rules, the final degree of membership equals the taxon's average membership value.

Table 2 Common descriptions on taxa's relative association to habitat and their assigned weighting factor. The weighting factor for 'other habitats' is assumed to be 0.1 when no information on habitat association is available.

Description	Weighting factor
Absent/rare	0.00
Occasionally, sometimes	0.25
Often, regularly, seasonally*	0.50
Usually, abundant in, prefer	0.75
Always, mostly, only occurs	1.00

* If a taxon occurs in a habitat, but no description on the strength of the association is found, we assume a default score of 0.5.

Table 3 Heuristic rules that define the maximum effective distance from the associated habitat. The bolded columns and rules represent the predicates (categories of maximum body size and taxon's versatility), while the italics represent the resulted categories of maximum effective distance.

	Maximum body size		
Versatility	**Small**	**Medium**	**Large**
Low	*Small*	*Small*	*Small*
Moderate	*Moderate*	*Moderate*	*Large*
High	*Moderate*	*High*	*High*

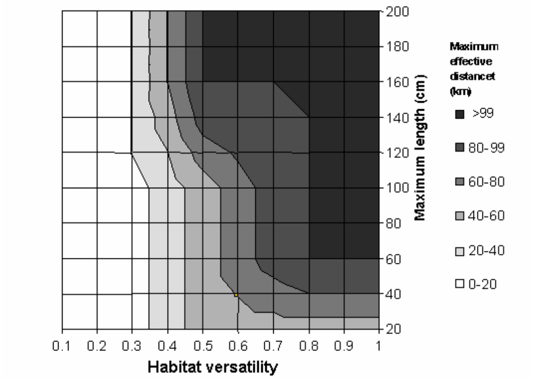

Figure 5 Maximum effective distance for Striped bass (*Morone saxatilis*) estimated from the habitat versatility and maximum length of that species (see text).

The maximum effective distance from the associated habitat can be estimated from the 'centroid value' of each conclusion categories, weighted by a taxon's degree of membership. The centroid values for small, medium and large maximum effective distances were defined as 1 km, 50 km and 100 km, respectively. Thus if, for example, a taxon has membership values of 0.2 and 0.5 to small and medium maximum effective distance, respectively, then the estimated maximum effective distance is: (0.2*1 + 0.5*50 + 0*100)/(0.2 + 0.5 + 0) = 36.1 km (Figure 5). The maximum effective distance is calculated for all exploited taxa in the database.

Estimating relative abundance in a spatial cell

Several assumptions are made to simplify the computations. Firstly, it is assumed that the habitat always occurs in the centre of a cell and is circular in shape. Secondly, the density of a taxon (per unit area) is assumed to be the same across any habitat types. Also, it is assumed that a linear decline in density from the habitat perimeter to the taxon's maximum effective distance occurs for each taxon. Given these assumptions, the total relative abundance of a taxon in a cell equals the sum of abundance on and around its associated habitat:

$$B'_T = (\alpha_j + \alpha_{j+1} \cdot (1 - \alpha_j)) \cdot (1 - A) \qquad \ldots 1)$$

where B'_T is the final abundances, α_j is the density away from the habitat from cell j, and A is the habitat area of the cell. The relative abundance resulting from the different habitat types is the sum of relative abundance, and is weighted by their importance to the taxon.

Although these assumptions on the relationship between maximum length, habitat versatility and maximum distance from the habitat may render predicted distributions at a fine spatial scale uncertain, this routine provides an explicit and consistent way to incorporate habitat considerations into distribution ranges.

Filter 6: Equatorial submergence

The submergence phenomenon was already known to Charles Darwin, who wrote that "we hear from Sir J. Richardson, that Arctic forms of fishes disappear in the seas of Japan & of northern China, are replaced by other assemblages in the warmer latitudes & reappear on the coast of Tasmania, southern New Zealand & the Antarctic islands" (Pauly 2004, p. 198).

Eckman (1967) gives the current definition: "animals which in higher latitudes live in shallow water seek in more southern regions archibenthal or live in shallow water seek in more southern regions archibenthal or purely abyssal waters [...]. This is a very common phenomenon and has been observed by several earlier investigators. We call it submergence after V. Haecker [1906-1908] who, in his studies on pelagic radiolarian, drew attention to it. In most cases, including those which interest us here, submergence increases towards the lower latitudes and therefore may be called equatorial submergence.

Submergence is simply a consequence of the animal's reaction to temperature. Cold-water animals must seek colder, deeper water layers in regions with warm surface water if they are to inhabit such regions at all."

Modifying the distribution ranges to account for equatorial submergence requires accounting for two constraints: (1) data scarcity; and (2) uneven distribution of environmental variables (temperature, light, food, etc.) with depth.

As noted above, there is little information on the depth distribution of most commercial species. As a result, only the following four data points were available for each taxon, namely: the shallow or 'high' end of the depth range (D_{high}), its deep or 'low' end (D_{low}) of the depth range, the poleward limit of the latitudinal range (L_{high}), and its lower latitude limit (L_{low}). These four data points are often available in FishBase for fishes, and can be readily inferred for commercial invertebrates, as noted above. If it is assumed that equatorial submergence is to occur, then it is logical to also assume that D_{high} corresponds to L_{high}, and that D_{low} corresponds to L_{low}.

Data scarcity can be further mitigated by assuming the shape of the function linking latitude and equatorial submergence. In this context, two parabolas are used, one for the upper limits of the depth distribution (P_{high}), and one for the lower limits (P_{low}), with the assumption that both P_{high} and P_{low} are symmetrical about the Equator. In addition, maximum depths are assumed not to change poleward of 60^{o} N and S.

The uneven distribution of the temperature gradient can be mimicked by constraining P_{high} to be less concave than P_{low}. This is achieved by setting D_{gm}, the geometric mean of D_{high} and D_{low}, as the lowest depth that P_{high} can attain. Furthermore, in the case of a distribution spanning both hemispheres, P_{low} will have its lowest point (D_{low}) at the Equator.

Finally, it is assumed that if a computed P_{high} intercepts zero depth at lower latitudes than 60^{o} N and S, then P_{high} is recomputed using the three points D_{oN}=0 at 60^{o} N, D_{oS} at 60^{o} S, and D_{high} and its latitude, which jointly define a parabola.

Figure 6 illustrates three cases of submergence based on different constraints. When this process is applied to a distribution range based on latitudinal range and depth that does not account for submergence, the plots in Figure 7 have the effect of 'shaving off' the shallow end depth values at low latitudes, and similarly, shaving off the deep end depth values at high latitudes. This will have the effect of narrowing the habitat temperature ranges of the corresponding species.

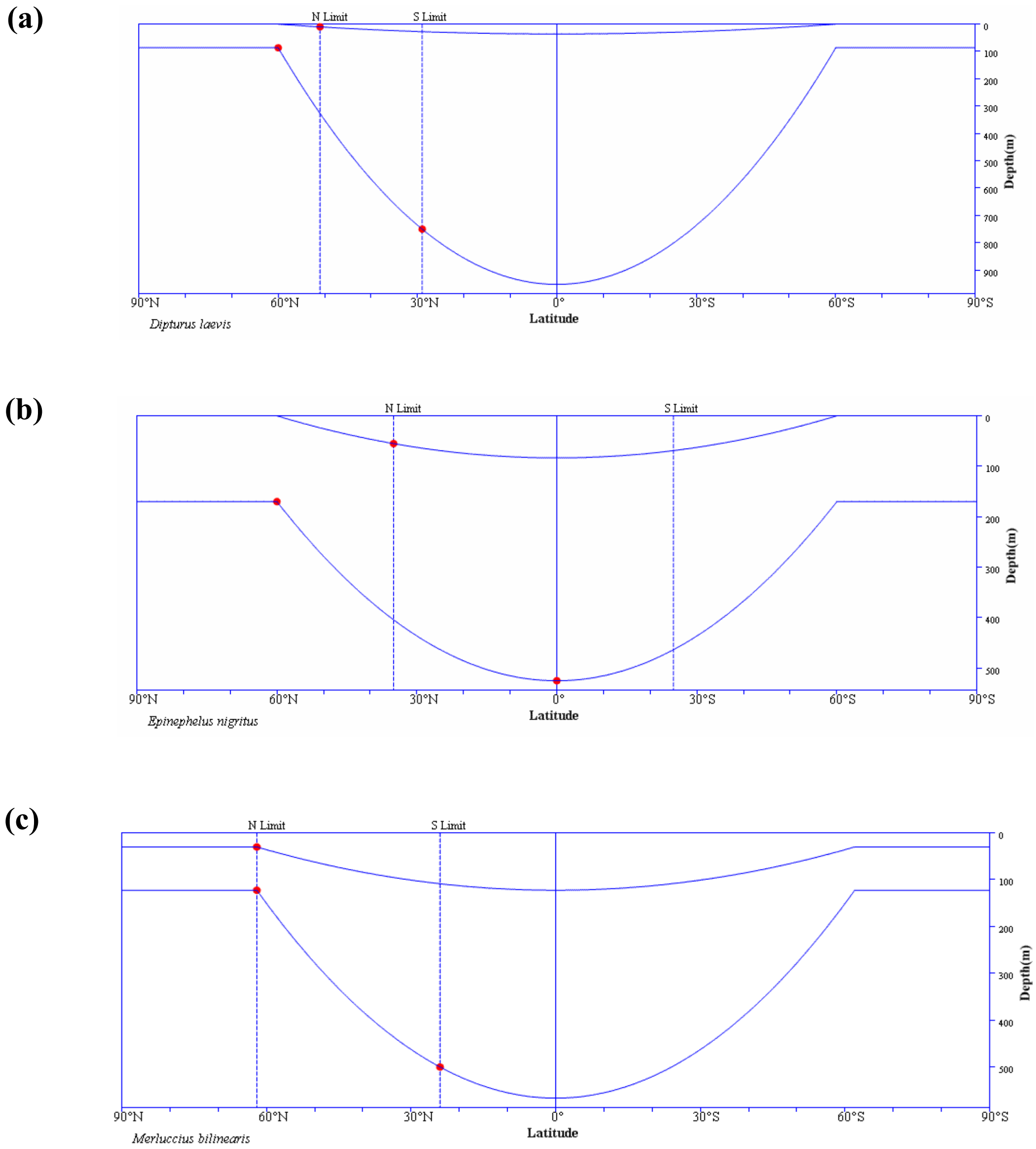

Figure 6 Illustrative representations of 'equatorial submergence', given different depth/latitude data: **(a)** Case 1: Barndoor skate (*Dipturus laevis)* – When the shallow end of the depth range (D_{high}) is at lower latitudes than 60° N and S, the upper limit of the depth distribution (P_{high}) is assumed to intercept zero at 60° N and S; **(b)** Case 2: When distribution range is spanning the North and South hemispheres, as in the case of the Warsaw grouper, *Epinephelus nigritus*, the lowest point of the lower limit (P_{low}) is at the Equator; **(c)** Case 3: Silver hake (*Merluccius bilinearis)*. The poleward limit of the latitudinal range (L_{high}) is at higher latitudes than 60° N and S.

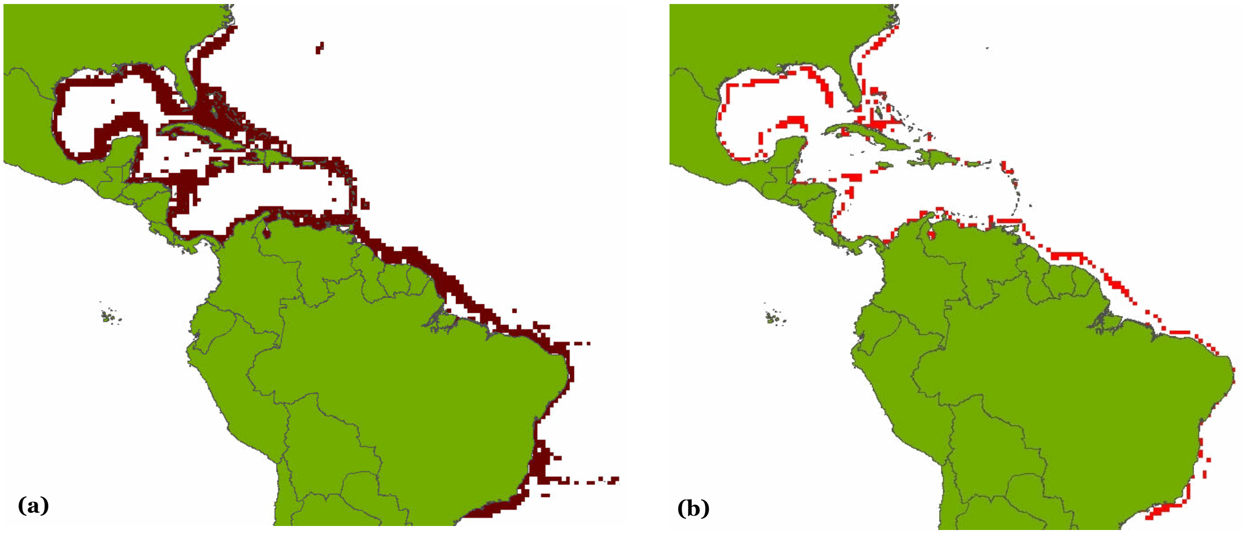

Figure 7 'Equatorial submergence' has the effect of 'shaving off' areas from the distribution range of the Warsaw grouper, *Epinephelus nigritus*: **(a)** Original Distribution; **(b)** Distribution adjusted for 'equatorial submergence'.

Results and Discussion

The results consist of distribution ranges generated through the above methods, incorporated in the *Sea Around Us* database, and available online (see www.seaaroundus.org). They can also be accessed (for fish species) via FishBase (click '*Sea Around Us* distributions' under the 'Internet sources' in the Species Table).

Most importantly, these distribution ranges will serve as basis for all spatial catch allocation done with the *Sea Around Us* Project. Therefore, we would be very thankful for feedback, i.e., suggested comments or corrections, which we will strive to implement as soon as possible.

Acknowledgement

The work documented here is an output of the *Sea Around Us* Project, initiated and funded by the Pew Charitable Trusts, Philadelphia. We thank the Marine Conservation Biology Institute for the support of Sally Hodgson who worked on the distribution ranges of deep sea fish. We thank, finally, Adrian Kitchingman and Ahmed Gelchu for their work on the first generation of *Sea Around Us* distribution ranges.

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A PRELIMINARY LIST OF ENGLISH COMMON NAMES FOR AS YET UNNAMED FISH FAMILIES[1]

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ABSTRACT

Of the 515 families recognized in the last edition (2006) of J. Nelson's *Fishes of the World*, 34 lack English common names, of which 20 have common names ending in 'id', i.e., no true common names. Similarly, of the 530 families recognized in W.N. Eschmeyer's 2006 edition of the *Catalog of Fishes*, 122 lack common names, while 8 have names ending in 'id'. Given the need for such names in FishBase and other applications, common names were coined for these families, mainly by translating and adapting the scientific names.

The common names proposed in this preliminary work do not overlap with already used English common names and meet the criteria of the American Fisheries Society's (AFS) Committee on Names of Fishes. They are presented here in two separate lists, i.e., those without common names and those ending in 'id', from Amarsipidae to Xenisthmidae, with the etymologies and, where required, reasons for the choices taken. We also include a list of common names included in the 2006 edition of J. Nelson's *Fishes of the World*, but not in the 1994 edition.

INTRODUCTION

Common names of organisms serve a number of functions, notably as bridge between specialists and the lay public (Palomares and Pauly, 1998). As such, common names must be widely understandable, and preferably, describe some peculiar and memorable features of the organisms in question.

Multiple common names exist for many organisms, and their standardization and stabilization, e.g., for legal purposes, merely involves a choice from a number of available names (see, e.g., Robins *et al.*, 1991 and Nelson *et al.*, 2004).

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[1] Cite as: Palomares, M.L.D., Bailly, N., Froese, R., Pauly, D., 2006. A preliminary list of English common names for as yet unnamed fish families. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 38-48. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

However, new, small or rare species and higher taxa of plants, animals and other organisms are rarely assigned common names in the scientific literature. In such cases, new common names must be coined. Robins *et al.* (1991) proposed a series of criteria for new common names in fishes, notably:

1. "A single vernacular name shall be accepted for each species or taxonomic unit included and no two species on the list shall have the same proposed name";

2. "Only clearly defined and well-marked taxonomic entities shall be assigned common names (which shall not be intimately tied to the scientific name) and names intended to honor persons are discouraged in that they are without descriptive value";

3. "Names shall not violate the tenets of good taste" and are appropriate if they are colorful, romantic, fanciful, metaphorical, distinctive and original and describe structural attributes, color and color patterns, ecological characteristics and geographic distribution;

4. Native names are welcome for adoption as common names. However, commonly-employed names adopted from traditional English usage are given considerable latitude in taxonomic placement;

5. "The duplication of common names of fishes and other organisms should be avoided if possible, but names in general use need not be rejected on this basis alone"; and

6. Common names ending in 'id', i.e., adaptation of the scientific name to English, e.g., Adrianichthyidae to adrianichthyids, are not considered as true common names.

The most recent edition (2006) of Nelson's *Fishes of the World* recognizes 515 families, 100 of which are broken down to 206 non-nominal subfamilies. Of these families, 34 do not have true common names; and of these, 7 have no common names, 20 have names ending in 'id', 7 are recategorized taxa. Similarly, the most recent edition (2006) of Eschmeyer's *Catalog of Fishes* recognizes 530 families, 72 of which are broken down into 138 non-nominal subfamilies. Of these families, 122 lack common names, while 8 have names ending in 'id'. Finally, the August 2006 version of FishBase (www.fishbase.org) recognizes 530 families, 79 of which are broken down into 170 non-nominal subfamilies. Of these families, 74 lack common names and 2 have names ending in 'id'.

Note that in this contribution, we only venture to propose common names for the currently-recognized fish families. Proposals for common names of currently-recognized subfamilies (and tribes) could be the subject of a future contribution. For instance, when a subfamily is raised to family level, a new common name is required (e.g., Dalatiidae: Etmopteriinae in Nelson, 1994, raised to Etmopteriidae in Nelson, 2006). The taxa of the family-group (super-, sub-, families and tribes) could carry over their common names irrespective of their rank and/or their parent taxon. On the other hand: when a family is split into subfamilies, the nominal subfamily sometimes takes the same common name as the whole family. When families are lumped into one family and are taken down to the subfamily level, the new family takes either the common name of the nominal subfamily or a list of the common names of all or some subfamilies. Note that the second case is not desirable, e.g, Scombridae with the composite common name of mackerels, tunas, bonitos, which is the list of common names of 3 tribes of one of the two subfamilies. It would then be difficult to choose between 'tunas' and 'mackerels' to represent the family. The common names aid in keeping trace of the taxa irrespective of the changes in taxonomic category.

Comparison of the lists mentioned above left us with 25 families for which no true common names are available and for which we suggest English common names. This list was generated with the intention that it should be subjected to the scrutiny of fish experts, and then encoded into FishBase.

MATERIALS AND METHODS

The scientific names of the families were translated using Greek and Latin dictionaries (notably *Perseus*, the online dictionary at www.perseus.tufts.edu/cgi-bin/resolveform), and/or by consulting the source of the family names, which usually also described and frequently gave the etymology of the type genus of the family. The main source here was the *Catalog of Fishes* database by W. Eschmeyer as included in FishBase and also accessible through the Internet (see www.calacademy.org).

The translations were then compared with the common names of species in the family, and with the English common names for species and higher taxa already in FishBase. Non-English common names were translated literally using Babel Fish (babelfish.altavista.com), e.g., Chinese names in Chinese characters. Note that not all of the literal translations made sense. Thus, only the recurring words used in the common names of species within a family were noted. If a translation led to a unique common name, and was acceptable using the criteria of Robins *et al.* (1991), the name was used. Otherwise, a new name was coined, based on marked attributes of the species in the family in question.

Also, the following were applied:

1. If a family is monotypic, the common name of the species is used, in plural, to distinguish it from the species name, and to avoid the need for changing the name should more species be joined to the family;

2. Similar to rule 16 of Robins *et al.* (1991), the common name of the respective order is used in composite names where appropriate;

3. Variations of existing family common names were used only within the same order, e.g., wasp scorpionfishes (new) and scorpionfishes are both in the order Scorpaeniformes;

4. Similar to rule 4 of Robins *et al.* (1991), simple names were preferred, such as 'Lutefishes' instead of 'Guitar characins' for Citharinidae;

5. Misleading family names are not perpetuated as common names, e.g., Bathyclupeidae translates straightforwardly to 'deep sea herrings'; however, species in this family belong to the Order Perciformes and to the Order Clupeiformes. Thus, the name 'deep-sea scalyfins' was coined instead from a prominent character of members of this family; and

6. As far as possible, names should be 'telling' and easy to remember, i.e., reflect obvious characters or relationships.

RESULTS

In the process of comparing the list of families currently included in FishBase with the lists of scientific and common names of Nelson (1994; 2006) and Eschmeyer (2006), we found 9 families which Nelson (2006) has recategorized into subfamilies or lumped with other families (Table 1). We also found that some of the families for which Nelson (2006) used common names ending in 'id' have FishBase English names. The families for which no common names were assigned are included in the lists of suggested common names presented in the following pages.

Table 1. Families recognized in FishBase (www.fishbase.org), Eschmeyer (2006) and Nelson (1994), but reclassified in Nelson (2006). Included also are families recognized in FishBase but with no proper common name in Nelson (2006).

Scientific name	Reclassification (Nelson, 2006)	Order	Common name	Source of common name
Adrianichthyidae	–	Beloniformes	Adrianichthyids; Ricefishes	Nelson (2006); FishBase (18 August 2006 version)
Aracanidae	Subfamily Aracaninae (p. 455)	Tetraodontiformes	–	–
Badidae	Subfamily Badinae (p. 382)	Perciformes	–	–
Bedotiidae	Subfamily Bedotiinae (p. 2710	Atheriniformes	Madagascar rainbowfishes	Nelson (1994); FishBase (18 August 2006 version)
Cottocomephoridae	Lumped with Cottidae (p. 334)	Scorpaeniformes	–	–
Dentatherinidae	Subfamily Dentatherininae (p. 273)	Atheriniformes	Tusked silversides	Nelson (1994); FishBase (18 August 2006 version)
Eschmeyeridae	Lumped with Scorpaenidae (p. 320)	Scorpaeniformes	–	–
Lateolabracidae	Lumped with Moronidae (p. 344)	Perciformes	Asian seaperches	Eschmeyer (2006)
Synaceiidae	Tribe Synaceiini (p. 324)	Scorpaeniformes	Stonefishes	Nelson (1994); FishBase (18 August 2006 version)
Zanclorhynchidae	Lumped with Congiopodidae (p. 327)	Scorpaeniformes	–	–

The following presents the scientific names (**in bold characters**) of the 59 families considered here, the Order in which they belong (in parenthesis), their etymology, the proposed common name (**in bold characters**), and where required, the reason for the choice of the proposed name. Separate lists are presented for: (i) 7 families for which Nelson (2006) has not included an English common name; (ii) 20 families whose common names end in 'id'; (iii) 7 families for which we would like to propose alternative common names to those used in Nelson (2006); and (iv) 25 families for which Nelson (1994) had no common names and the corresponding common names published in Nelson (2006), as well as the likely rationale for the choices that Nelson (2006) made in coining the common names.[2]

(i) Families without English common names

Apistidae (Scorpaeniformes, scorpionfishes and flatheads): Greek, 'apistos', i.e., 'suspicious' (Romero, 2002); Latin 'apis', i.e., 'bee' (Liddel and Scott, 1889). **Wasp scorpionfishes**. English names are available only for *Apistus carinatus* (Bloch and Schneider, 1801) and *Apistops caloundra* (De Vis, 1886) and these include the word 'waspfish'. 'Wasp fishes' is preoccupied by Family Tetrarogidae (Scorpaeniformes). *Apistus carinatus* is distinguished by a brightly-colored and long pectoral fin which, when spread, deters predators (Kuiter and Tonozuka, 2001).

Cottocomephoridae (Scorpaeniformes, scorpionfishes and flatheads): Greek, 'kottos', i.e., a river fish, derived from 'kotta', i.e., 'head'; Greek, 'komê', 'komes', i.e., 'hair', 'mane'; Greek, 'pherein', i.e., 'to carry' (Romero, 2002). **Bighead sculpins**. 'Sculpins' is preoccupied by Family Cottidae (Scorpaeniformes) and 'bullhead' is in the composite common name for Family Heterodontidae (Heterodontiformes). Some available Russian common names include the word 'bighead', while some Chinese common names include the word 'frog head' and 'shell-lake'.

Neosebastidae (Scorpaeniformes, scorpionfishes and flatheads): Greek, 'neos', i.e., 'new'; Greek, 'sebastes', i.e., 'august', 'admirable', epithet given to the Roman emperor Augustus (Romero, 2002). **Gurnard scorpionfishes**. Many of the available common names include the words 'gurnard perch'.

Omosudidae (Aulopiformes, grinners): Greek, 'omo', i.e., 'shoulder'; Latin, 'sudis', 'i.e., esox, fish of the Rhine, cited by Plinius 9.15; also 'stake' (Romero, 2002). **Hammerjaws**. Members of this species are characterized with dentaries each with one huge fang (Nelson, 1994). Sole representative, *Omosudis lowii* Günther, 1887 assigned the FishBase English name of 'hammerjaw'.

Parabembridae (Scorpaeniformes, scorpionfishes and flatheads): Greek, 'para', i.e., 'from the side of', 'from', 'beside', 'alongside'; Greek, 'bembras', 'membras', i.e., a kind of sprat or anchovy (Liddle and Scott, 1889). **Sprat-like flatheads**. Members are characterized with a depressed head and pelvic fins below the pectoral base (Nelson, 1994).

Plectrogenidae (Scorpaeniformes, scorpionfishes and flatheads): Greek, 'plektron', i.e., anything to strike with, e.g., 'stick'; Greek, 'genos', 'gene', i.e, 'race' (Romero, 2002). **Stinger flatheads**. Members of this family have heads usually with spines and ridges, and venom gland in dorsal, anal and pelvic spines (Nelson, 1994). Some Chinese common names include the word 'flathead'.

Setarchidae (Scorpaeniformes, scorpionfishes and flatheads): Latin, 'saeta', i.e., a thick, stiff hair on an animal, 'bristle' (Liddel and Scott, 1889); and 'arch'. **Deep-sea bristly scorpionfishes**. Description of the family is not available in FishBase. Available common names include the words 'scorpionfish', 'rockfish' and 'deep-sea'. Four of the 5 species in FishBase are all found in deep waters; the exception is a pelagic species.

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[2] Proposed English common names for families included in an earlier version of this paper provided to J. Nelson before the publication of the 2006 edition of *Fishes of the World* are marked with asterisks.

(ii) Families with common names ending in 'id'

Acestrorhynchidae (Characiformes, characins): Greek, 'akestra', i.e., 'needle'; Greek, 'rhyngchos', i.e., 'jaw' (Romero, 2002). **Smallscale pike characins**. Members of this family are characterized by very elongate (pike-like) bodies covered with small scales, conical teeth and strong canines are present on the premaxilla (Nelson, 1994). Available Chinese common names include the words 'fat carp', Spanish, Portuguese, German and French names include the word 'dog' and 'tooth'. Note that 'dogtooth' is used in composite common names by some species of cardinalfishes, grenadiers, groupers, herrings, lampfishes, snappers and tunas and proposed as English name for Family Cynodontidae (see below). 'Pike characin' is used by two species of *Oligosarcus* (Characidae, Characiformes) and two species of *Acestrorhynchus*. 'Pike characids' is preoccupied by Family Ctenoluciidae (Characiformes).

Amarsipidae (Perciformes, perch-likes): Greek, 'a', i.e., without; Greek, 'marsipos', i.e., 'bag' (Romero, 2002). **Bagless glassfishes**. These species have translucent bodies without coloration and do not have pharyngeal sacs (Nelson, 1994). Only one common name is available, i.e., for *Amarsipus carlsbergi* Haedrich, 1969, in Chinese, and which translates to 'non-pouch pomfret'. 'Glassfish' is used in composite names of species in the Family Ambassidae (Perciformes). 'Pomfrets' is preoccupied by the Family Bramidae (Perciformes). 'Silver pomfret' is preoccupied by *Pampus argenteus* (Euphrasen, 1788) (Stromateidae, Perciformes).

Aphyonidae (Ophidiiformes, cusk eels): Greek, 'aphyo', 'aphye', i.e., 'sardine', 'anchovy', in the sense of whitish, with the color of sardine (Romero, 2002). **Blind cusk eels**. The only English name available, for *Aphyonus gelatinosus* Günther, 1878, is 'gelatinous blindfish'. In addition, many of the available Chinese names in FishBase include the root word 'blind', which corroborates with the diagnosis that the eyes of members of this Family are rudimentary (Nelson, 1994).

Bathyclupeidae (Perciformes, perch-likes): Greek, 'bathys', i.e., 'deep'; Latin, 'clupea', i.e., 'sardine' (Romero, 2002). **Deep-sea scalyfins**. Members of this family have dorsal and anal fins covered with scales. Some of the available common names include the words 'deep water', 'bottom' and 'herring'. 'Herrings' is preoccupied by Order Clupeiformes. 'Scalyfin' is used in composite common names as adjectives for some members of Pomacentridae, Sciaenidae, Haemulidae and Serranidae (all Perciformes).

Bathysauroididae (Aulopiformes, grinners): Greek, 'bathys', i.e., 'deep'; Greek, 'saurodes', similar to a lizard (Romero, 2002). **Largescale deep-sea lizardfishes**. 'Deep-sea lizardfish' is preoccupied by *Bathysaurus ferox* Günther, 1878 (Synodontidae, Aulopiformes). 'Largescale lizardfish' is used by *Saurida undosquamis* (Richardson, 1848) and *Saurida brasiliensis* Norman, 1935. The available Chinese common name for the sole representative, *Bathysauroides gigas* (Kamohara, 1952), translates to 'Large-scale deep sea nine spines fish'.

Bathysauropsidae (Aulopiformes, grinners): Greek, 'bathys', i.e., 'deep'; Greek, 'sauros', i.e., 'lizard'; Greek, 'opsis', i.e., 'appearance' (Romero, 2002). **Lizard greeneyes**. New family in Nelson (2006; not in August 2006 version of FishBase). Members of this family are mesobenthic and widespread (Nelson, 2006). The available Chinese common name for one of the three species in this family, *Bathysauropsis gracilis* (Günther, 1878) translates to 'filament body deep sea nine spines fish', while the other available English names are 'black lizardfish' (retained as the FishBase name) and 'deep-water greeneye'. 'Greeneyes' is preoccupied by Family Chlorophthalmidae (Aulopiformes), which are also found in deep waters.

Citharinidae (Characiformes, characins): Greek, 'kitharia', i.e., 'cittern', a Renaissance stringed instrument like a guitar with a flat pear-shaped body, also 'guitar' and 'lute' (Merriam-Webster online dictionary). **Lutefishes**. 'Guitarfishes' is preoccupied by Family Rhinobatidae (Rajiformes).

Cynodontidae (Characiformes, characins): Greek, 'kyon', 'kyonos', i.e., 'dog'; Greek, 'odous', i.e., 'teeth' (Romero, 2002). **Dogtooth characins**. Members of this family are carnivorous with dentary canines to stab prey (Nelson, 1994). Many of the available Brazilian common names include the word 'dog' while many of the Chinese common names include 'carp'. 'Daggertooths' is preoccupied by Anotopteridae (Aulopiformes), 'sabertooth fishes' by Evermannellidae (Aulopiformes), 'fangtooths' by Anoplogasteridae (Beryciformes), and 'sawtooths' by Serrivomeridae (Anguilliformes).

Diplophidae (Stomiiformes, lightfishes and dragonfishes): Greek, 'diploos', i.e., 'double'; Greek, 'phos', i.e., 'light' (Romero, 2002). **Porthole lightfishes**. New family in Nelson (2006; not in August 2006 version of FishBase). The available Chinese common names include the words 'double', 'light', and 'lamp'. The available English name includes 'porthole', which is used in composite names by: *Gonostoma elongatum* Günther, 1878 and *Cyclothone microdon* (Günther, 1878) (Gonostomatidae, Stomiiformes); *Dianema longibarbis* Cope, 1872 (Callichthyidae, Siluriformes) and *Hemisorubim platyrhynchos* (Valenciennes, 1840) (Pimelodidae, Siluriformes); and *Poeciliopsis gracilis* (Heckel, 1848) (Poeciliidae, Cyprinodontiformes).

Erethistidae (Siluriformes, catfishes): Greek, 'erethismos', 'erethizein', i.e., 'irritate' (Romero, 2002). **South Asian river catfishes**. Members of this family have four pairs of barbels and the adipose fin is usually large (Nelson, 1994), found in rivers, streams and moving freshwaters of southern Asia (Nelson, 2006). Note that 'river catfish' is used in composite names of other siluriform catfishes, e.g., *Clupisoma garua* (Hamilton, 1822) (Schilbeidae), *Corydoras metae* Eigenmann, 1914 (Callichthyidae), *Hemibagrus nemurus* (Valenciennes, 1840) (Bagridae), *Pangasius pangasius* (Hamilton, 1822) (Pangasidae) and *Porochilus meraukensis* (Weber, 1913) (Plotosidae).

Hemiodontidae (Characiformes, characins): Greek, 'hemi', i.e., 'half'; Greek, 'odous', i.e., 'tooth', 'teeth' (Romero, 2002). **Halftooths**. Members of this family have small and toothless lower jaws (Nelson, 1994). Available Chinese common names include the words 'half tooth fat carp'.

Heptapteridae (Siluriformes, catfishes): Greek, 'hepta', i.e., 'seven'; Greek, 'pteron', i.e., 'fin' (Romero, 2002). **Three-barbeled catfishes**. A speciose family whose members are not externally differentiable with members of the Family Pimelodidae (long-whiskered catfishes; see Nelson, 2006). Members of this family usually have naked skin, three pairs of barbels, large adipose fin and a deeply forked caudal fin (Nelson, 2006). Available common names do not have any root words in common.

Hispidoberycidae (Stephanoberyciformes, pricklefishes, bigscales and gibberfishes): Latin, 'hispidus', i.e., 'rough', 'shaggy', 'hairy', 'bristly' (Whitaker, 1998-2000). **Spiny-scale pricklefishes**. This family is monospecific. *Hispidoberyx ambagiosus* Kotlyar, 1981 is a deep sea fish with spinulose scales, operculum with a long, stout spine, the dorsal with 4-5 spines and the anal fin with 3 spines (Kotlyar, 2004). 'Pricklefishes' is preoccupied by Family Stephanoberycidae (Beryciformes), 'spinyfins' by Family Diretmidae (Beryciformes).

Lophichthyidae (Lophiidormes, anglerfishes): Greek, 'lophos', i.e., 'crest'; Greek, 'ichthys', i.e., 'fish' (Romero, 2002). **Crested frogfishes**. Members of this family have no humped nape, the first dorsal spines are modified to an illicium (i.e., lure) and have palatine teeth (Nelson, 1994). The only representative is *Lophichthys boschmai* Boeseman, 1964 (FishBase common name: Boschma's frogfish). The available Chinese common name includes the word 'wave', i.e., 'crest'.

Myrocongridae (Anguiliformes, eels and morays): Greek, 'myros', i.e., male of moray eel; Latin, 'conger', i.e., 'conger' (Romero, 2002). **Atlantic red eels**. This family is monogeneric. 'Moray' is preoccupied by Family Muraenidae (Order Anguiliformes) and 'conger' is preoccupied by Family Congridae (Order Anguiliformes).

Normanichthyidae (Scorpaeniformes, scorpionfishes and flatheads): Named after John Roxburgh Norman, British ichthyologist 1898-1944 (Romero, 2002). **Barehead scorpionfishes**. Members of this family have armorless heads, one spine on pelvic fin and lack ribs (Nelson, 1994).

Ostracoberycidae (Perciformes, perch-likes): Greek, 'ostrakon', i.e., an earthern vessel, tile, also the hard shell of testaceous animals, as snails, muscles, tortoises (Liddle and Scott, 1889). **Shellskin alfonsinos**. Members of this family have a prominent spine extending backward from the lower limb of preopercle (Nelson, 1994). 'Alfonsinos' is preoccupied by Family Berycidae (Beryciformes, sawbellies).

Parodontidae (Characiformes, characins): Greek, 'para', i.e., 'the side of'; Greek, 'odous', i.e., 'teeth' (Romero, 2002). **Scrapetooths**. Members of this family have ventral mouths with teeth modified for scraping algae off rocks, highly mobile and enlarged premaxillaries, no adipose eyelid and with expanded and flattened pectoral fins (Nelson, 2006). Available Chinese common names include the words 'cheek', 'tooth', and 'fat carp'. Some of the available Spanish common names include the word 'mouse'. Some of the Brazilian Portuguese common names include the word 'pen knife'.

Tetrabrachiidae (Lophiiformes, anglerfishes): Greek, 'tetra', i.e., 'four'; Greek, 'brachion', i.e., 'arm' (Romero, 2002). **Four-armed frogfishes**. FishBase English name of sole species in FishBase, *Tetrabrachium ocellatum* Günther, 1880, is 'four-armed frogfish'.

Xenisthmidae (Perciformes, perch-likes): Greek, 'xenos', i.e., 'strange', 'rare'; Greek, 'isthmia', i.e., 'neck', 'throat', 'narrow passage' (Romero, 2002). **Collared wrigglers**. Available common names include the word 'wriggler'.

(iii) Alternative common names for families with common names in Nelson (2006)

Centracanthidae (Perciformes, perch-likes): Greek, 'kentron', i.e., 'thorn', 'sting'; Greek, 'akantha', i.e., 'thorn' (Romero, 2002). **Picarels**. Most of the species in this family have composite English names including the word 'picarel'. Nelson (2006) uses 'picarel porgies'. The name 'picarels' is not preoccupied and is simpler than 'picarel porgies'.

Champsodontidae (Perciformes, perch-likes): Greek from Egyptian, 'champsai', i.e., 'crocodile'; Greek, 'odous', i.e., 'teeth' (Romero, 2002). **Crocodile toothfishes**. The only available English common name is 'gaper' for *Champsodon capensis* Regan, 1908. Available Chinese common names include the word 'toothfish'. 'Crocodilefish' is preoccupied by *Cymbacephalus beauforti* (Knapp, 1973) and 'toothfish' is preoccupied by several species of the Family Nototheniidae (Perciformes). 'Gaper' which is used in Nelson (2006) is also preoccupied by *Serranus cabrilla* (Linnaeus, 1758) (Serranidae, Perciformes) and used in the composite name of *Chaunax stigmaeus* Fowler, 1946 (Chaunacidae, Lophiiformes). However, 'crocodile toothfish' is not preoccupied by any species.

Chaudhuriidae (Synbranchiformes, spiny eels): From 'chaudhuria', i.e., a Burmese local name for a fish (Romero, 2002), named after B.L. Chaudhuri, an Indian Ichthyologist. **Spineless eels**. Members of this family have no dorsal or anal fin spines. Several of the available English composite common names include the words 'spineless eel'. Nelson (2006) used 'earthworm eels', 'earthworm' being used in the composite common name for *Yirrkala lumbricoides* (Bleeker, 1853) (Ophichthidae, Anguiliformes). We believe that 'spineless eel' represents the most striking morphological character of this group without having to refer to another animal, e.g., 'earthworm'.

Chiasmodontidae (Perciformes, perch-likes): Greek, 'chiasma', i.e., 'cross', 'chiasmos', i.e., 'diagonal'; Greek, 'odous', i.e., 'tooth', 'teeth' (Romero, 2002). **Snaketooth fishes**. Some of the available English common names include the word 'swallower', the name used in Nelson (2006) but which is preoccupied by Family Saccopharyngidae (Saccopharyngiformes). Some of the available Chinese common names include the words 'snake-toothed' and occasionally 'fork-toothed' and 'long-toothed'.

Curimatidae (Characiformes, characins): From 'Curimatá', a locality in Piauí State, Brazil, and used in Creole French as a local name for a fish in French Guyana (Romero, 2002). **Toothless characins**. Available Chinese common names include the words 'toothless fat carp' while Spanish common names include 'smallmouth'. A distinct characteristic of the members of this family is the loss or the reduction of dentition on the fifth upper pharyngeal tooth plate (Nelson, 1994). The word 'characin' probably came from Latin, 'characias', 'characiae', i.e., 'reed' for making 'stakes', a kind of 'spurge' (Whitaker, 1998-2000; Pliny the Elder, 1906), derived from Greek, 'charax', i.e., 'a pointed stake', 'a vine-prop or pole' (Liddle and Scott, 1889). Romero (2002) provides the following: Greek, 'charax', i.e., a marine fish; Latin, 'forma', i.e., 'shape'. Members of this family are usually found in riverine and lacustrine habitats and feed on organic matter, microdetritus, microvegetation, and filamentous algae common in those habitats (Nelson, 1994). 'Reedfish' is preoccupied by *Erpetoichthys calabaricus* Smith, 1865 (Polypteridae, Polypteriformes); 'smallmouth' is preoccupied by *Haemulon chrysargyreum* Günther, 1859 (Haemulidae, Perciformes). 'Carps' is preoccupied by Order Cypriniformes. Nelson (2006) used 'toothless characiforms'; the word 'characiforms' deviates from 'characins'.

Ereuniidae (Scorpaeniformes, scorpionfishes and flatheads): Greek, 'ereyn', 'aireoo', i.e., 'to catch'; also Greek, 'ereyna', 'ereynes', i.e., 'inquiry', 'search' (Romero, 2002). **Deepwater bullhead sculpins**. The available Chinese names include the word 'bullhead', which is appropriate as members of this family have large heads compared to their narrow and long tails (Nelson, 1994). 'Bullhead' is used in the composite name for 'bullhead sharks' (Heterodontidae, Heterodontiformes). Nelson (2006) used 'deepwater sculpins', which is used by *Myoxocephalus thompsonii* (Girard, 1851) (Cottidae, Scorpaeniformes); note that the word 'sculpin' is also preoccupied by Family Cottidae (Scorpaeniformes).

Monognathidae (Saccopharyngiformes, swallowers and gulpers): Greek, 'monos', i.e., 'only'; Greek, 'gnathos', i.e., 'jaw' (Romero, 2002). **Onejaws**. Members of this family lack maxilla and premaxilla (Nelson, 1994). 'Gulpers' is preoccupied by Family Eurypharyngidae (Saccopharyngiformes). Nelson (2006) used 'onejaw gulpers'.

Valenciidae (Cyprinodontiformes, rivulines, killifishes and live bearers): Available common names include the words 'Valencia' and 'Spain', indicating that the family name might have been derived from the name of the city. **Toothcarps**. The two species represented have common names which include 'toothcarp'. 'Toothcarp' also used in composite names for some species of Family Cyprinodontidae (pupfishes) and Poeciliidae (poeciliids) both belonging to the Order Cyprinodontiformes. Nelson (2006) used 'Valencia toothcarps'.

(iv) Families without common names in Nelson (1994) and which have new names in Nelson (2006)[3]

Banjosidae (Perciformes, perch-likes): English, 'banjo', i.e., musical instrument with a drumlike body, a fretted neck, and usually four or five strings (Merriam-Webster Online Dictionary; www.m-w.com/cgi-bin/dictionary). **Banjofishes*** from 'Banjofish' for *Banjos banjos* (Richardson, 1846).

Bathylutichthyidae (Scorpaeniformes, scorpionfishes and flatheads): Greek, 'bathys', i.e., 'deep'; Greek, 'louso', 'louteon', i.e., 'bath', 'to inmerse'; Greek, 'ichthys', i.e., 'fish' (Romero, 2002). **Antarctic sculpins**. Known only from South Georgia Island, Antarctica.

Centrogeniidae (Perciformes, perch-likes): Greek, 'kentron', i.e., 'thorn', 'sting'; Greek, 'genos', i.e., 'race' (Romero, 2002). **False scorpionfishes***. Taken from the English name of *Centrogenys vaigiensis* (Quoy and Gaimard, 1824), sole representative of this family.

Centrophoridae (Squaliformes, bramble, sleeper and dogfish sharks): Greek, 'kentron', i.e., 'thorn', 'sting'; Greek, 'pherein', i.e., 'to carry' (Romero, 2002); Latin, 'phor', 'phoreo', with several meanings including 'putting food into one's mouth'. **Gulper sharks***. Many of the available English names include the words 'dogfish' and 'gulper'. However, 'dogfishes' (Squalidae, Squaliformes) and 'gulpers' (Eurypharyngidae, Saccopharyngiformes) are both preoccupied.

Colocongridae (Anguilliformes, eels and morays): Greek, 'kolos', i.e., 'tail'; Latin, 'conger', i.e., 'sea eel' (Romero, 2002). **Short-tail eels***. 'Short tail conger' is preoccupied by *Paraconger similis* (Wade, 1946) (Congridae, Anguiliformes). The available Chinese and Czech common names include the words 'short tail conger eel' and 'serpentine'.

Draconettidae (Perciformes, perch-likes): Greek, 'drakos', 'drakaina', i.e., 'dragon'; Greek, 'nessa', 'netta', i.e., 'duck' (Romero, 2002). **Slope dragonets***. Members of this family have relatively big eyes compared to their small heads, two nostrils on each side of the head, with relatively broad gill openings and one straight strong spine on both opercle and subopercle; they are uncommon or relatively rare and are found on the edge of the continental shelf or on seamounts (Nelson, 1994). The available Chinese names include the words 'thick thorn lizard'. 'Lizardfishes' is preoccupied by the Family Synodontidae (Aulopiformes), 'dragonets' by the Family Callionymidae (Perciformes).

Gymnarchidae (Osteoglossiformes, bony tongues): Greek, 'gymnos', i.e., 'naked'; Greek, 'archo', i.e., the extreme of the anus (Romero, 2002). **Abas***. This family is monospecific and the fish has a toothless tongue. The proposed English common name is the chosen FishBase common name for the sole representative, *Gymnarchus niloticus* Cuvier, 1829 and is based on the Ijo language (Nigerian) common name.

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[3] See footnote (2) on p. 41.

Hepsetidae (Characiformes, characins): Greek, 'epsetas', i.e., 'boiled'; also Greek, 'oí epsetoi', i.e., 'certain fishes'; may be related to 'psetta', i.e., 'grouper' (Romero, 2002). **African pikes**. This family is monospecific and is found widespread in Africa from Senegal to Angola including Niger, Volta, Chad, Ogowe, Democratic Republic of the Congo and upper Zambezi Rivers, as well as in the Cunene, Okavango, and Kafue systems; also widespread in central and West Africa but absent in the Nile River, Zambian Congo and the Great Lakes (Skelton, 1993).

Heterenchelyidae (Anguilliformes, eels and morays): Greek, 'heteros', i.e., 'other'; Greek, 'enchelys', i.e., 'eel' (Romero, 2002). **Mud eels***. Members of this family have large mouths and are scaleless (Nelson, 1994). Available Chinese common names include the words 'short', 'cheek', and 'python'. Nelson (2006) took the AFS official common name and accepted as the FishBase common name for *Pythonichthys asodes* Rosenblatt & Rubinoff, 1972.

Hypopomidae (Gymnotiformes, knifefishes): Greek, 'hypo', i.e., 'under'; Greek, 'pomas', 'pomatos', i.e., 'cover' (Romero, 2002). **Bluntnose knifefishes**. Members of this family have no teeth on both jaws, snout moderate to short length, small eyes. They resemble eels because they have no caudal or dorsal fin but have the anal-fin origin ventral or posterior to pectoral fin-base. They also possess an electric organ which discharges discrete pulses (Albert, 2003). Nelson (2006) took the English common name used for *Brachyhypopomus brevirostris* (Steindachner, 1868).

Indostomidae (Gasterosteiformes, sticklebacks and seamoths): Latin, 'induere', i.e., 'to cover'; Greek, 'stoma', i.e., 'mouth' (Romero, 2002). **Armored sticklebacks**. Members of this family have slender bodies with a covering of bony scutes; operculum with spines and also has a series of 5 isolated dorsal spines (Nelson, 1994). 'Pricklebacks' is preoccupied by Family Stichaeidae (Perciformes) and 'sticklebacks' by Family Gasterosteidae (Gasterosteiformes).

Ipnopidae (Aulopiformes, grinners): Greek, 'ipnos', i.e., 'oven', 'kiln' (Romero, 2002). **Deep-sea tripod fishes**. Members of this family have eyes which can be minute or large or plate-like and without lenses; the pectoral, pelvic and caudal rays can be elongated on which they stand, and the jaw extends past the orbit of the eye (Nelson, 1994). Most of the common names available for this family include the words 'deep-sea', 'tripodfish', 'spiderfish' and 'deep-pool fish', while some include the words 'stove eye', 'grid eye', 'net eye'. 'Tripodfish' used in composite common names in the Family Triacanthidae (Tetraodontiformes).

Lebiasinidae (Characiformes, characins): Greek, 'lebias', i.e., a kind of fish (Romero, 2002). **Pencilfishes***. Members of this family have elongate, cylindrically-shaped bodies with fairly large scales, lacking a frontal/parietal fontanel and the cheek well covered by orbital and opercular bones (Nelson 1994). Many of the available common names include 'pencilfish', 'fat carp' and 'tetra'. 'Pencil' used in composite names by the Family Trichomycteridae (Siluriformes), 'carp' is preoccupied by Order Cypriniformes and 'tetra' is used in composite names for fishes of the Family Alestiidae (Characiformes).

Microstomatidae (Osmeriformes, smelts): Greek, 'mikros', i.e., 'small'; Greek, 'stoma', i.e., 'mouth' (Romero, 2002). **Pencil smelts**. Members of this family have large eyes (more than twice the length of snout), small mouths, have spineless fins (Nelson, 1994). Available common names include the words 'south', 'argentine', and 'pencilsmelt'. 'Argentine' is used in the composite name for the Family Argentinidae (Salmoniformes), 'pencil' is used in composite names by the Family Trichomycteridae (Siluriformes) and 'smelt' is preoccupied by Family Osmeridae (Salmoniformes).

Neoscopelidae (Myctophiformes, lanterfishes): Greek, 'neos', i.e., 'new'; Greek, 'skopelos', i.e., the name of a fish cited by Cuvier, 1817; Greek, 'skopelos', i.e., 'reef', 'rock' (Romero, 2002). **Blackchins**. Some members of this family have photophores (Nelson, 1994). Many of the available common names include the word 'lanterfish', 'glowfish', 'lampfish'. 'Lanternfishes' is preoccupied by Family Myctophidae (Myctophiformes) and 'lampfish' is used in composite names of the Family Myctophidae. Nelson (2006) adapted the FAO English and accepted FishBase common name for *Scopelengys tristis* Alcock, 1890.

Odontobutidae (Perciformes, perch-likes): Greek, 'odont', i.e., tooth; Latin, 'buttos' from 'butinê', i.e., a flask covered with plaited osier (Liddell and Scott, 1889). **Freshwater sleepers**. Members of this family may be distinguished from other goboid families by the large scapula which excludes the proximal radial from contact with the cleithrum, has six branchiostegal rays and lack of lateral line (Nelson, 1994). Some of the available names include the word ‘sleeper’ and ‘pond’. ‘Sleeper’ is preoccupied by Family Eleotridae (Perciformes).

Pseudotrichonotidae (Aulopiformes, grinners): Greek, ‘pseudes’, i.e., ‘false’, ‘falsely’; Greek, ‘thirx’, i.e., ‘hair’; Greek, ‘noton’, i.e., ‘back’ (Romero, 2002). **Sand diving lizardfishes**. ‘Sanddivers’ is the name used for Family Trichonotidae (Perciformes).

Psilorhynchidae (Cypriniformes, carps): Greek, ‘psilos’, i.e., ‘bald’, ‘hairless’; Greek, ‘rhynchos’, i.e., ‘jaw’ (Romero, 2002). **Mountain carps**. Members of this family have small inferior mouths, fleshy lips and no barbells and are usually found in mountain streams.

Radiicephalidae (Lampriformes, velifers, tube-eyes and ribbonfishes): Latin, ‘radius’, i.e., ‘radius’; Greek, ‘kephale’, i.e., ‘head’ (Romero, 2002). **Tapertails***. Members of this family have elongated scaleless bodies, compressed and attenuated posteriorly to a thin caudal filament. The sole representative of this family is *Radiicephalus elongatus* Osório, 1917, whose FishBase English common name is ‘tapertail’. This is used in composite English names for some members of Family Trachipteridae (Lampriformes) and Family Engraulidae (Clupeiformes).

Samaridae (Pleuronectiformes, flatfishes): Latin, ‘samara’, i.e., seed of the elm (Romero, 2002). Could also be Greek, ‘sêma’, i.e., ‘sign’, ‘mark’, ‘token’ of the star on a horse’s head (Liddel and Scott, 1889). **Crested flounders**. Most available English common names include the words ‘righteye flounder’. ‘Right-eye flounder’ is used in composite name for Family Pleuronectidae (Pleuronectiformes). Nelson (2006) adapted a modified form of the scientific name.

Schindleriidae (Perciformes, perch-likes): Named after Dr. D.W. Schindler, University of Alberta, Canda (Eschmeyer, 2006). **Infantfishes**. Members of this family are small and neotenic, with transparent bodies and many undeveloped cartilage and bones. Some of the available common names include the words ‘infant’ and ‘precocious’.

Scombrolabracidae (Perciformes, perch-likes): Latin, ‘scomber’, i.e., ‘mackerel’; Latin, ‘labrus’, i.e., ‘lip’ (Romero, 2002). **Longfin escolars**. Members of this family are deep water fishes which have serrated operculum and preoperculum and a protusible maxilla (Nelson, 1994). The sole representative, *Scombrolabrax heterolepis* Roule, 1921 has the FishBase common name ‘longfin escolar’. ‘Escolar’ is used in composite names in the Family Gempylidae (Perciformes).

Sternoptychidae (Stomiiformes, lightfishes and dragonfishes): Greek, ‘sternon’, i.e., ‘chest’, ‘breast’; Greek, ‘ptyx’, ‘ptychose’, i.e., ‘fold’, ‘crease’ (Romero, 2002). **Marine hatchetfishes**. Members of this family have branchiostegal photophores and pseudobranch (Nelson, 1994). Available common names include the words ‘hatchetfish’, ‘hatchet belly’, ‘axe’, ‘pearlside’, and ‘bristle mouth’. ‘Hatchetfish’ is also used by the Family Gasteropelecidae, i.e., freshwater hatchetfishes.

Symphysanodontidae (Stomiiformes, lightfishes and dragonfishes): Greek, ‘symphysis’, i.e., ‘grown together’; Greek, ‘an’, i.e., ‘without’; Greek, ‘odous’, i.e., ‘teeth’ (Romero, 2002). **Slopefishes***. Available common names include the words ‘slope’, ‘shelf’, ‘covered tooth’.

DISCUSSION

The names presented here are, as mentioned above, suggestions that can and will be discussed in the ichthyological community, then will be entered into FishBase. Following current practice, they also serve as basis for coining new common names for species that lack such names, e.g., by adding modifiers to the family common names. This may contribute to the fishes being the first very speciose group of organisms with all species having common names.

ACKNOWLEDGEMENTS

The authors wish to acknowledge Dr Konstantinos Stergiou for checking the Greek translations and Mr William Cheung for checking the translation and interpretation of Chinese common names.

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GROWTH, REPRODUCTION AND FOOD OF THE MUDSKIPPER, *PERIOPHTHALMUS BARBARUS* ON MUDFLATS OF FREETOWN, SIERRA LEONE[1]

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ABSTRACT

This study, based on 364 specimens of mudskipper, *Periophthalmus barbarus* (Linnaeus, 1766) (Family Gobiidae) sampled from July 1992 to April 1993 on a small mudflat near Freetown, deals with the morphometrics, growth, reproduction and feeding habits of a species that is often studied in terms of its interesting amphibious behavior, but which, in Sierra Leone, represents a food resource for coastal dwellers. Results include length-weight relationships for females and males, a seasonally oscillating growth curve (TL_∞ = 17 cm, K = 0.89 ± 0.30 year^{-1}, C = 0.75 and WP = 0.95), with a strong end-of-year reduction of growth related to the cold 'Harmattan' wind, and a spawning peak in May-June, at the onset of the rainy season. First maturity occurs at about 8 cm; the food consists of small crustaceans, polychaets, insects, mollusks and detritus.

INTRODUCTION

The Atlantic mudskipper, *Periophthalmus barbarus* (Linnaeus, 1766) (Family Gobiidae, SubFamily Oxudercinae, Order Perciformes, Figure 1, insert) is the most abundant fish in the mangrove swamps along the coast of Sierra Leone. People, notably around the coastal villages of Bonthe, Wale, Yeloboya and Shenge, catch mudskipper, locally known as 'jumbo fish', using traps made of binodal segments of bamboo cane. One node is cut off, and the cane is driven into the mud. Then, leaves and mud are used to turn the opening into the mouth of a trap (Figure 1).

Powdered okra or a substance locally known as 'gballar' is then used to smoothen the surface of the leaves, which may also be baited by a sprinkling of powder-dried crab, or additional 'gballar'. In neighboring Guinea, a broad leaf and a piece of broom stick are used, instead of bamboo cane, to construct a gear similar in operation to the above-described trap.

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[1] Cite as: Turay, I., Vakily, J.M., Palomares, M.L.D., Pauly, D., 2006. Growth, food and reproduction of the mudskipper, *Periophthalmus barbarus* on mudflats of Freetown, Sierra Leone. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 49-54. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

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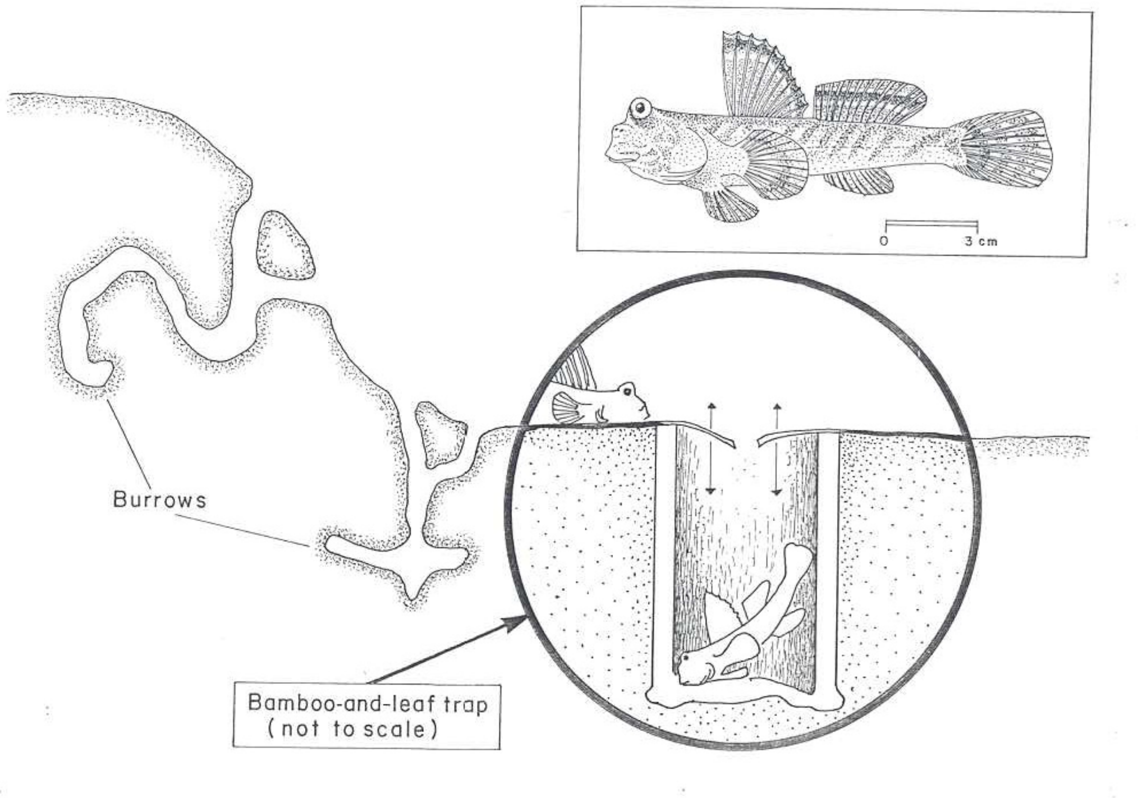

Figure 1 The mudskipper, *Periophthalmus barbarus* (Linnaeus, 1766) (Family Gobiidae, insert adapted from FAO), with schematic representations of burrows and of the bamboo-and-leaves trap used in Sierra Leone (adapted from Den-Khadhri, 1984).

MATERIALS AND METHODS

Catch composition statistics relating to the mudskipper do not appear to exist, and this study is thus entirely based on 364 specimens caught by the first author from July 1992 to April 1993 by digging into mudskipper burrows in the mudflat of Congotown, a 'quartier' of Freetown (8° 29' 10' N; 13° 15' 30' E).

Morphometric measurements were done on 348 samples, to the nearest mm, using a vernier caliper; the measurements taken included total (TL) and standard length (SL) and some others presented in Turay (1993), but the measurements presented below refer to TL in cm. Individual fish weights were determined to the nearest 0.01 g. The length-frequency analyses were all performed using the FiSAT software (Gayanilo *et al.*, 1996).

Reproduction was studied by noting gonad maturity stages, by computing gonadosomatic indices (GSI = gonad weight·100/body weight) and by estimating 'fecundity', i.e., the number of eggs in the gonads of mature female mudskipper.

Food and feeding habits were studied through examination of stomach contents, and the 'point' and 'occurrence' methods (Hynes, 1950).

RESULTS AND DISCUSSION

The largest mudskipper observed was a male of 15.4 cm; the largest female measured 13.0 cm. Figure 2A shows the length-weight relationship of female and male mudskippers; the corresponding relationship for the population as a whole is $W = 0.0072 \cdot TL^{3.19}$ for which $n = 348$ and whose log linear version has an $r^2 = 0.961$. The relationship between standard length and total length is given by:

$SL\ (cm) = 0.86 \cdot TL\ (cm)^{-0.0914}$ (Figure 2B)

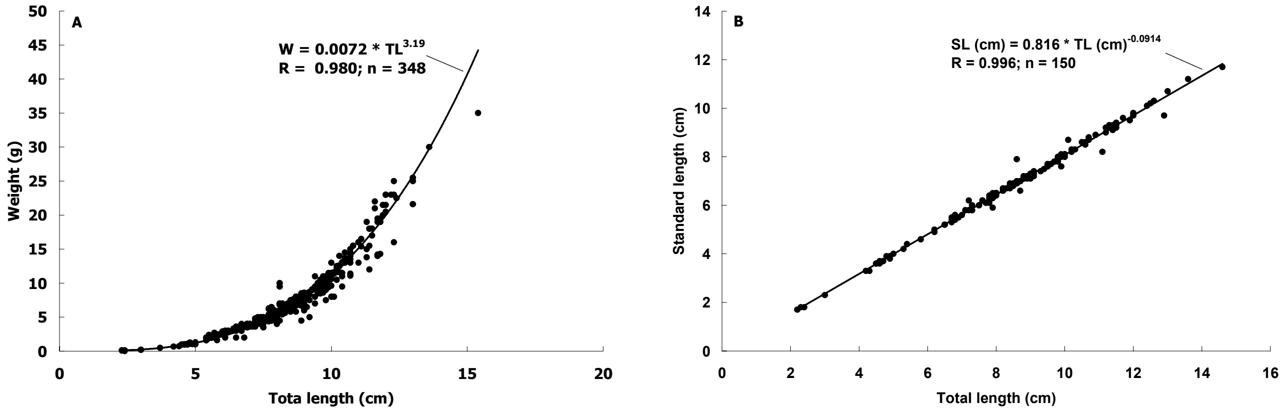

Figure 2 Relationships of length to weight (A) and total to standard lengths (B) of male and female *Periophthalmus barbarus* (Linnaeus, 1766) (Family Gobiidae), removed from their burrows in the mudflats of Congotown, Freetown, Sierra Leone from July 1992 to April 1993.

Table 1 Length-frequency data for 348 mudskippers, Periophthalmus barbarus (Linnaeus, 1766) (Family Gobiidae), removed from their burrows in the mudflats of Congotown, Freetown, Sierra Leone.

Midlength (TL, cm)	Jul 1992	Aug	Oct	Nov	Dec	Jan 1993	Feb	Mar	Apr
0.25	0	0	0	0	0	0	0	0	0
0.75	0	0	0	0	0	0	0	0	0
1.25	0	0	0	0	0	0	0	0	0
1.75	0	0	0	0	0	0	0	0	0
2.25	5	1	0	0	0	0	0	0	0
2.75	1	1	0	0	0	0	0	0	0
3.25	0	0	0	0	0	0	0	0	0
3.75	0	0	1	0	0	0	0	0	0
4.25	1	2	1	0	0	0	0	0	0
4.75	2	4	1	2	2	0	0	0	1
5.25	1	1	3	1	0	1	0	0	0
5.75	0	2	1	2	2	1	1	1	1
6.25	0	2	2	1	2	3	1	4	1
6.75	3	5	1	1	2	0	2	9	0
7.25	1	3	2	1	3	2	2	8	2
7.75	4	6	3	1	2	3	1	16	1
8.25	5	3	4	2	4	1	3	5	4
8.75	10	8	1	2	2	5	1	11	2
9.25	4	2	2	1	4	1	4	6	1
9.75	10	3	4	2	2	3	4	4	1
10.25	4	3	2	3	2	1	5	2	1
10.75	1	1	1	1	1	2	2	1	2
11.25	3	4	1	0	1	0	3	0	0
11.75	5	2	3	4	0	0	1	1	1
12.25	1	0	1	1	1	0	0	0	1
12.75	1	0	1	1	0	0	0	0	0
13.25	0	0	0	0	0	0	0	0	0
13.75	1	0	0	0	0	0	0	0	0
14.25	0	0	0	0	0	0	0	0	0
14.75	0	0	0	0	0	0	0	0	0
15.25	0	0	0	0	0	0	0	0	1
15.75	0	0	0	0	0	0	0	0	0
16.25	0	0	0	0	0	0	0	0	0
Total	63	53	35	26	30	23	30	68	20

Table 1 summarizes the length-frequency (L/F) data used for the growth analyses, whose results are given in some details (including some intermediate outputs), as they nicely illustrate how gentle ‘massaging’ of an L/F data set can lead to improved estimates of growth parameters, here those of the von Bertalanffy model (von Bertalanffy, 1938) and one of its seasonally oscillating variants (Pauly, 1987).

The method of Wetherall (1986) was applied to an accumulation of the data in Table 1; it led to estimates of L_∞ ranging from 16 to 18 cm, depending on which length range was included in the analysis. Hence a value of $L_\infty = 17$ cm was retained for all analyses using ELEFAN, a routine of the FiSAT software.

A first pass of the ELEFAN subroutine in which K values are scanned, in very small steps, from $K = 0.1$ to $K = 10$ year^{-1}, yielded an essentially flat structure (Figure 3a). This was attributed to the class interval (0.5 cm) of the L/F data in Table 1, which was too small to clearly indicate the progression of cohorts. Subsequent analysis of L/F files with gradually increasing intervals did not yield a marked improvement (Figures 3b-3g, easily done with the 'slicing' routine of FiSAT).

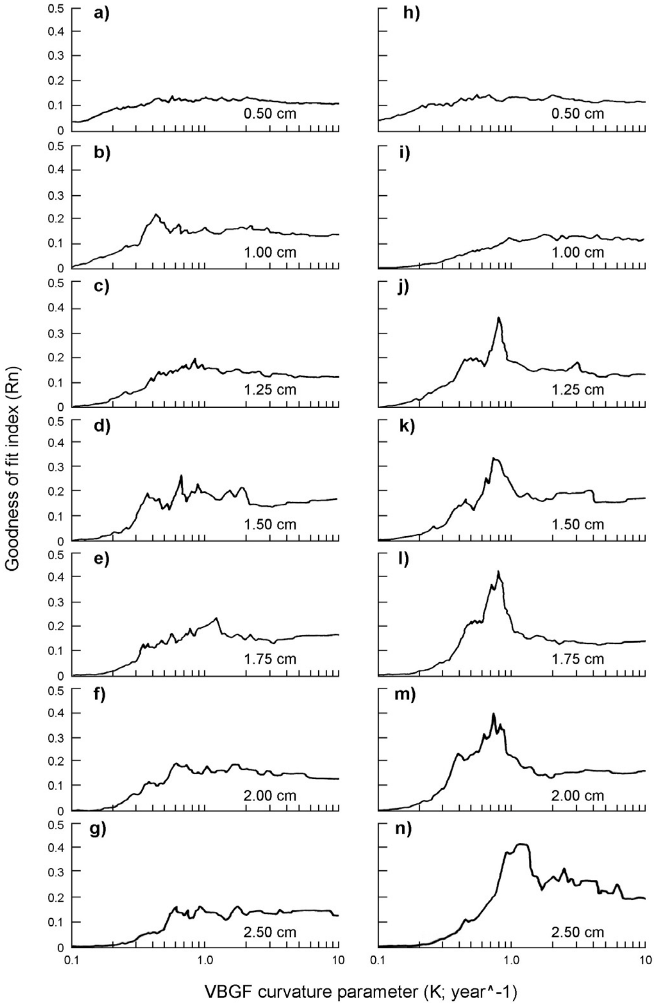

Figure 3 Response surface analysis of the parameter K of the von Bertalanffy growth function showing the increasing resolution of ELEFAN following modification of the length-frequency data in Table 1, for TL_∞ =17 cm.

The second pass, which assumed seasonal growth (C = 0.5, WP = 0.2, commonly occurring in fish) led to the identification of a peak, associated with K = 0.80 $year^{-1}$ and a class interval of 1.25 cm (Figure 3j). This was used, along with L_∞ = 17 cm, to (partly) correct the L/F file for the effect of incomplete selection by and incomplete recruitment to the gear, using the catch-curve approach of Pauly (1987).

This led, in the third pass, to the emergence of a clear peak, centered around K = 0.81 $year^{-1}$.

The fourth and final pass consisted of optimizing the parameter related to seasonal growth oscillations, likely to occur in fish exposed to seasonal differences in (air) temperature of about 10°C (Findlay, 1978). This was done using the 'automatic search routine' of ELEFAN, with K, C and WP as free parameters, then using the best estimates of C and WP thus obtained, by running the K scanning routine with C and WP fixed at 0.75 and 0.95, respectively (and L_∞ at 17 cm as for all previous analyses).

Figure 4 (upper panel) shows the growth curve obtained as a result of this work. The asymptotic length (L_∞) is 17 cm, K = 0.89 $year^{-1}$ is the rate at which L_∞ is approached, C = 0.75 expresses the amplitude of the seasonal growth oscillations, which are here rather strong given that C can take values between 0 and 1, and where WP = 0.95 is the 'winter point', i.e., the time of the year (expressed as fraction of 1) when growth is slowest; WP corresponds here to late November 1992, which falls in the wet, 'intermediate' season (Vakily and Pauly, 1993).

This growth curve, which also fits very small mudskippers, has its origin in mid June, suggesting this period as the main spawning season. There is some indication of a second minor spawning at the end of the year, leading to a second, minor cohort (lower panel of Figure 4).

Table 2 presents the key results of the maturity study, from which a length at first maturity of about 9 cm can be inferred for the females and 7 cm for the males. The means of these two values yield L_m/L_∞ = 0.65. as estimate of the 'reproductive load' (Cushing 1981) for mudskippers.

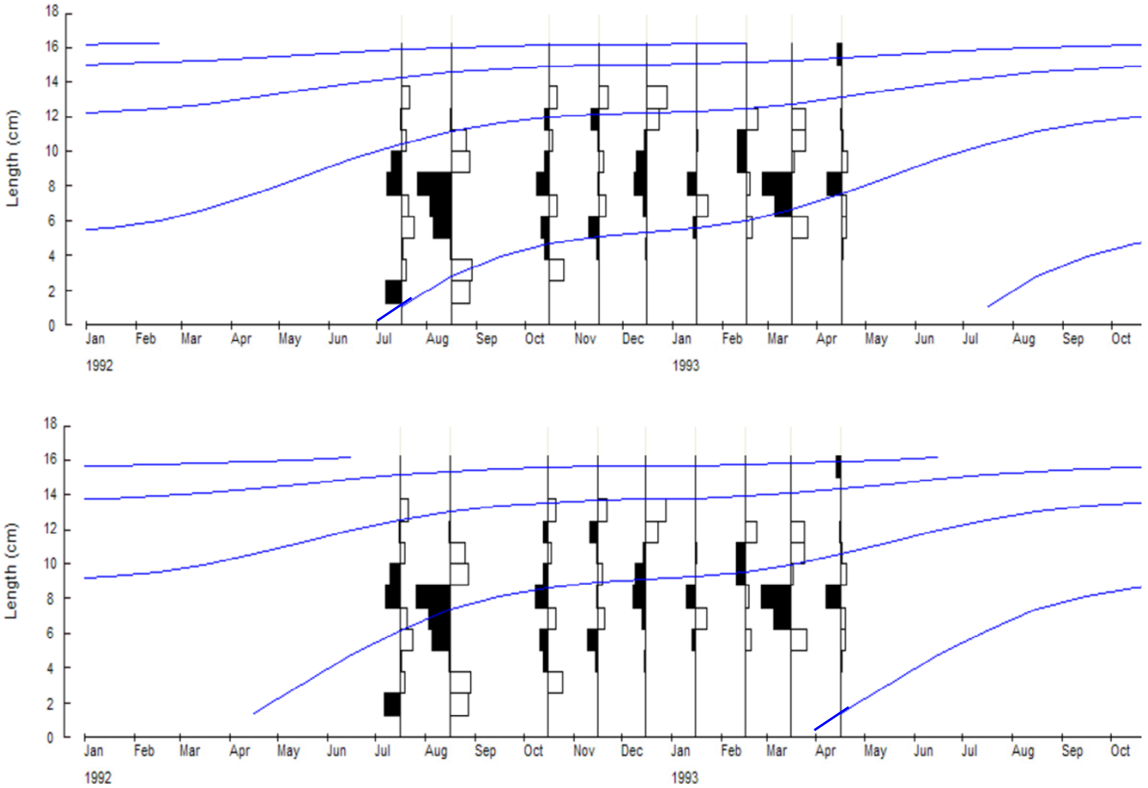

Figure 4 Von Bertalanffy Growth Function for *Periophthalmus barbarus* (Linnaeus, 1766) (Family Gobiidae), removed from their burrows in the mudflats of Congotown, Freetown, Sierra Leone from July 1992 to April 1993, with TL_∞ = 17 cm, K = 0.89 year^{-1}, C = 0.75 and WP = 0.95. Upper panel: main cohort, originating in June. Lower panel: second cohort, originating earlier in the year.

GSI ranged in females from 2.0 to 3.5, with a mean of 2.5 GSI and % of mature fish were plotted against months. However, low sample size and gaps in the series rendered these data inconclusive; all that emerged is that they did not contradict the timing of the spawning season(s) proposed above.

Apparent fecundity was 11400 eggs g^{-1} of female gonads, in fish of 8 cm TL, i.e., about 2,100 eggs g^{-1} body weight. However, spawning probably occurs several times during (and outside) the main spawning season, and hence this estimate of fecundity represents only a minimum.

Table 2 Relative frequency of immature and mature mudskipper, *Periophthalmus barbarus* (Linnaeus, 1766) (Family Gobiidae), removed from their burrows in the mudflats of Congotown, Freetown, Sierra Leone from July 1992 to April 1993.

Midlength (TL, cm)	Females Immature/mature	Males Immature/mature
3.0	0/0	2/0
5.0	1/0	20/0
7.0	10/0	24/44
9.0	22/56	17/47
11.0	3/38	10/19
13.0	0/7	0/6
15.0	0/0	0/1

The food items occurring most frequently in mudskipper stomachs were crustaceans (3 1%), polychaets (26%), insects (9%), and mollusks (3%) with detritus forming the rest. There was a slight tendency for the occurrence of crustaceans to increase and for polychaets to decrease with increasing mudskipper size.

ACKNOWLEDGEMENTS

The field work upon which this paper is based was performed by the first author for a BSc (Honours) thesis supervised by Professor D.E.B. Claytor, Fourah Bay College, University of Sierra Leone, Freetown. The first author would also like to thank Mr. Dean-Kadri, whose own thesis on mudskipper proved extremely helpful.

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NOTE ON THE WEIGHT OF BODY PARTS, INCLUDING FINS, OF THE SMALLTOOTH SAWFISH *PRISTIS PECTINATA*[1]

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In July 1976, I became by default the scientific leader of a demersal survey conducted by *R/V Mutiara 4* in the southern Indonesian part of the South China Sea (south and east of Singapore), documented in Pauly *et al.* (1996).

During the cruise, we captured a large sawfish (Family Pristidae), which we identified as the smalltooth sawfish *Pristis pectinata* Latham 1794 (Figure 1). At the time, all large sharks we caught were finned by the Indonesian crew of the *Mutiara 4*, the fins hanged to dry, garland-like, from the ship's rigging, and later sold on the 'soup fin' market by the crew as bonus. The saw was sold separately for the curios market.

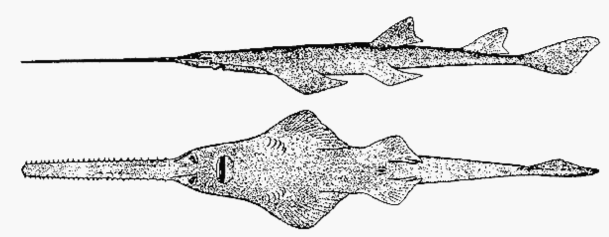

Figure 1 The smalltooth sawfish, *Pristis pectinata* Latham 1794, Family Pristidae (drawing from Massey and Harper, 1993).

This sawfish, of 270-300 cm (total length, i.e., including the saw-like snout), differed from others in that I weighted its different body parts. The results of this rather bloody exercise are given in Table 1.

Table 1 Weight (in kg and as % of the total body weight, i.e., 201.7 kg) of different body parts of a mature female smalltooth sawfish, caught on June 18, 1976, at Station 154 (~0°25'S; 103°54'E, 15 m depth) in Pauly *et al.* (1996)

Body part	Weight	%	Body parts (extremities)	Weight	%
Head	47.5	23.5	Saw	2.0	1.0
Trunk	95.0	47.1	Dorsal fins (2)	3.5	1.7
Liver	26.0	12.9	Pectoral fins (2)	10.0	5.0
Other inner organs	8.2	4.1	Ventral fins (2)	5.0	2.5
Blood (recovered)	~1.0	0.5	Caudal fin	3.5	1.7

Thirty years later, the smalltooth sawfish is 'Critically endangered' on the IUCN Redlist (Baillie *et al.*, 2004), both because it is caught as by-catch by trawlers fishing for shrimps and fish (as was the *Mutiara 4*), and targeted for its fins.

Little did we know.

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[1] Cite as: Pauly, D., 2006. Note on the weight of body parts, including fins, of the smalltooth sawfish *Pristis pectinata*. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), p. 55. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

AN OVERVIEW OF BIOLOGICAL DATA RELATED TO ANCHOVY AND SARDINE STOCKS IN GREEK WATERS[1]

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ABSTRACT

European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) are the most important small pelagic species in Greek waters. We present here a brief overview of available data sources and studies concerning their biology and ecology. Some new analyses are also presented concerning lengths at first maturity.

INTRODUCTION

European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) are the two most important small-sized pelagic species in Greek waters, making up 30% of the total Greek landings and 59% of the total purse seine landings (Stergiou *et al.*, 1997a). Despite their importance for the Greek fisheries, their stocks have never been studied systematically, nor has their exploitation been monitored on a yearly basis, with the exception of their landings (see e.g., Stergiou, 1989, 1990, 1991, 1992; Stergiou *et al.*, 1997). In general, most of their landings in Greek waters derive from the purse seine fleet. Fishing with pelagic trawlers is prohibited, i.e., the percentage of small pelagic fish in the total marketable fraction of demersal trawlers cannot exceed 5%. Management measures to protect these species include a closed season for purse seiners from the 10th of December to the end of February.

In this paper we attempt to present a brief overview of the available biological and ecological data concerning anchovy and sardine in Greek waters.

GENETIC STRUCTURE

Various studies conducted in recent years indicate a significant genetic structuring for anchovy in the eastern Mediterranean and Black Seas (Spanakis *et al.*, 1989; Magoulas *et al.*, 1996; Machias *et al.*, 2000a). This is not the case for sardine which conforms to a panmictic population (Machias *et al.*, 2001b). Surveys of genetic variation in mitochondrial DNA (Magoulas *et al.*, 1996; Machias *et al.*, 2000a) provide

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[1] Cite as: Somarakis, S., Tsianis, D.E., Machias, A., Stergiou, K.I., 2006. An overview of biological data related to anchovy and sardine stocks in Greek waters. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 56-64. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

consistent evidence that the anchovy stocks do not form a genetically homogeneous population. Barriers for gene flow have been suggested between the northern and southern Aegean, and between the northern Adriatic and Ionian Seas. Two different genetic stocks of anchovy are currently recognized in Greek waters: the eastern stock (Aegean type) and the western stock (Ionian type).

REPRODUCTION

Information on spawning time and grounds of anchovy and sardine has been obtained from 1992 to 2001 within the framework of three EU and one national research projects. These projects aimed, among others, at delimiting the spawning grounds and times of these species in Greek waters, and the development and application of ichthyoplankton-based methods, specifically the daily egg production method (DEPM), for estimating the spawning biomass of the stocks (Tsimenides *et al.*, 1995a; 1998; Machias *et al.*, 2000a; 2001b).

The spawning period of anchovy in the Greek Seas extends from May to September (Somarakis, 1993; 1999; Machias *et al.*, 2000a; Tsianis *et al.*, 2003), but some spawning activity can be observed up to December in the central Aegean Sea (S. Somarakis, unpublished data). Spawning peaks at around June in all areas studied so far (Figure 1): 1992, north Aegean Sea, (Somarakis, 1993); 1998, central Aegean Sea (Machias *et al.*, 2000a); 1998, central Ionian Sea (Machias *et al.*, 2000a); 2002, NW Aegean Sea (Tsianis, 2003). The major spawning grounds of anchovy in the Aegean Sea are located in areas characterized by wide continental shelf and enrichment processes associated with the outflow from large rivers or the Black Sea Water (BSW) in the north Aegean (Somarakis, 1993; Somarakis *et al.*, 2000a; Ramfos *et al.*, 2000) (see also Stergiou and Georgopoulos, 1993, for the relationship between distribution of phytoplankton pigments and landings of small pelagics in the Greek Seas). Consequently, the highest egg densities have been typically observed over the northern Aegean Sea continental shelf (Figure 2a). A potential spawning location for anchovy around the island of Lemnos has never been surveyed. Nevertheless, it is likely to be an important spawning ground, since this area is under the direct influence of BSW and the associated enhancement of biological production (Somarakis, 1999).

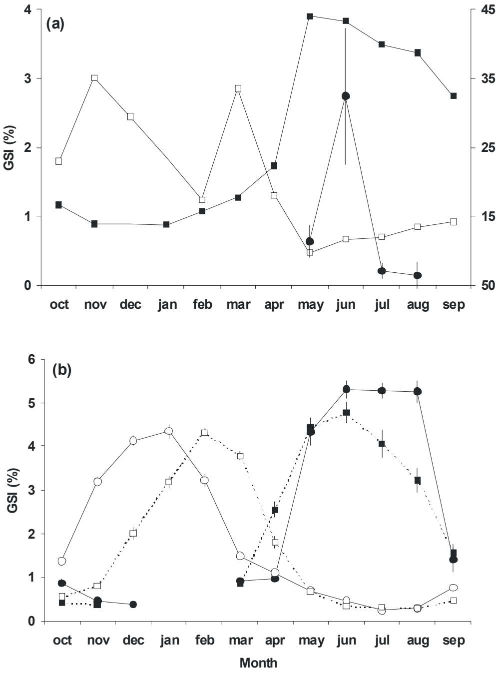

Figure 1 Data relevant to anchovy and sardine spawning periods in the Greek Seas: (a) north Aegean Sea. Monthly evolution of the gonosomatic index (GSI=100*ovary weight/ovary-free weight) for sardine (□) and anchovy (■) and mean abundance of anchovy eggs in the plankton (●). Data from Somarakis (1993), Voulgaridou and Stergiou (2003) and Tsianis (2003); (b) central Aegean and Ionian Seas. Monthly evolution of the gonosomatic index (GSI=100*ovary weight/eviscerated weight) for sardine in the Aegean (○) and the Ionian (□) as well for the anchovy in the Aegean (●) and the Ionian Sea (■).Data from Machias *et al.* (2000a; 2001b). Bars: ±SE.

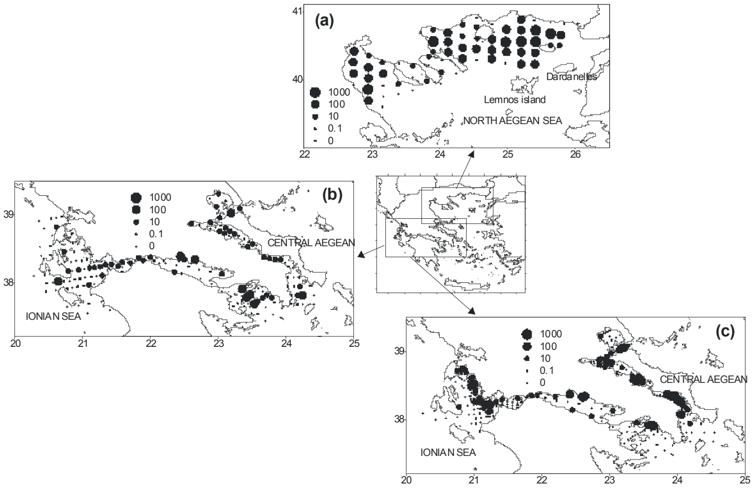

Figure 2 Distribution and abundance of anchovy and sardine eggs from ichthyoplankton surveys. (a) Anchovy, north Aegean Sea, June 1996. (b) Anchovy, central Aegean and Ionian Seas, June 1999. (c) Sardine, central Aegean and Ionian Seas, winter 2000-2001. Data from Tsimenides *et al.* (1998), Somarakis *et al.* (2001, 2002).

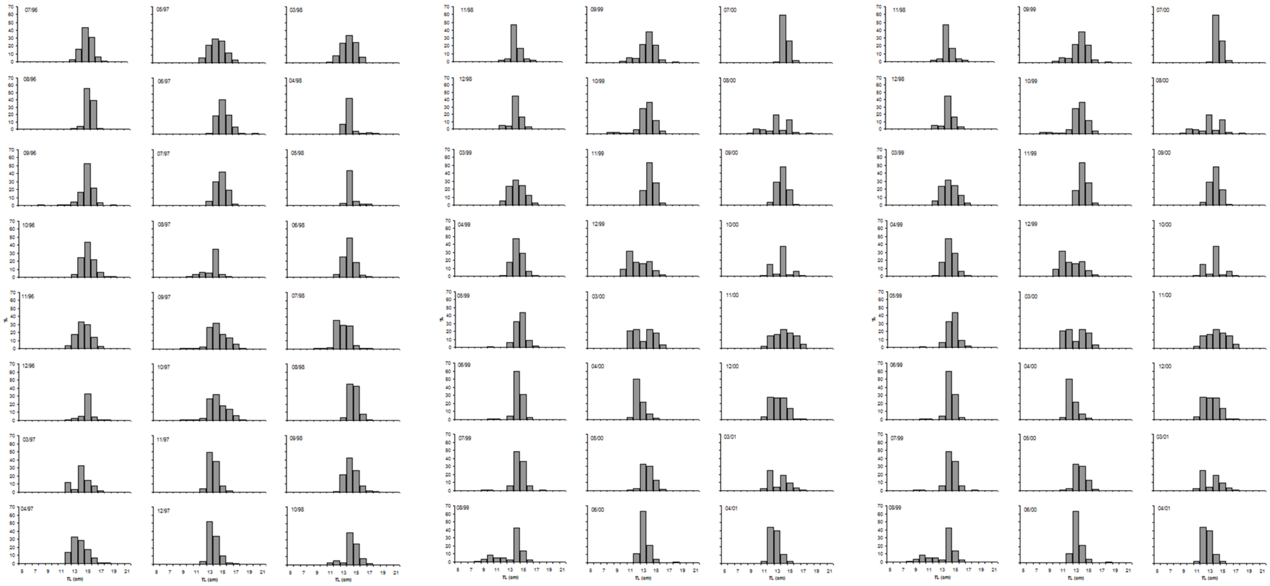

Figure 3 Biweekly mean total length (in cm) of sardine in NW Aegean, 07/1996-05/2003 (from Voulgaridou and Stergiou 2003; Tsianis, 2003).

Data on the spawning period of sardine exist for the coastal areas of the central Aegean and Ionian Seas as well as for the north Aegean Sea (Machias *et al.*, 2001b; Ganias, 2003; Ganias *et al.*, 2003b; Voulgaridou and Stergiou, 2003; Tsianis 2003) (Figure 1). In the coastal waters of central Greece, spawning takes place from October to May but it peaks earlier in the Aegean (November-January) than in the Ionian Sea (January-February) (Figure 1b). The gonadosomatic index data for sardine in the north Aegean Sea (Figure 1a) suggest the existence of two spawning peaks: one in November-December and another in March. The importance of the second peak increased during the period 1996-2000 (Tsianis, 2003). This is attributed to the decrease in the mean total length with time (Figure 3; Tsianis, 2003) given that, in general, smaller sardines spawn later than larger ones (Ganias, 2003). During the 1999 and 2000-2001 ichthyoplankton surveys in the central Aegean and Ionian Seas (Ganias *et al.*, 2001; Somarakis *et al.*, 2001), the highest egg abundance values were found inshore, mainly in waters shallower than 100 m depth (Figure 2c).

Available studies suggest that the reproductive tactics of anchovy and sardine in Greek waters differ substantially (Somarakis, 1999; Ganias, 2003). Sardines seem to rely mainly on fat reserves stored in the muscles and viscera during summer to reproduce during the winter. They are characterized by low seasonal and interannual variability in batch fecundity and spawning frequency (Somarakis *et al.*, 2002, Ganias, 2003, Ganias *et al.*, 2003a; 2004). On the other hand, the reproductive effort of summer spawning anchovy seems to be closely associated with adult prey fields (meso-zooplankton), i.e., the energy allocated to reproduction derives primarily from the food intake. In comparing batch fecundity and spawning frequency estimates between June 1993 and June 1995 over the NE Aegean Sea continental shelf, Somarakis (1999) showed

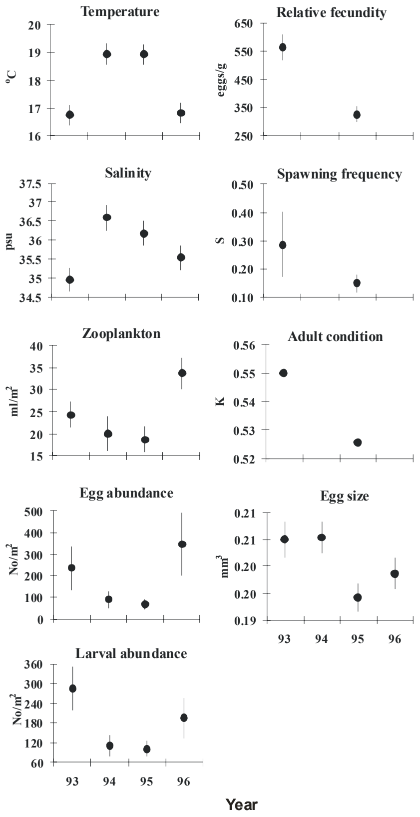

Figure 4 Means (±95% confidence intervals) for temperature (0-40 m); salinity (0-40 m); zooplankton displacement volumes, anchovy egg and larval abundance; and egg size from ichthyoplankton surveys and fecundity, spawning frequency and somatic condition of anchovy females from concurrent adult surveys in the Thracian Sea (NE Aegean Sea). Redrawn from Somarakis (1999).

that adult food availability was higher in 1993, when waters were significantly cooler and of lower salinity.

Concurrently, female anchovies were in better condition, producing numerous large-sized eggs at a higher spawning frequency (short inter-spawning interval) (Figure 4). These observations were consistent with a ration-related reproductive tactic in anchovy (Somarakis *et al.*, 2000b; Maraveya *et al.*, 2001; Somarakis, 2005).

Lengths at first maturity of anchovy and sardine have been estimated for the central Aegean and Ionian Seas from samples collected experimentally during DEPM surveys (Figure 5 and see Appendix for method). Anchovy reach maturity at approximately 105 mm total length and sardine at around 115 mm, i.e., at the completion of the first year of life.

AGE AND GROWTH

There are very few age and growth studies for anchovy and sardine in Greek waters and otolith readings have not been generally validated (Table 1). Published growth curve comparisons among stocks, areas, and years have not shown any significant differences for either anchovy or sardine (Tserpes and Tsimenides, 1991; Nikoloudakis *et al.*, 2000). Von Bertalanffy growth parameters (Table 1) estimated from samples collected from landings, experimental trawling, and onboard the commercial fishing fleet clearly indicate that commercial catches might be biased with respect to lengths-at-age, at least for the one and two year old fish (Figure 6). Indeed, selection of larger anchovy schools by the Greek purse seine fishery in the north Aegean Sea was evident when comparing length frequencies obtained from the commercial landings with those of experimental trawling (with 'a proportional to abundance' allocation of pelagic trawl samples) during a DEPM survey in June 1995 (Figure 7).

Since 1996, the Laboratory of Ichthyology of the Aristotle University of Thessaloniki has been collecting biweekly data on length, weight, sex ratio, gonadosomatic index and condition of both species in the NW Aegean Sea. The results clearly indicate that the mean length of sardine (Voulgaridou and Stergiou, 2003; Tsianis 2003) and anchovy (Loukmidou and Stergiou, 2000) in the NW Aegean Sea has declined in recent years (e.g., Figure 3). The potential effect of

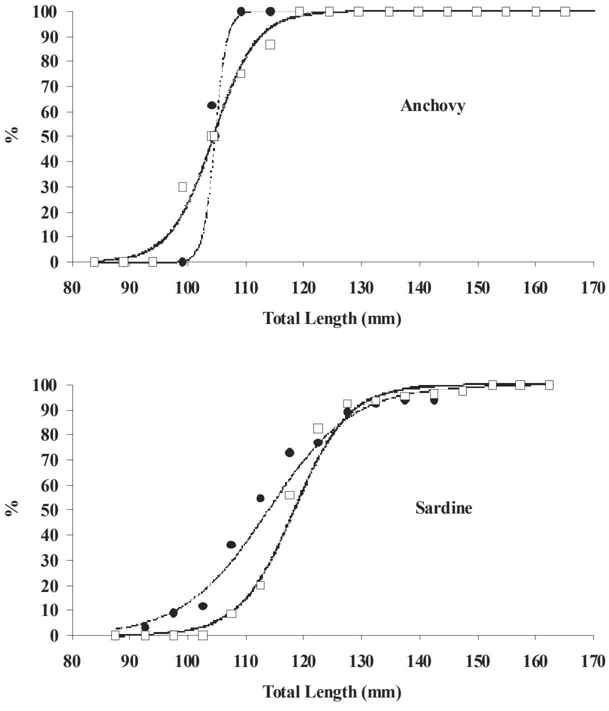

Figure 5 Length at first maturity (at 50%) of anchovy and sardine. Percent of mature females per length class in the central Aegean (□) and Ionian (●) Seas. Fitted logistic curves are also shown.

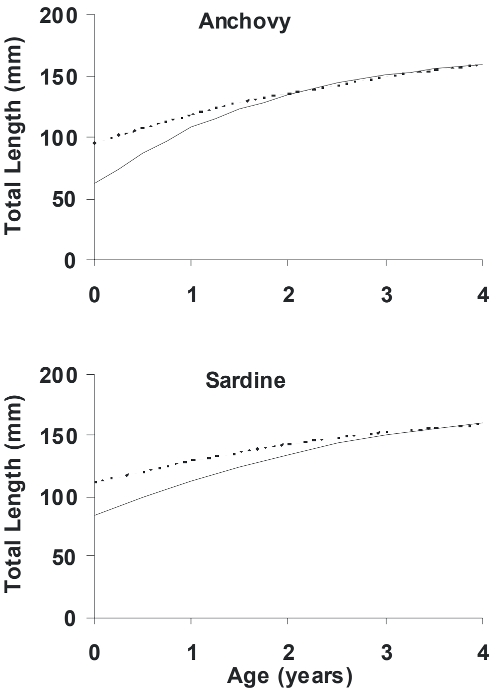

Figure 6 Von Bertalanffy growth curves for anchovy and sardine in Greek waters. Parameters of the models are given in Table 1. Solid lines: estimation based on experimental sampling (Machias *et al.*, 2000a, 2001b). Broken and dotted lines: estimation based on sampling the landings (Tsimenides *et al.*, 1995a, Tserpes and Tsimenides, 1991; Kalliantiotis *et al.*, 2003 respectively).

environmental variability on such a decline is under investigation.

Table 1 Estimates of the von Bertalanffy growth parameters for anchovy and sardine in Greek waters.

Species	Area	Year	K ($year^{-1}$)	L_∞ (mm)	t_0	Sampling	Method	Reference
Anchovy	North Aegean Sea	1993	0.280	191	-2.480	Purse seine landings	Otoliths	Tsimenides *et al.* (1995a)
	NW Aegean Sea	1997-1998	0.75	200		Purse seine landings	Length-frequency analysis	Loukmidou (1998)
	NW Aegean Sea	2000-2003	0.77	175		Purse seine landings	Length-frequency analysis	Tsianis *et al.* (2003)
	Thracian Sea	2000-2001	0.49	176	-1.276	Purse seine landings	Otoliths	Kallianiotis *et al.* (2003)
	Central Aegean and Ionian Seas	1998-1999	0.509	175	-0.888	Experimental pelagic trawl samples and onboard sampling	Otoliths	Machias *et al.* (2000a)
Sardine	NW Aegean Sea	1996-2003	0.80	219		Purse seine landings	Length-frequency analysis	Tsianis (2003)
	NW Aegean Sea	1996-1999	0.86	208		Purse seine landings	Length-frequency analysis	Voulgaridou and Stergiou (2003)
	Aegean and Ionian Seas	1983-1984	0.300	181	-3.210	Purse seine landings	Scales	Tserpes and Tsimenides (1991)
	Central Aegean and Ionian Seas	1999-2001	0.314	191	-1.839	Experimental pelagic trawl samples and onboard sampling	Otoliths	Machias *et al.*, (2001b)

BIOMASS ESTIMATES

Direct biomass estimates for anchovy and sardine through acoustic and/or egg surveys have been obtained in recent years in the framework of various EU and national projects (Tsimenides *et al.*, 1995a; 1998; Machias *et al.*, 2000a; 2001b). First acoustic surveys were conducted in north Aegean in 1987-1988, in the central Aegean in 1989-1990, and in south Aegean in 1991, all aiming to study the echo-distribution of small pelagic fish assemblages (Tsimenides, 1989; Tsimenides *et al.*, 1995b). Later surveys in 1995-2001 were focused on the study of vertical and horizontal distribution and the estimation of biomass of anchovy and sardine in the north Aegean and the coastal areas of the central Aegean and Ionian Seas (Machias *et al.*, 1996; 1997; 2000a, b; 2001a, b; Giannoulaki *et al.*, 1999; 2001; 2003; Tsimenides *et al.*, 1998; Maravelias *et al.*, 1997). The acoustic method has been applied concurrently with DEPM for the estimation of biomass of anchovy in the north Aegean during June 1995, and in the central Aegean and Ionian Seas in June 1999, as well as for the estimation of the biomass of sardine in the latter area in winter 2000-01 (Tables 2 and 3).

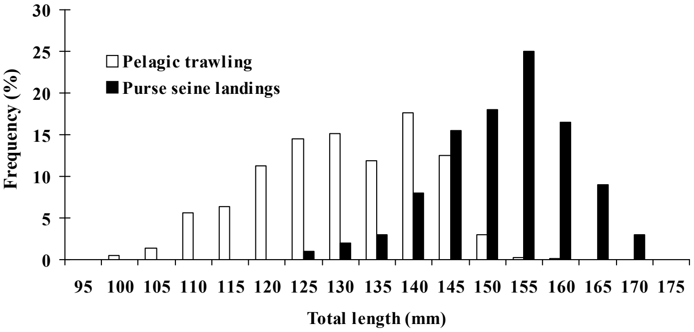

Figure 7 North Aegean Sea, June 1995. Length frequency distributions of anchovy from experimental pelagic trawling during an acoustic survey and from purse seine landings. Data from Tsimenides *et al.* (1998).

The abundance estimates of anchovy ranged between 40000 and 45000 t in the north Aegean and between 11000 and 15000 t in the central Aegean and Ionian Seas. The estimates of sardine biomass (total or spawning biomass) in the central Aegean and Ionian Seas ranged from 20000 to 32000 t.

Table 2 Biomass estimates of anchovy stocks in the Greek Seas (in tonnes, with CVs in parentheses). DEPM: Daily egg production method. LVPA: Length-based virtual population analysis.

Year	Month of direct surveys	Region	Acoustic survey	DEPM survey (spawning biomass)	LVPA	References
1993	June	North Aegean		40643 (0.276)	40236	Tsimenides *et al.* (1995a, 1998)
1995	June	North Aegean	44601 (0.120)	42708 (0.181)		Tsimenides *et al.* (1998) Machias *et al.* (1997) Somarakis *et al.* (1997)
1996	June	North Aegean	39475 (0.132)			Tsimenides *et al.* (1998)
1998	July	Central Aegean and Ionian Seas	14261 (0.298)		13446	Machias *et al.* (2000a, 2001a)
1999	June	Central Aegean and Ionian Seas	14511 (0.280)	11861 (0.278)	13044	Machias *et al.* (2000a, 2001a) Somarakis *et al.* (2002)

Table 3 Biomass estimates for sardine stocks in the Greek Seas (central Aegean and Ionian Sea; in tonnes with CVs in parentheses). DEPM: Daily egg production method. LVPA: Length-based virtual population analysis.

Year	Month of direct surveys	Acoustic survey	DEPM survey (Spawning Biomass)	LVPA	References
1999	December		32594 (0.301)	27086	Machias *et al.* (2001b)
2000-2001	December-February	19826 (0.429)	24207 (0.225)	30317	Machias *et al.* (2001b) Somarakis *et al.* (2001)

SUMMARY

Based on the above-mentioned studies, it is clear that there is a lack of regular, long-time series of data on biomass and biological parameters of anchovy and sardine throughout the Greek waters. Indeed, experimental sampling and surveys have been generally highly discontinuous in time and space, mainly linked to the existence of on-going projects and ending with the specific project that initiated them. This represents an impediment to the study of the effect of fishing and environmental variability on small pelagic fishes (see, e.g., Stergiou and Lascaratos, 1992; Stergiou *et al.*, 1997), and thus, to their management, which is based exclusively on technical measures.

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APPENDIX: ESTIMATION OF LENGTH AT FIRST MATURITY

Length at first maturity of anchovy and sardine was estimated from samples collected during the peak of the spawning season (during DEPM surveys) in summer 1999 and winter 2000-2001, respectively. Fish were collected with a pelagic trawl and maturity was assessed histologically in female specimens (Somarakis *et al.*, 2001; 2002). The size at which 50% of females were mature (size at maturity, L_{50}) was estimated from the relationship between percentage P of mature fish at length class L. This relationship, widely used for maturity studies (e.g., Stergiou *et al.*, 1996), is described by the logistic function: $P = e^{(v1+v2\ L)} / (1+e^{(v1 + v2 \cdot L)})$,and the value of L_{50}, L_{25}, L_{75} can be estimated from the expressions: $L_{50} = -v_1/v_2$, $L_{25} = [-Ln(3)-v_1]/v_2$, $L_{75} = [Ln(3)-v_1]/v_2$.

The proportion of mature fish for each 10 mm length class was calculated by sex and v_1, v_2 were calculated using Fryer's (1991) algorithm by maximising the log–likelihood, ln(L) (Petrakis and Stergiou, 1997). A test for over–dispersion was obtained by estimating the deviance statistic Δ and comparing it to a χ^2 distribution on N-2 degrees of freedom (Petrakis and Stergiou, 1997). The data are over–dispersed if $\Delta > \chi^2$. The standard errors and the 95% confidence intervals of the estimated value of L_{50} were calculated following procedures described in Petrakis and Stergiou (1997). Results of the analysis are given in Table A1.

Table A1 Estimated parameters for the size at maturity, L_{50}. SE: Standard error; CI: 95% confidence intervals; Δ: deviance statistic; df: degrees of freedom. All lengths are total lengths in mm.

Parameter estimates	Anchovy		Sardine	
	Aegean Sea	Ionian Sea	Aegean Sea	Ionian Sea
v_1	-28.175	-100.739	-24.992	-15.554
v_2	0.270	0.963	0.211	0.137
SE v_1	2.957	8.536	2.505	1.147
SE v_2	0.028	0.082	0.021	0.010
L_{50}	104.41	104.62	118.39	113.83
CI L_{50}	102.9–105.6	104.3-104.9	116.5-120.3	111.9–115.7
L_{25}	100.34	103.48	113.18	105.79
L_{75}	108.48	105.77	123.59	121.87
Δ	12.610	7.941	22.708	22.637
Df	13	13	14	14
χ^2	22.362	22.362	23.685	23.684

A COMPARISON OF GROWTH PARAMETERS OF AUSTRALIAN MARINE FISHES NORTH AND SOUTH OF 28° SOUTH[1]

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ABSTRACT

Estimated growth parameters in fish contribute to knowledge of fish biology, and assist in the appropriate management of commercial fisheries resources. Parameters can also be used to test theories of organic growth. Here, one such test is conducted, of the theory that the availability of oxygen to the internal tissues of fish limits their rate of growth, as proposed earlier by the second author. More precisely, what is being tested is a follow-up of that theory, i.e., that, other things being equal, fishes in the cold, high-latitude part of their overall distribution range will have von Bertalanffy growth parameters (L_∞, K) different (higher L_∞, lower K) from those in the warm, low-latitude part of that distribution range. To test this, growth parameters of Australian fishes were assembled from FishBase, and complemented with growth parameters from other sources, notably unpublished documents from Australian government agencies. All growth parameter sets, corresponding to fish populations north or south of 28°S, were assigned a mean water temperature, and analyzed using multiple log-linear regression of K *vs.* temperature and L_∞. The result was a multiple regression in which both L_∞ and temperature had a significant effect on K. Thus, environmental temperature, which varies strongly along the east and west coast of Australia, had an effect on the growth parameters of Australian fishes, as predicted by the theory tested here.

INTRODUCTION

Growth parameters of fish are an important source of information on the biology of fish, and for management of fisheries. Few studies have looked simultaneously at the growth of a large number of species, in spite of the valuable insights this can provide (Cury and Pauly, 2000).

The purpose of this study was to compare the growth parameters of Australian fishes along a latitude (i.e., temperature) gradient as a way of indirectly testing the theory formulated by Pauly (1981, 1984, and see Pauly, 2006, this volume), which states that the growth of fish is linked with their oxygen supply. Other things being equal, fish at low temperature should use less of the oxygen available to them for maintenance, and hence can devote more of it to growth, with the result that they reach larger size (Figure 1). In the von Bertalanffy equation (see below), asymptotic length, L_∞, is positively and closely correlated with maximum size, and inversely correlated with the parameter K. Hence, at low temperatures, L_∞ should be high, and K low, and the converse should apply at high temperatures (Longhurst and Pauly, 1987).

To test this, growth parameters of Australian fishes were assembled from FishBase, and complemented with growth parameters from other sources, notably unpublished documents from Australia. All growth

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[1] Cite as: Andersen, C., Pauly, D., 2006. A comparison of growth parameters of Australian marine fishes north and south of 28° South. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 65-68. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

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parameter sets, corresponding to fish populations north or the south of 28° S, were assigned a mean water temperature.

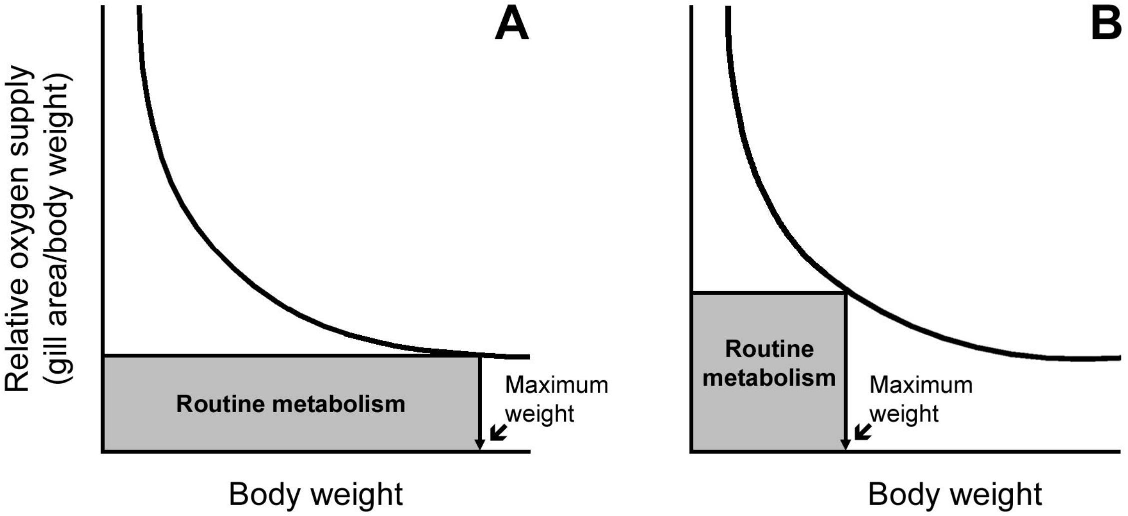

Figure 1 Schematic representation of the relationship between relative gill area (and hence relative oxygen supply) and body weight in fishes. Maintenance metabolism determines the maximum size that can be reached because relative gill area (and hence oxygen supply) *must* decline with body weight. **A**: A fish exposed to low environmental temperature will have a low maintenance metabolism and reaches a larger size. **B**: Exposure of a fish of the same species to high temperatures causes rapid denaturation of body protein, requiring more O_2 to be diverted to protein synthesis, and hence to maintenance of metabolism. Other things being equal, this fish will remain smaller than that in A (see also Pauly 2006, this volume).

MATERIALS AND METHODS

Growth parameters were obtained from the POPGROWTH Table of FishBase (www.fishbase.org). These were complemented with growth parameters from other sources, notably various published and unpublished documents from Australia (see References).

The von Bertalanffy growth function (VBGF) for length has the form:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \quad \ldots 1)$$

where L_t is the predicted mean length at time t, L_∞ is the asymptotic length, or the mean length the fish would reach if they were to grow a very long time (indefinitely, actually), K is a coefficient of dimension time^{-1}, expressing the rate at which L_∞ is approached, and t_0 is the (usually negative) age the fish would have had at length zero if they had always grown in the manner predicted by the equation (which they usually do not).

The length-at-age data from which these growth curves paramaters were usually obtained from reading otoliths or vertebrae. Growth parameters were also inferred from length-frequency and tagging-recapture data. When this was not available from FishBase or the references below, a temperature was assigned to all growth parameter sets, corresponding to the mean water temperature at the sampling using the sampling location and depth (actual or inferred), based on data available from the Australian Oceanographic Data Centre (www.aodc.gov.au/).

RESULTS AND DISCUSSION

The following multiple regression was obtained from the 190 sets of growth parameters obtained:

$$\log K = 0.1652 + 0.0245 \cdot \text{Temp} - 0.681 \cdot \log L_\infty \quad \ldots 2)$$

where K is in year^{-1}, Temp in °C, L_∞ in cm, and log refers to base 10. The r^2 value was 0.544 and the effect of temperature was significant ($P<0.01$), in addition to L_∞, in predicting K. This was solved for logK using different temperatures, as shown in Figure 2, i.e., a plot of logK *vs.* logL_∞, with isotherms at 30, 20, and 10°C superimposed.

As might be seen, the fish in the high K – low L_∞ quadrant of Figure 2 stem overwhelmingly from Australian waters north of 28° S, while the fish with growth parameters in the opposite quadrant were sampled south of 28°S.

These findings are compatible with a number of biological mechanisms. The most likely mechanism, however, is that high temperature reduces the scope for growth of fishes, by increasing their metabolic rate, and hence the amount of water having to be passed across the gills in order for their respiratory requirements to be met. This task is made even more difficult by the fact that less oxygen is dissolved in warm than in cold water (Pauly 1981).

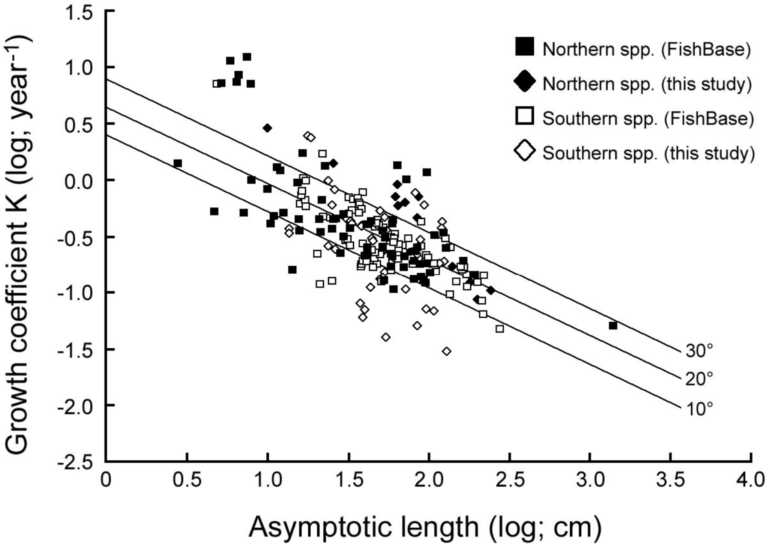

Figure 2 Plot of the von Bertalanffy parameter (log) K *vs.* the parameter L_∞ in 190 population of Australian marine fishes north and south of 28° South. The warm-water populations from the North tend to have lower L_∞ and higher K than those in the South, and *vice versa* for those in the colder South. The isotherms for 10, 20 and 30°C were drawn using Equation 2 (see text).

The different habitats of fishes, whether estuarine, coastal, neritic or oceanic, offer them food of different suitability and in different densities. However, there is no reason to assume that the suitability or density of food available to fish of different species should change, along the Australian coasts, in a close relationship to temperature or latitude (Longhurst and Pauly, 1987). Rather, food can be assumed to vary randomly, and to represent one of the causes for the variability around the values predicted by the multiple regression (Equation 1) and consequently, in Figure 2.

We thus feel that the evidence we presented support the existence of a strong linkage between fish growth and respiration.

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GROWTH PARAMETERS AND LENGTH-LENGTH RELATIONSHIPS OF GREEK FRESHWATER FISHES[1]

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ABSTRACT

In this paper, we gathered from the literature: (a) a total of 80 length-length relationships for 20 Greek freshwater fish species and one hybrid; and (b) von Bertalanffy growth parameters for 54 freshwater fish stocks, belonging to 22 species and one hybrid. The relationship between $\log_{10}L_\infty$ and $\log_{10}K$ for all stocks, excluding one outlier, was: $\log_{10}K = -1.07 \cdot \log_{10}L_\infty + 0.77$ ($r^2 = -0.66$, $n = 53$, $P < 0.05$).

INTRODUCTION

Relationships between different types of lengths (length-length relationships) are very important for comparative growth studies (Froese and Pauly, 2000; www.fishbase.org). In addition, growth parameters and maximum observed length, L_{max}, and age, t_{max}, are also important for management, comparative growth studies, and testing life-history theories, with L_{max} being used for the estimation of plethora biological parameters using existing empirical equations (e.g., Pauly, 1998; Froese and Binohlan, 2000).

In this paper, we gathered from the literature 80 length-length relationships referring to 20 Greek freshwater fish species and one hybrid (from nine lakes, three rivers and two lagoons) and L_{max} and t_{max} values and the von Bertalanffy growth parameters for 54 Greek freshwater fish stocks, belonging to 22 species and one hybrid, from twelve lakes and two rivers in Greece.

MATERIALS AND METHODS

We gathered articles with biological data pertinent to Greek freshwater fish using the Aquatic Sciences and Fisheries Abstracts (ASFA), which cover peer-reviewed as well as grey literature articles. We also used any available unpublished theses and other technical reports. The following type of information was collected: (a) length-length relationships, expressed in cm; (b) maximum observed length and age, L_{max} and t_{max}, in cm and year respectively; and (c) the von Bertalanffy growth parameters K, L_∞ and to, in year^{-1}, cm and year, respectively. The word 'stock' is used here to indicate sets of parameters corresponding to different sexes, years, and areas.

Growth in length has been described using the von Bertalanffy (1938) growth function (VBGF):

$$L_t = L_\infty(1-e^{-K(t-to)}) \qquad \text{... 1)}$$

where L_∞ is the asymptotic length, i.e., the length a fish would reach if it were to grow indefinitely; K is the rate at which L_∞ is approached (in year^{-1}); and t_0 is the theoretical origin of the curve, i.e., the age of the fish at zero length (in year). When the authors did not estimate VBGF growth parameters, we estimated them from the back-calculated length-at-ages provided by the authors, using the non-linear least-squares method (Gayanilo *et al.*, 1994).

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[1] Cite as: Kleanthidis, P.K., Stergiou, K.I., 2006. Growth parameters and length-length relationships of Greek freshwater fishes. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 69-77. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

RESULTS AND DISCUSSION

Overall, 80 length-length relationships between total, fork and standard length were collected from the literature (Table 1), corresponding to 20 fish species and 1 hybrid from 9 lakes, 3 rivers, and 2 lagoons. The sample size ranged from 9 individuals, for *Knipowitschia caucasica* in the Evros River, to 2575 individuals, for *Atherina boyeri* in Trichonis Lake (Table 1). Sample size was not reported for 15 cases (Table 1). In 24 cases, the sample size was less than 200 individuals (Figure 1). For 49 cases, length-length relationships referred to both sexes combined, for 30 cases they were sex-specific (15 for males and 15 for females) and for 1 case it referred to immature fish (Table 1).

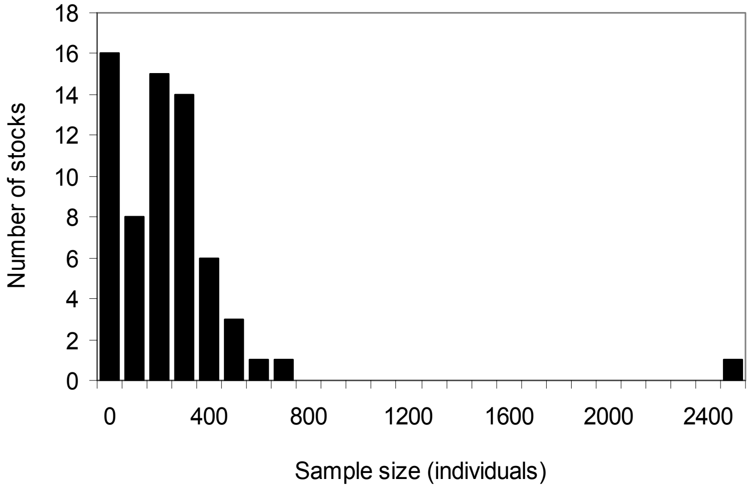

Figure 1 Sample size (i.e., number of individuals) for the cases shown in Table 1.

Table 2 summarizes the biological parameters collected for the 54 fish stocks, belonging to 22 species and one hybrid, from twelve lakes and two rivers in Greece. With respect to sampling frequency, samples were collected mainly on a monthly basis (in 22 cases) or based on a single sampling event (in 17 cases), and, to a lesser extent, on a seasonal or other basis (in 7 and 4 cases, respectively) (Table 2). Sampling frequency was not reported in 4 cases (Table 2). Age and growth were derived mainly from scale readings (in 43 cases) and to a lesser extent from other hard skeletal elements (i.e., opercular bones: 4 cases; fin spines: 3 cases; combination of skeletal elements: 4 cases) (Table 2). The von Bertalanffy growth parameters were provided in the original studies for 11 cases only, estimated using the non-linear method (in 7 cases), the Ford-Walford plot (in 3 cases) and Rafail's (1973) method (in 1 case) using back-calculated length-at-ages (Table 2). In the remaining 43 cases we estimated growth parameters from the back-calculated (in 41 cases) or the observed (in 2 cases) length-at-ages provided in the original studies, using the non-linear regression method. Growth parameters referred to combined sexes for 22 cases (Table 2).

L_{max} was provided in 44 cases and ranged from 9.5 cm, for *Pseudorasbova parva* in Lake Mikri Prespa, to 76 cm, for *Cyprinus carpio* in Lake Vistonis (Table 2). It exhibited a primary mode at 20-25 cm and a secondary one at 35-40 cm (Figure 2a). A value of t_{max} was provided in 50 cases and ranged from 3 year, for *Pseudorasbova parva* in Lake Mikri Prespa, to 14 year for *Barbus albanicus* in Lake Kremasta (Table 2). For 34 cases, t_{max} ranged between 6 and 9 year (Figure 2b). The von Bertalanffy L_∞ values ranged from 11.8 to 88 cm (median = 28.8 cm), with a primary mode between 25-30 cm and a secondary one at 40-50 cm (Figure 2c). The K values ranged from 0.081 to 0.577 year^{-1} (median = 0.139 year^{-1}), with a mode at 0.10-0.15 year^{-1} (Figure 2d). Finally, t_0 values ranged from -3.218 to 0.236 year (median = -0.798 year), with a mode at -1.0 to -0.5; 41 cases had values between -1 and 0 (Figure 2e). The L_{max}/L_∞ ratio ranged between 0.60 and 1.76 (mean = 0.84; median = 0.85), with a mode between 0.8-0.9. The relationship between L_{max} and L_∞ was $\log L_\infty = 0.972 \cdot \log L_{max} + 0.123$ ($r^2 = 0.83$, $n = 44$, $P < 0.05$). The relationship between logK and $\log t_{max}$ was $\log K = -0.939 \cdot \log t_{max} + 0.038$ ($r^2 = 0.39$, $n = 50$, $P < 0.05$).

The relationship between logK *vs.* $\log L_\infty$, excluding one stock, which seems to be an outlier (i.e., *Cyprinus carpio* in Lake Vistonis; Figure 3), was: $\log K = -1.07 \cdot \log L_\infty + 0.77$ ($r^2 = -0.66$, $n = 53$, $P < 0.05$).

The above mentioned relationships can be used for estimating one variable from the other for various freshwater fish species in Greece for which data are lacking. For this to yield reliable estimates, it will, however, be necessary to expand the data set by including more stocks and species.

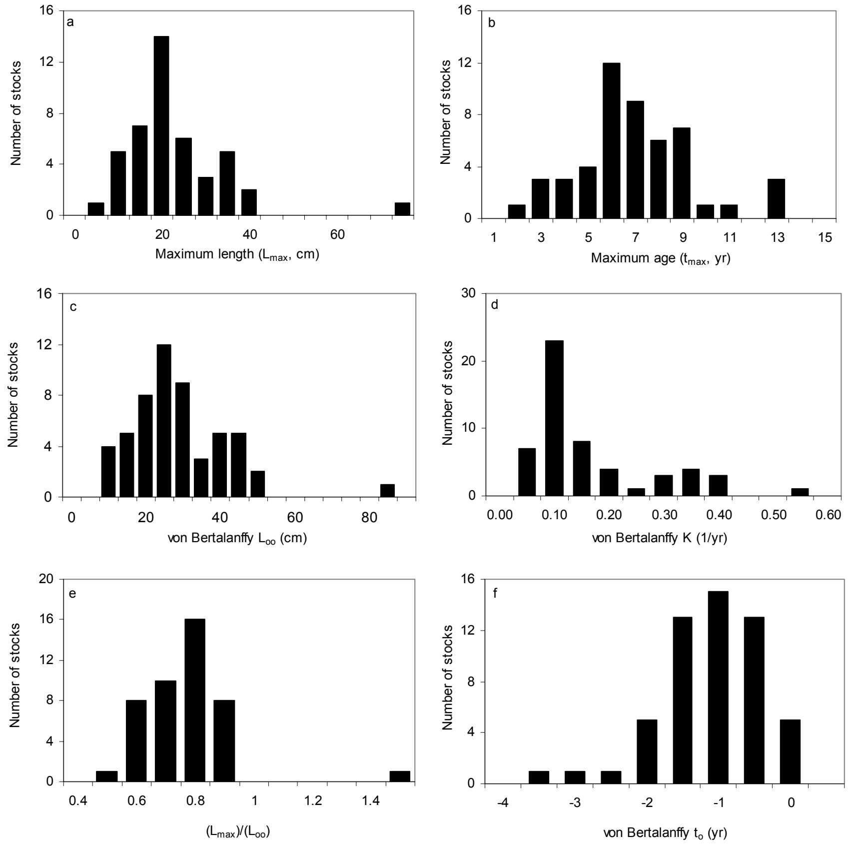

Figure 2 Distribution of the values of (a) L_{max}, (b) t_{max}, (c) L_{oo}, (d) K, (e) L_{max}/L_{oo}, and (f) t_o for the Greek freshwater fish stocks analysed in this study.

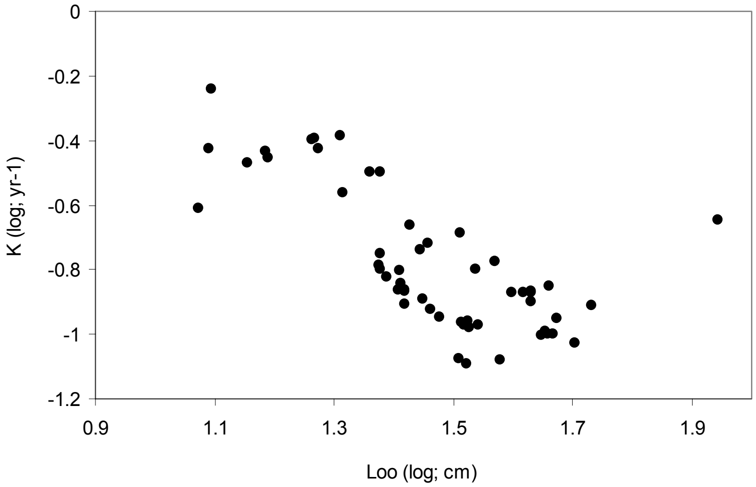

Figure 3 Plot of logK *vs*. logL_∞ for 54 Greek freshwater fish stocks.

Table 1 Parameters of the length-length relationships (Y = a+bX, in cm; TL = total length; FL = fork length; SL = standard length) of 20 Greek freshwater fish species and one hybrid in nine lakes, three rivers and two lagoons. Sex (M = males; F = females; C = sexes combined; I = immature fish); N, sample size.

Species	Area	Year	Sex	N	Y	X	b	a	Reference
Abramis brama	Lake Volvi	1989-91	C	631	TL	FL	1.102	0.8459	Valoukas and Economidis (1996)
Abramis brama	Lake Volvi	1989-91	C	74	SL	FL	0.897	-0.2175	Valoukas and Economidis (1996)
Abramis brama	Lake Volvi	1989-91	C	68	SL	TL	0.805	-0.8822	Valoukas and Economidis (1996)
Alburnus alburnus	Lake Koronia	1986-88	C	449	TL	FL	1.095	0.1606	Politou (1993)
Alburnus alburnus	Lake Koronia	1986-88	C	449	TL	SL	1.202	0.5005	Politou (1993)
Alburnus alburnus	Lake Mikri Prespa	1985	C	60	FL	SL	0.956	0.0296	Crivelli and Dupont (1987)
Alburnus alburnus	Lake Mikri Prespa	1985	C	60	TL	SL	0.944	0.0458	Crivelli and Dupont (1987)
Alosa caspia vistonica	Lake Vistonis	-	C	38	FL	TL	0.866	0.5217	Economidis and Sinis (1986)
Alosa caspia vistonica	Lake Vistonis	-	C	38	SL	TL	0.783	0.5505	Economidis and Sinis (1986)
Alosa macedonica	Lake Volvi	1978	M	123	TL	SL	1.282	-0.3980	Sinis (1981)
Alosa macedonica	Lake Volvi	1978	F	211	TL	SL	1.276	-0.3710	Sinis (1981)
Alosa macedonica	Lake Volvi	1978	C	334	TL	SL	1.272	-0.3120	Sinis (1981)
Alosa macedonica	Lake Volvi	1978	M	123	TL	FL	1.165	-0.5670	Sinis (1981)
Alosa macedonica	Lake Volvi	1978	F	211	TL	FL	1.159	-0.4960	Sinis (1981)
Alosa macedonica	Lake Volvi	1978	C	334	TL	FL	1.164	-0.5640	Sinis (1981)
Aphanius fasciatus	Messolonghi lag. (Rebakia)	1989-91	M	343	TL	SL	1.180	0.0900	Leonardos (1996)
Aphanius fasciatus	Messolonghi lag. (Rebakia)	1989-91	F	456	TL	SL	1.170	0.1130	Leonardos (1996)
Aphanius fasciatus	Messolonghi lag. (Rebakia)	1989-91	C	799	TL	SL	1.170	0.1200	Leonardos (1996)
Aphanius fasciatus	Etolikon lag. (Astrovitsa)	1989-91	M	219	TL	SL	1.190	0.0800	Leonardos (1996)
Aphanius fasciatus	Etolikon lag. (Astrovitsa)	1989-91	F	235	TL	SL	1.170	0.1200	Leonardos (1996)
Aphanius fasciatus	Etolikon lag. (Astrovitsa)	1989-91	C	454	TL	SL	1.170	0.1400	Leonardos (1996)
Aphanius fasciatus	Messolonghi lag. (Alykes)	1989-91	M	283	TL	SL	1.180	0.1200	Leonardos (1996)
Aphanius fasciatus	Messolonghi lag. (Alykes)	1989-91	F	297	TL	SL	1.190	0.0900	Leonardos (1996)
Aphanius fasciatus	Messolonghi lag. (Alykes)	1989-91	C	580	TL	SL	1.180	0.1100	Leonardos (1996)
Atherina boyeri	Lake Trichonis	1989-90	C	2575	FL	TL	0.915	0.0823	Stoumboudi *et al.* (1997)
Barbus albanicus	Lake Kremasta	1982	M	-	TL	FL	1.120	0.1380	Daoulas *et al.* (1987)
Barbus albanicus	Lake Kremasta	1982	F	-	TL	FL	0.980	2.6650	Daoulas *et al.* (1987)
Barbus albanicus	Lake Kremasta	1982	C	-	TL	FL	1.000	2.1200	Daoulas *et al.* (1987)
Barbus albanicus	Lake Kremasta	1982	M	-	TL	SL	1.190	0.3440	Daoulas *et al.* (1987)
Barbus albanicus	Lake Kremasta	1982	F	-	TL	SL	1.160	0.7700	Daoulas *et al.* (1987)
Barbus albanicus	Lake Kremasta	1982	C	-	TL	SL	1.170	0.6400	Daoulas *et al.* (1987)
Chalcalburnus belvica	Lake Mikri Prespa	1990-91	C	369	TL	FL	1.120	-0.159	Sinis and Petridis (1995)
Chalcalburnus belvica	Lake Mikri Prespa	1990-91	C	369	SL	TL	0.816	-0.164	Sinis and Petridis (1995)
Chalcalburnus belvica	Lake Mikri Prespa	1990-91	C	369	SL	FL	0.917	-0.338	Sinis and Petridis (1995)
Chalcalburnus chalcoides	Lake Volvi	1983	M	90	FL	TL	0.899	-0.0530	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Volvi	1983	F	280	FL	TL	0.913	-0.3310	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Volvi	1983	C	370	FL	TL	0.907	-0.2080	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Volvi	1983	M	90	FL	SL	1.070	0.1850	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Volvi	1983	F	280	FL	SL	1.050	0.4790	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Volvi	1983	C	370	FL	SL	1.050	0.3980	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Vistonis	1983	M	260	FL	TL	0.933	-0.3290	Kokkinakis (1992)

Table 1 continued.

Species	Area	Year	Sex	N	Y	X	b	a	Reference
Chalcalburnus chalcoides	Lake Vistonis	1983	F	253	FL	TL	0.921	-0.1080	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Vistonis	1983	C	513	FL	TL	0.926	-0.1970	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Vistonis	1983	M	260	FL	SL	1.030	0.8260	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Vistonis	1983	F	253	FL	SL	1.060	0.2940	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Vistonis	1983	C	513	FL	SL	1.050	0.5150	Kokkinakis (1992)
Knipowitschia caucasica	Evros River	1983-84	M	230	SL	TL	0.837	0.0224	Kevrekidis *et al.* (1990)
Knipowitschia caucasica	Evros River	1983-84	F	158	SL	TL	0.853	-0.0198	Kevrekidis *et al.* (1990)
Knipowitschia caucasica	Evros River	1983-84	I	9	SL	TL	0.686	0.2063	Kevrekidis *et al.* (1990)
Knipowitschia caucasica	Evros River	1983-84	C	397	SL	TL	0.847	-0.0032	Kevrekidis *et al.* (1990)
Leuciscus cephalus	Rihios Stream	1984	C	489	FL	SL	1.209	-0.2517	Neophitou (1988)
Leuciscus cephalus	Rihios Stream	1984	C	489	TL	FL	0.956	-0.3828	Neophitou (1988)
Perca fluviatilis	Lake Koronia	1975	C[1]	24	SL	TL	0.766	0.0245	Papageorgiou (1977)
Perca fluviatilis	Lake Koronia	1975	C[2]	120	SL	TL	0.853	-0.0303	Papageorgiou (1977)
Perca fluviatilis	Lake Koronia	1975	C[3]	230	SL	TL	0.886	-0.0870	Papageorgiou (1977)
Perca fluviatilis	Lake Doirani	1989-92	C	317	SL	TL	0.821	0.5710	Neophitou (1993a)
Perca fluviatilis	Lake Doirani	1989-92	C	317	FL	TL	0.977	0.6300	Neophitou (1993a)
*Phoxinellus pleurobipunctatus**	Lake Kremasta	1982	M	-	TL	FL	0.780	4.6110	Daoulas *et al.* (1987)
*Phoxinellus pleurobipunctatus**	Lake Kremasta	1982	F	-	TL	FL	0.700	6.3920	Daoulas *et al.* (1987)
*Phoxinellus pleurobipunctatus**	Lake Kremasta	1982	C	-	TL	FL	1.080	0.1530	Daoulas *et al.* (1987)
*Phoxinellus pleurobipunctatus**	Lake Kremasta	1982	M	-	TL	SL	1.160	0.4450	Daoulas *et al.* (1987)
*Phoxinellus pleurobipunctatus**	Lake Kremasta	1982	F	-	TL	SL	1.030	2.3050	Daoulas *et al.* (1987)
*Phoxinellus pleurobipunctatus**	Lake Kremasta	1982	C	-	TL	SL	1.150	0.4080	Daoulas *et al.* (1987)
Pseudorasbora parva	Lake Mikri Prespa	1990	C	245	SL	FL	0.901	0.0540	Rosecchi *et al.* (1993)
Rutilus rubilio	Lake Mikri Prespa	1985	C	60	FL	SL	0.978	0.0201	Crivelli and Dupont (1987)
Rutilus rubilio	Lake Mikri Prespa	1985	C	60	TL	SL	0.968	0.0345	Crivelli and Dupont (1987)
Rutilus rubilio X *Alburnus alburnus*	Lake Mikri Prespa	1985	C	60	FL	SL	0.970	0.0242	Crivelli and Dupont (1987)
Rutilus rubilio X *Alburnus alburnus*	Lake Mikri Prespa	1985	C	60	TL	SL	0.981	0.0290	Crivelli and Dupont (1987)
Rutilus rutilus	Lake Volvi	1978	C[4]	102	SL	TL	0.770	-0.1386	Papageorgiou (1979)
Rutilus rutilus	Lake Volvi	1978	C[5]	110	SL	TL	0.780	0.2647	Papageorgiou (1979)
Rutilus rutilus	Lake Volvi	1978	C[6]	21	SL	TL	0.810	0.0157	Papageorgiou (1979)
Rutilus ylikiensis	Lake Lysimachia	-	C	314	TL	FL	1.080	0.0880	Leonardos *et al.* (2000b)
Salaria fluviatilis	Lake Trichonis	1988-91	M	32	TL	SL	1.200	-0.0410	Psarras *et al.* (1997)
Salaria fluviatilis	Lake Trichonis	1988-91	F	159	TL	SL	1.170	0.1200	Psarras *et al.* (1997)
Salaria fluviatilis	Lake Trichonis	1988-91	C	191	TL	SL	1.180	0.0830	Psarras *et al.* (1997)
Salmo trutta fario	Aspropotamos stream	1981-82	C[7]	-	FL	SL	1.050	0.6470	Papageorgiou *et al.* (1983)
Salmo trutta fario	Aspropotamos stream	1981-82	C[8]	-	FL	SL	1.180	-1.1190	Papageorgiou *et al.* (1983)
Salmo trutta fario	Aspropotamos stream	1981-82	C[9]	-	FL	SL	1.190	-1.2360	Papageorgiou *et al.* (1983)
Scardinius erythropthalmus	Lake Kastoria	1980	C[10]	342	SL	TL	0.780	-0.0112	Papageorgiou and Neophitou (1982)
Scardinius erythropthalmus	Lake Kastoria	1980	C[11]	342	SL	TL	0.870	-0.1007	Papageorgiou and Neophitou (1982)

* referred as *Rutilus pleurobipunctatus*.

[1] TL = 80-110 mm. [2] TL = 110-150 mm. [3] TL = 150-230 mm. [4] TL<120 mm. [5] TL = 121-180 mm. [6] TL>181 mm. [7] SL<100 mm. [8] SL = 101-175 mm. [9] SL>175 mm. [10] TL<100 mm. [11] TL>101 mm.

Table 2 Biological parameters for 22 Greek freshwater fish species and one hybrid, from twelve lakes and two rivers. K in year^{-1}, L_∞ in cm, and t_0 in year, are the von Bertalanffy parameters. F, frequency of sampling (M = monthly; S = seasonal; B = bimonthly; O = one single sampling; T = two samplings; U = undefined); Sex (M = males; F = females; C = sexes combined); MEP, method used for the estimation of the von Bertalanffy parameters (FW = Ford-Walford plot: Sparre et al. 1989; R = Rafail, 1973; NL = non-linear regression; asterisk denotes that von Bertalanffy parameters were calculated in this study); L_{max} and t_{max}, maximum body length in cm and age in year respectively; SA, element used for ageing (S = scales; OB = opercular bones; V = vertebrae; FS = fin spines); L, length used for the estimation of the parameters (B = back-calculated; TL = total length; FL = fork length; SL = standard length).

Species	Area	Year	F	Sex	K	L_∞	t_0	MEP	L_{max}	t_{max}	SA	L	L_{max}/L_∞	Reference
Abramis brama	Lake Volvi	1989-91	M	M	0.102	45.2	-0.351	FW	40.5	14	S	B. FL	0.90	Valoukas and Economidis (1996)
Abramis brama	Lake Volvi	1989-91	M	F	0.094	50.7	-0.406	FW	42.2	14	S	B. FL	0.83	Valoukas and Economidis (1996)
Alburnus alburnus	Lake Koronia	1986-88	M	M	0.577	12.4	-0.153	R	11.6	4	S	B. TL	0.94	Politou (1993)
Alburnus alburnus	Lake Koronia	1986-88	M	F	0.369	15.3	-0.232	NL	14.9	7	S	B. TL	0.97	Politou (1993)
Alburnus alburnus	Lake Koronia	1986-88	M	C	0.352	15.5	-0.284	NL	14.9	7	S	B. TL	0.96	Politou (1993)
Alosa macedonica	Lake Volvi	1978	O	M	0.402	18.3	-1.270	NL*	-	-	S	B. TL	-	Sinis (1981)
Alosa macedonica	Lake Volvi	1978	O	F	0.403	18.5	-1.494	NL*	-	-	S	B. TL	-	Sinis (1981)
Alosa macedonica	Lake Volvi	1978	O	C	0.374	18.8	-1.505	NL*	33.1	10	S	B. TL	1.76	Sinis (1981)
Atherina boyeri	Lake Trichonis	1992-93	U	C	0.375	12.3	0.018	FW	11.0	4	S	B. FL	0.89	Leonardos *et al.* (1993)
Barbus albanicus	Lake Kremasta	1982	S	M	0.144	25.8	-0.805	NL*	20.1	9	OB. S	B. FL	0.78	Daoulas and Economidis (1989)
Barbus albanicus	Lake Kremasta	1982	S	F	0.083	37.9	-0.903	NL*	28.8	14	OB. S	B. FL	0.76	Daoulas and Economidis (1989)
Barbus cyclolepis[1]	Rihios stream	1984	B	C	0.168	37.1	-0.179	NL*	26.0	6	S	B. FL	0.70	Neophitou (1987)
Chalcalburnus belvica	Lake Mikri Prespa	1990-91	M	M	0.340	14.3	-1.745	NL*	13.6	4	S	B. FL	0.95	Sinis and Petridis (1995)
Chalcalburnus belvica	Lake Mikri Prespa	1990-91	M	F	0.110	33.5	-1.405	NL*	22.0	8	S	B. FL	0.66	Sinis and Petridis (1995)
Chalcalburnus belvica	Lake Mikri Prespa	1990-91	M	C	0.107	34.9	-1.257	NL*	22.0	8	S	B. FL	0.63	Sinis and Petridis (1995)
Chalcalburnus chalcoides	Lake Volvi	1983	O	M	0.128	28.1	-2.133	NL*	19.4	7	S	B. FL	0.69	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Volvi	1983	O	F	0.137	25.6	-3.218	NL*	22.5	8	S	B. FL	0.88	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Volvi	1983	O	C	0.137	26.2	-2.628	NL*	22.5	8	S	B. FL	0.86	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Vistonis	1983	O	M	0.105	33.6	-1.821	NL*	20.0	6	S	B. FL	0.60	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Vistonis	1983	O	F	0.109	32.6	-1.654	NL*	23.7	8	S	B. FL	0.73	Kokkinakis (1992)
Chalcalburnus chalcoides	Lake Vistonis	1983	O	C	0.107	33.0	-1.729	NL*	23.7	8	S	B. FL	0.72	Kokkinakis (1992)
Cyprinus carpio	Lake Vistonis	1973	O	C	0.226	88.0	-0.769	NL*	76.0	7	OB	B. TL	0.86	Tsimenidis (1976)
Leuciscus cephalus	Rihios stream	1984	U	C	0.141	45.8	-0.586	NL*	37.0	8	S	B. FL	0.81	Neophitou (1988)
Leuciscus cephalus albus	Lake Mornos	1987-88	B	M	0.182	27.9	-0.832	NL*	-	5	S	B. FL	-	Economou *et al.* (1997)
Leuciscus cephalus albus	Lake Mornos	1987-88	B	F	0.192	28.7	-0.569	NL*	-	5	S	B. FL	-	Economou *et al.* (1997)
Leuciscus 'svallize'	Lake Kremasta	1982	S	M	0.412	20.4	0.236	NL*	18.4	6	S	B. FL	0.90	Economou *et al.* (1991)
Leuciscus 'svallize'	Lake Kremasta	1982	S	F	0.317	22.9	0.112	NL*	20.8	7	S	B. FL	0.91	Economou *et al.* (1991)

Table 2 continued.

Species	Area	Year	F	Sex	K	L_∞	t_0	MEP	L_{max}	t_{max}	SA	L	L_{max}/L_∞	Reference
Perca fluviatilis	Lake Doirani	1989-92	U	C	0.317	23.9	-1.260	NL*	23.0	5	OB. S	B. TL	0.96	Neophitou (1993a)
Perca fluviatilis	Lake Koronia	1976	O	M	0.164	23.7	-0.952	NL*	-	9	S	B. TL	-	Papageorgiou (1977)
Perca fluviatilis	Lake Koronia	1976	O	F	0.150	24.5	-1.212	NL*	-	9	S	B. TL	-	Papageorgiou (1977)
Perca fluviatilis	Lake Koronia	1976	O	C	0.159	23.9	-1.086	NL*	23.0	9	S	B. TL	0.96	Papageorgiou (1977)
Phoxinellus pleurobipunctatus2	Lake Kremasta	1982	S	M	0.136	26.2	-0.640	NL*	17.6	7	OB	B. FL	0.67	Daoulas *et al.* (1987)
Phoxinellus pleurobipunctatus2	Lake Kremasta	1982	S	F	0.119	28.9	-0.748	NL*	20.1	9	OB	B. FL	0.70	Daoulas *et al.* (1987)
Pseudorasbora parva	Lake Mikri Prespa	1984-85 1991-92	U	C	0.245	11.8	-1.373	NL*	9.5	3	S	O. FL	0.81	Rosecchi *et al.* (1993)
Rutilus rubilio	Lake Trichonis	1978-79	M	M	0.124	26.2	-1.219	NL*	18.8	7	S	B. FL	0.72	Daoulas (1981)
Rutilus rubilio	Lake Trichonis	1978-79	M	F	0.113	30.0	-1.040	NL*	25.8	9	S	B. FL	0.86	Daoulas (1981)
Rutilus rubilio	Lake Pamvotis	1983-84	M	C	0.275	20.6	-1.216	NL*	20.5	8	OB	B. FL	1.00	Neophitou and Theochari (1989)
Rutilus rubilio X *Alburnus alburnus*	Lake Mikri Prespa	1985	O	C	0.157	25.7	-0.902	NL*	18.5	6	S	B. FL	0.72	Crivelli and Dupont (1987)
Rutilus rutilus	Lake Volvi	1978	O	C	0.081	33.3	-1.295	NL*	23.0	12	S	B. TL	0.70	Papageorgiou (1979)
Rutilus ylikiensis	Lake Lysimachia	-	S	C	0.084	32.3	-0.126	NL	28.5	10	S	B. FL	0.88	Leonardos *et al.* (2000b)
Salmo trutta fario	Aspropotamos stream	1981	O	C	0.218	26.7	-0.417	NL*	24.0	8	S	B. SL	0.90	Papageorgiou *et al.* (1983)
Scardinius acarnanicus[3]	Lake Trichonis-Lysimachia	1977-79	M	M	0.159	34.5	-0.155	NL*	27.0	7	S	B. TL	0.78	Iliadou (1981)
Scardinius acarnanicus[3]	Lake Trichonis-Lysimachia	1977-79	M	F	0.136	42.6	0.094	NL*	33.0	7	S	B. TL	0.77	Iliadou (1981)
Scardinius acarnanicus[3]	Lake Trichonis-Lysimachia	1977-79	M	C	0.134	42.6	0.055	NL*	33.0	7	S	B. TL	0.77	Iliadou (1981)
Scardinius acarnanicus	Lake Trichonis	-	M	M	0.126	42.8	-0.830	NL	-	-	S	B. FL	-	Leonardos *et al.* (2000a)
Scardinius acarnanicus	Lake Trichonis	-	M	F	0.134	39.7	-1.180	NL	-	10	S	B. FL	-	Leonardos *et al.* (2000a)
Scardinius acarnanicus	Lake Lysimachia	-	M	M	0.112	47.1	-0.790	NL	-	-	S	B. FL	-	Leonardos *et al.* (2000a)
Scardinius acarnanicus	Lake Lysimachia	-	M	F	0.134	41.4	-0.700	NL	-	11	S	B. FL	-	Leonardos *et al.* (2000a)
Scardinius erythrophthalmus	Lake Kastoria	1980	O	C	0.178	23.9	-0.521	NL*	18.0	7	S	B. TL	0.75	Papageorgiou and Neophitou (1982)
Silurus aristotelis[4]	Lake Trichonis-Lysimachia	1977-79	M	M	0.099	44.5	-0.305	NL*	39.0	10	FS	B. TL	0.88	Iliadou (1981)
Silurus aristotelis4	Lake Trichonis-Lysimachia	1977-79	M	F	0.100	46.4	-0.337	NL*	40.0	10	FS	B. TL	0.86	Iliadou (1981)
Silurus aristotelis[4]	Lake Trichonis-Lysimachia	1977-79	M	C	0.100	45.5	-0.321	NL*	40.0	10	FS	B. TL	0.88	Iliadou (1981)
Tinca tinca	Lake Pamvotis	1988	M	C	0.205	32.4	-0.401	NL*	29.0	10	S	B. FL	0.90	Neophitou (1993b)
Tinca tinca	Lake Vegoritis	1988	T	C	0.123	54.0	-0.790	NL*	36.6	7	OB.S.V	O. TL	0.68	Sinis et al (1999)

[1] referred as *Barbus meridionalis*. [2] referred as *Rutilus pleurobipunctatus*. [3] referred as *Scardinius erythrophthalmus*. [4] referred as *Parasilurus aristotelis*.

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ASSESSMENT OF GROWTH AND APPARENT POPULATION TRENDS IN GRAND CANYON NATIVE FISHES FROM TAG-RECAPTURE DATA[1]

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ABSTRACT

Mean growth curves and individual variation in asymptotic body length are estimated for the humpback chub (*Gila cypha*), flannelmouth sucker (*Catostomus latippinus*), and bluehead sucker (*C. discobolus*), from growth of fish tagged in the Colorado River. Age distributions for 1991-1994 are back-calculated from the individual growth curves, to provide assessments of apparent natural mortality rates and/or recruitment trends. Declines in relative abundance with age are consistent with natural mortality rates predicted from the growth parameters for populations with stable recruitment, but there are relatively more old chubs and bluehead suckers than would be expected from natural mortality rate estimates based on tag-recapture models. Either the tag-recapture methods have overestimated natural mortality rate, or chubs and bluehead suckers have had considerable decline in recruitment rates since the mid-1980s.

INTRODUCTION

Beginning in 1963, cold water releases from Glen Canyon Dam (GCD) may have caused declines in native warm-water fish species of the Colorado River, especially the humpback chub (*Gila cypha*) (listed as endangered under the US Endangered Species Act), flannelmouth sucker (*Catostomus latippinus*), and bluehead sucker (*C. discobolus*). Presumption of continued decline has prompted expensive proposals to restore more favorable physical habitat conditions for these fishes, by altering operation of Glen Canyon Dam (warm water releases, restoration of seasonality in flows, even restoration of turbidity by transport of materials past Lake Powell). Such proposals would be not only directly costly to implement, but also destructive to some ecological values that have developed in conjunction with clear, cold water releases from the dam (rainbow trout fishery, riparian bird community including peregrine falcons).

While abundances may have dropped initially after GCD was filled, there is little evidence to support claims of continued decline toward extinction. Intensive fisheries monitoring programs have been carried out by various agencies since the late 1970s, including tagging studies, size distribution monitoring, and

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[1] Cite as: Walters, C., Douglas, M., Persons, W.R., Valdez, R.A., 2006. Assessment of growth and apparent population trends in Grand Canyon native fishes from tag-recapture data. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 78-88. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

index sampling for juvenile and adult densities using various fishing gears. For most sampling sites, the size structure data show evidence of continued recruitment, and no clear trend toward larger body sizes (older fish) as would be expected from non-recruiting adult populations. There are no clear trends in the density sampling data, though changes in methods and sites make long-term comparisons suspect. Mark-recapture estimates have been obtained since the late 1980s for the humpback chub 'subpopulation' spawning in the Little Colorado River; these estimates are highly variable and show no consistent trend. Low ratios of juveniles to adults in size-frequency samples have been cited as evidence of low recruitment (Valdez and Ryel, 1995), but this ratio comparison is not valid since juveniles and adults are collected by different methods, in different habitats, with unknown differences in sampling rates (proportions of total population collected by each method).

This paper shows that tag recovery data from the 1990s are consistent with the hypothesis that chub, flannelmouth, and bluehead sucker populations are relatively stable, and are not consistent with an assumption of continued rapid population decline. The analysis is based on substantial samples of fish that were tagged and subsequently (0.5-6.8 years later) recovered for growth and survival estimation. From changes in size of these fish and the assumption that fish grow according to von Bertalanffy curves, we can back-calculate an apparent age at tagging for each individual, and construct an age distribution for each tag sample. Assuming the tagged fish were a representative sample of the population age structure (at least for older fish), the age distributions can then be compared to expected age distributions under various hypotheses about recruitment success and rate of population decline. Specifically, the age distribution data give estimates of apparent annual mortality rate, and these estimates are surprisingly close to mortality rate predictions from growth parameters (Pauly, 1980) though lower than rates estimated from tag-recapture models. Were populations declining during the 1980s, we would expect considerably higher apparent survival rates (relatively older fish and fewer young ones).

METHODS

The tag-recovery data used in this analysis are from a variety of tagging programs carried out by contractors to the Grand Canyon Monitoring and Research Center (Arizona Department of Fish and Game, Arizona State University, U.S. Fish and Wildlife Service) mainly during 1991-94, archived on a database at Arizona State University. We also analyzed much smaller data sets collected by Arizona Department of Fish and Game during the 1980s (ADFG, 1987), but do not report those results separately because sample sizes were only large enough for growth analysis and growth parameter estimates were very similar to those from the larger, more recent data set. Though fish were tagged and recovered throughout the Grand Canyon from Glen Canyon Dam to Lake Mead, most of the tagging and recovery was from in or near the mouth of the Little Colorado River (LCR). Of 9191 total chub tag recoveries in the data base, we considered 1676 records usable for the analysis (no obvious recording errors, at least one year of growth from time of tagging to recovery), along with 386 of 1127 flannelmouth sucker records (at least 6 months of growth) and 148 of 184 bluehead sucker records (again at least 6 months growth). The very large number of 'immediate' (within a few days of tagging) chub and flannelmouth recoveries were used to assess length measurement error patterns, and this assessment indicated the average measurement error for typical-sized fish (200-400 mm) was roughly 4 mm (8 mm standard deviation of differences between immediate length measurements).

Growth in length of fishes is generally very well described by a von Bertalanffy growth function of the form (Hilborn and Walters, 1992):

$$L_a = L_\infty \cdot (1 - e^{-K(a-a_o)}) \qquad \ldots 1)$$

where L_a = length at age a; a = age (years), relative to the apparent age at zero body length; a_o = age correction for non-zero length at age 0 (positive if growth is less than von Bertalanffy prediction for young fish); L_∞ = asymptotic body length (at infinite age); K = 'growth' (actually metabolism) parameter.

For analysis of tag recovery data, where fish tagged at lengths L_S are recovered after time periods T at lengths L_R, Fabens (1965) showed that the von Bertalanffy model can be written as:

$$L_R = L_S + (L_\infty - L_S) \cdot (1 - e^{-KT}) \qquad \ldots 2)$$

This equation provides a nonlinear regression model for estimation of L_∞ and K given a set of L_R, L_S observations. A key reason for the common use of Equation (2), besides allowing for variable times T to recovery, is that it expresses the growth curve in a form that does not depend explicitly on current age a, which is most often unknown. Various improvements in this method have been suggested to account for individual variation in the L_∞, K parameters, most notably an extension of the Fabens model that accounts at least for variation in L_∞ (Wang *et al.*, 1995; Wang, 1998). We tried the Wang (1998) method, but found it gave poor estimates for the nuisance parameter representing variance in L_∞. We then decided to use a modification of the Wang *et al.* (1995) maximum likelihood method, based on assuming a normal distribution of L_∞ values among individual fish. In this method, the growth observation $G_i = L_R - L_S$ for each individual i is assumed to be $G_i = (L_\infty + E_i - L_S) \cdot (1 - e^{-KT})$, which is the Equation (2) prediction, but with a mean-zero normally-distributed deviation E_i in the asymptotic size for individual i from the population asymptotic average size L_∞, i.e., $L^{(i)}_\infty = L_\infty + E_i$.

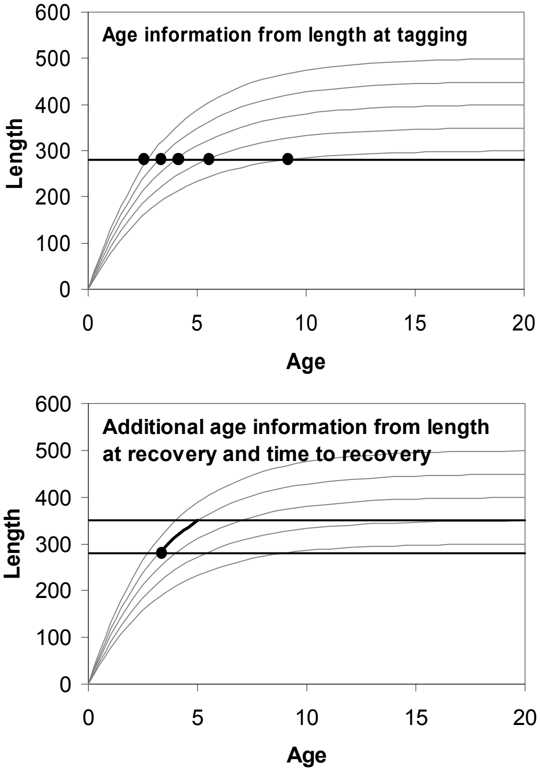

Figure 1 Illustration of how tag-recapture data can provide improved estimates of fish age. Individual variation in growth curves implies that age is highly uncertain given only length at first capture (top panel). But given length at second capture and time until that capture, the individual's growth curve and hence age can be determined much more accurately, at least for younger fish.

Additionally, for chub we constrained the estimates of L_∞, K to pass through independent estimates of age-1 length L_1 based on scale analysis and analysis of modal progression in seasonal juvenile length frequency samples (chub estimate from Valdez and Ryel, 1995). For flannelmouth suckers, we were unable to use such a constraint to improve the estimation, since we found the L_1 from modal progression analysis (around 80-90 mm) to be considerably lower than the age 0-1 growth that would be predicted from observed annual growth of tagged fish in the 200-300 mm size range (most likely ages 2-3). Here, 'constrained' means varying only L_∞ in the nonlinear growth regression, while calculating K from the relation $K = -\log(1 - L_1 / L_\infty)$.

Wang *et al.* (1995) suggest that variation among individuals in K should generally be quite small compared to variation in L_∞. If so, the apparent $L^{(i)}_\infty$ and age $a^{(i)}$ of each individual fish i can be calculated from its L_S, L_R data and K using the following relationships derived from Equations (1) and (2), provided the population K and L_∞ are known:

$$L^{(i)}_\infty = L_\infty + E_i = L_S + (L_R - L_S)/(1 - e^{-KT}) \qquad \ldots 3)$$

$$a^{(i)} = -(1/K)\log(1 - L_S/L^{(i)}_\infty) \qquad \ldots 4)$$

Note here that errors in estimation of K will tend to cause ages for all individuals to change in the same way (K too low causes all ages to be too high, K too high makes all fish look too young). Equations (3) and (4) essentially provide an individual-based 'age-length key' for converting length to age, given information from growth after initial tagging about individual variation in L_∞. This age calculation is illustrated in Figure 1, which shows how large age uncertainty given only L_S 'shrinks' when additional information (G_i, T) is provided about the individual's $L^{(i)}_\infty$.

The 'age' distribution sample resulting from application of Equations (3) and (4) can be expressed as estimated age proportions p_a of the sample ($p_a = n_a/n$, n_a = estimated number of age a fish and n = sample size). For further analysis, we need to make some assumptions or alternative hypotheses about the population proportions P_a from which the p_a were sampled. We note that these population proportions are

$P_a = v_aN_a/(\Sigma v_aN_a)$ ... 5)

where v_a is an age-specific vulnerability to sampling. That is, P_a is the vulnerable number v_aN_a of age a fish in the population, divided by the total vulnerable population size summed over ages, Σv_aN_a. Based on inspection of the data and discussions with experienced Grand Canyon scientists about how fish shift their distributions and become vulnerable to sampling as they grow, we assume that vulnerability v_a increases asymptotically from 0 to 1.0 with age, according to a sigmoid function. For convenience, we assume the following form:

$v_a = a^v/(a_h^v+a^v)$ ... 6)

where a_h is age at 50 % vulnerability (age where v = 0.5) and the power parameter v represents steepness of the sigmoid function (high v values imply a steeper, more 'knife-edged' vulnerability curve around the age a_h). Luckily, we found the results presented below to be largely insensitive to choices a_h and v. Thus, and for maximum likelihood analysis, we elected to assume $v_a = 0$ for ages 0 and 1, and $v_a = 1$ for ages 2 and older (4 and older for bluehead sucker); this simplification can cause modest underestimation of mortality rates and hence favor the hypothesis that population size has been declining (see below).

In a stable population with annual age-independent survival rate S ($= e^{-M}$, where M is the annual instantaneous natural mortality rate), it is easy to predict the N_a of Equation (5). These should be related according to

$N_a = N_1S^{a-1} = N_1e^{-M(a-1)}$ ... 7)

where N_1 is average age 1 recruitment. We can take $N_1 = 1$ without loss of generality since absolute numbers cancel in the calculation of P in Equation (5). In contrast, for a population that is growing or declining exponentially at annual rate r ($N_{t+1} = N_te^r$), the N_a should be related by

$N_a = N_{a-1}Se^{-r} = N_{a-1}e^{-M-r}$ ... 8)

i.e., abundances at successive ages should contain effects of both survival rate and population growth. The apparent survival rate (N_a/N_{a-1}, P_a for high a) from an age composition sample will be higher than S if the population is declining (r<0). If we examine only data for 'fully recruited' ages ($v_a = 1$, $a \geq a_{min}$), eqs. (7) and (8) imply that the stable age proportions should vary as $P_a = e^{-(M+r)(a-amin)}(1 - e^{-M-r})$ if age is treated as a discrete variable, or $P_a = e^{-(M+r)(a-amin)}(M + r)$ if age is treated as continuous (here the terms $1 - e^{-M-r}$ and M+r represent the sum and integral of N_a over ages).

For initial analyses of age vulnerability patterns, we defined a simple sum of squares criterion to compare goodness of fit of alternative hypotheses about P_a to the estimated age proportions p_a:

$SS = \Sigma_a(p_a - P_a)^2$ ... 9)

We then used a simple search procedure (Solver in Microsoft Excel) to search for estimates of annual survival rate S and the vulnerability parameters a_h and v that would minimize SS, with P_a calculated using the stable population 'null' predictions of N_a from Equation (7). This approach allows definition of at least ranges of S that would predict sample age proportions anywhere near the estimated ones, and it indicated that the assumption of 'knife-edge' selection ($v_a = 1$, $a \geq a_{min}$) is reasonable for the chub and flannelmouth data. S estimates much higher than obtained by other methods would imply r<<0, i.e., the sample p_a had come from a declining population (or some unknown problem with those independent estimates of S). S estimates much lower than from other methods might indicate an increasing population, but might also indicate some decrease in vulnerability of larger, older animals to tagging or recapture (failure in monotonic vulnerability assumption, Equation (6)).

Using the above relationships and an approach suggested by Wang *et al.* (1995), we then developed likelihood functions for the (L_S, G) data in relation to the parameters L_∞, K and Z = M + r (Appendix 1). These functions involve transformation from assumptions about the random variables E_i and age at capture, for which we can make reasonable statistical assumptions (E_i normal, age at capture sampled from exponential proportions at age), to the (L_S, G, T) data. Various simplified sum of squares and reduced likelihood functions for fitting the data were also tested for accuracy and bias using Monte Carlo procedures (Appendix 2), and these generally gave similar results for the relatively large sample sizes available for analysis.

Monte Carlo tests of the likelihood estimation procedure indicate that it is quite robust to errors in measurement of individual fish lengths and to variation among individuals in the growth K parameter. These sources of variation apparently do not cause bias in estimates of population mean growth parameters K and L_∞ , or apparent total mortality rate Z, though they do cause considerable variation in estimated ages for older fish (Figure 2).

A key advantage of the likelihood approach is that it allows use of Bayesian assessment methods to provide probability distributions for the parameters, integrating uncertainty over sample variation in individual growth rates and over a range of possible estimates for the auxiliary data L_1. This method gives a more conservative assessment of statistical uncertainty (wider statistical limits) than would simpler approaches like bootstrapping, since there is no simple way to include uncertainty about L_1 in such procedures. Standard Bayes techniques (Gelman *et al.*, 1995) and derivations in Walters and Ludwig (1994) imply the marginal likelihood integrated over the 'nuisance' variance of E_i, should be proportional to the log(l) derived in Appendix 1. Summing such likelihood values over a numerical grid of (L_∞, Z, K) values gives an approximate marginal likelihood of the data given each parameter; this 'likelihood profile' can be treated as a posterior probability distribution for the parameter, in essence assuming a flat (uninformative) prior for it. In intuitive terms, the marginal distribution for Z is wider than it would be if we estimated Z only from apparent age composition estimated using only the most likely K, L_∞, since the marginal distribution accounts for uncertainty in these parameters as well.

RESULTS

Results from fitting the growth data are presented in Table 1 and Figures 3-4. Despite much obvious variation in measured growth rates, the maximum likelihood method gives a reasonably good fit to the overall growth rate *vs.* length at tagging relationship (Figure 3). There is not much indication of nonlinearity in this relationship (which would invalidate the von Bertalanffy model), though there is apparently high variation in individual asymptotic lengths. Reconstructed age-size observations (Equation (4) ages) also show reasonable fits to the von Bertalanffy model (Figure 4), with the caveats that

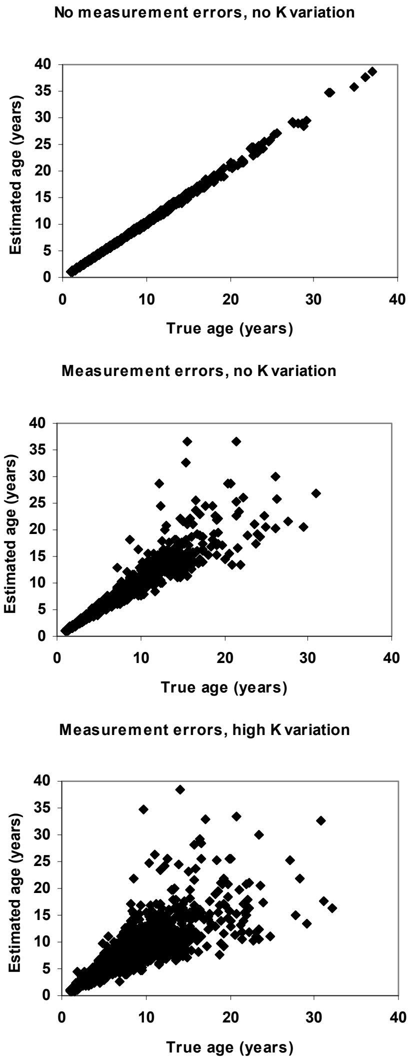

Figure 2 Simulated effect of estimation and measurement errors on true *vs.* calculated ages of individual fish, assuming sample size of 100 fish used in estimation of population mean K, L_∞. Simulated data generated using standard deviation of 60 mm among individual L_∞ values. First panel shows that even this high growth variation does not cause bias or appreciable error in age estimation (variation due solely to variation in estimates of population K, L_∞). Second panel shows spread in estimated ages, especially for older fish, caused by having length measurement errors with 4 mm standard deviation at each capture (observed standard deviation in measurements of individual fish recaptured within a few days after tagging). Third panel shows additional spread caused by having both measurement errors and variation in individual K values; individual K values assumed to have multiplicative normal variation with a coefficient of variation of 0.5 (somewhat higher than estimated for individual fish that were captured more than once).

(1) samples for younger ages are missing (except for L_1 constraint mentioned above), and (2) the flannelmouth data suggest lower growth rate for at least the first year of life than predicted by the von Bertalanffy model for older fish. Marginal probability distributions for the parameters (Figure 5) indicate that L_∞ and K are fairly well determined for all three species, though there is more uncertainty for bluehead sucker due to smaller sample size and lack of smaller fish in the tag sample. Estimated K parameters (Table 1) and natural mortality rates calculated from K, L_∞, and average water temperature (10°C, mean mainstem Colorado temperature below Glen Canyon Dam) using the Pauly (1980) equation are reasonable for fish that have been called relatively long-lived and slow-growing.

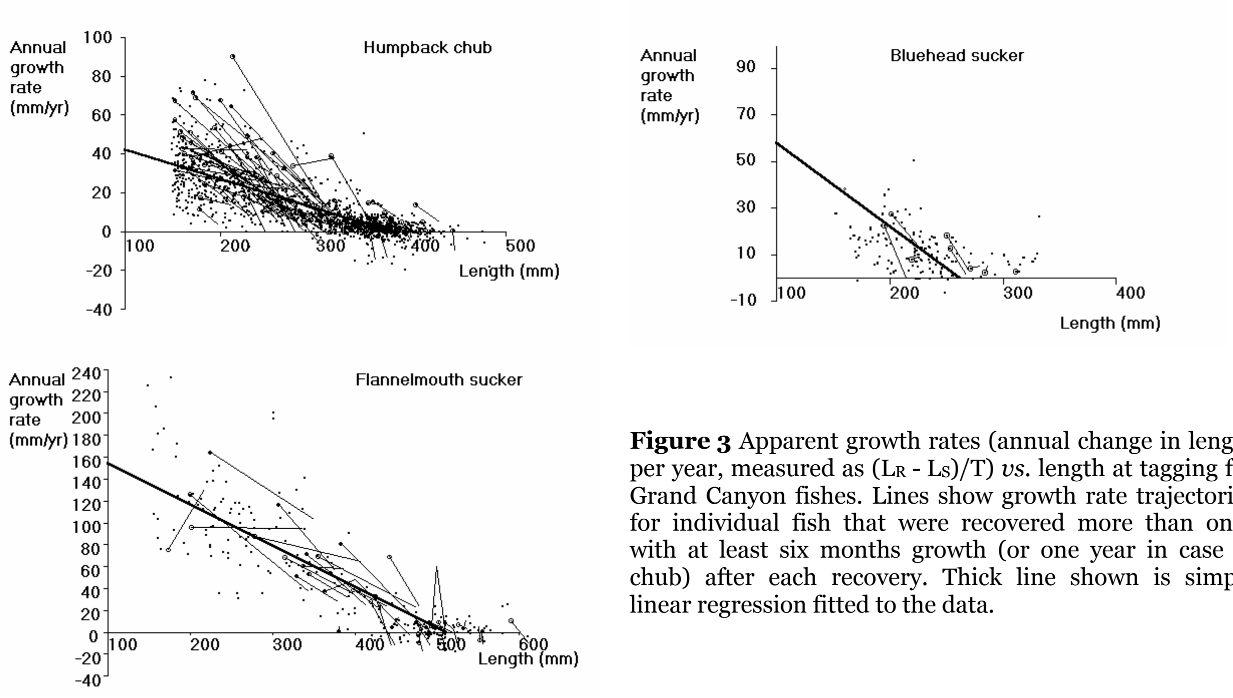

Figure 3 Apparent growth rates (annual change in length per year, measured as $(L_R - L_S)/T$) *vs.* length at tagging for Grand Canyon fishes. Lines show growth rate trajectories for individual fish that were recovered more than once with at least six months growth (or one year in case of chub) after each recovery. Thick line shown is simple linear regression fitted to the data.

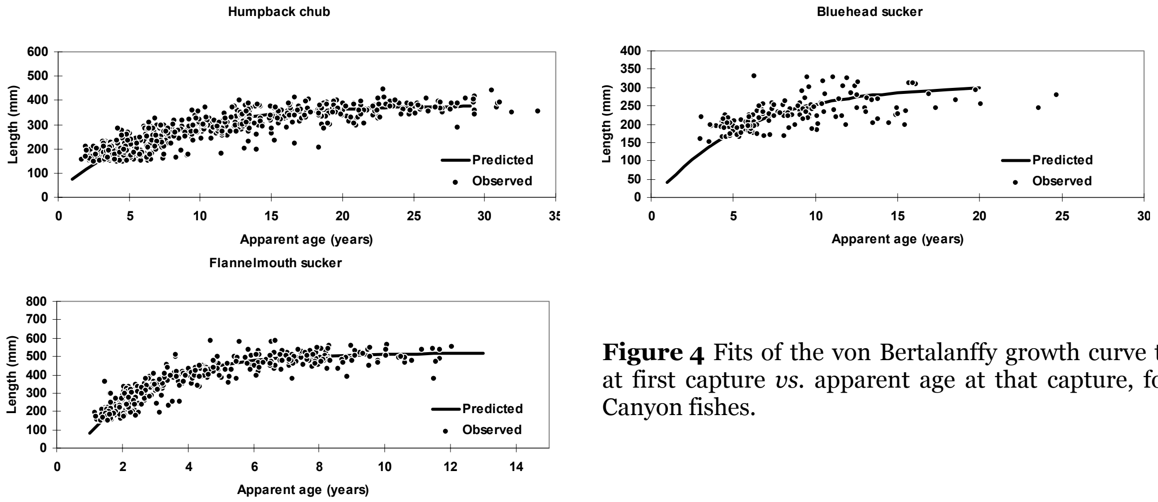

Figure 4 Fits of the von Bertalanffy growth curve to length at first capture *vs.* apparent age at that capture, for Grand Canyon fishes.

Growth rate *vs.* length trajectories for individual fish that were recaptured more than once (Figure 3) indicate some violation of the assumption that all fish have the same growth K parameter. There are not enough multiple recaptures for detailed analysis of variation in K among individuals; for chub and flannelmouth, individual K estimates from growth rate *vs.* length regressions have a coefficient of variation of about 0.3, which is enough to cause considerable random error in age estimation for older fish (Figure 2) but not enough to cause bias in Monte Carlo tests of mortality rate estimation. For chub and bluehead sucker, there is a worrisome tendency for fish recaptured a second time less than 1 year after initial capture to show considerably lower growth rate after the second capture (apparent high K values), indicating a possible short-term effect of handling on growth rate.

Table 1 Estimates of growth parameters and natural mortality rate. G-L regression estimates of K and L_∞ are from simple linear regression of annual growth rate ($(L_R - L_S)/T$) on length at tagging; growth likelihood estimates of these parameters are from likelihood function for growth ($L_R - L_S$) only. Total likelihood estimates are with the likelihood function derived in Appendix 1. Regression estimates of apparent total mortality rate (Z) are slopes of fitting numbers at age to the exponential decay model $N_a = N_0e^{-Za}$.

Parameter	Estimation procedure	Humpback chub	Flannelmouth sucker	Bluehead sucker
K	G-L regression	0.15	0.38	0.089
	Growth likelihood	0.16	0.41	0.32
	Total likelihood	0.22	0.46	0.34
L_∞	G-L regression	381	512	355
	Growth Likelihood	387	522	280
	Total Likelihood	376	538	262
Z ($S = e^{-Z}$)	Age regression	0.11	0.22	0.40
	Total Likelihood	0.12	0.32	0.37
	Pauly (1980)	0.16-0.18	0.27-0.31	0.14-0.30

Apparent age distributions are presented in Figure 6, with 'best fit' predicted population proportions P_a based on maximum likelihood estimates of apparent total mortality rate Z = M+r. A good visual fit is not expected for such distributions, since the sample sizes for p_a are small. The estimates of Z are relatively insensitive to uncertainty about the K, L_1, L_∞ estimates used to reconstruct apparent individual ages (see marginal probability distributions, Figure 5). The Z estimates can also be made to vary by about 0.02-0.05 by changing the minimum age included in mortality rate estimates (younger ages apparently less vulnerable at least for chub and bluehead). These sensitivity tests all indicate that M, or more precisely the sum M+r, is fairly well determined by the data. Note, in Figure 6, that the humpback chub age distribution appears to have systematic underrepresentation of younger ages and overrepresentation of older ages, hinting at possible recruitment decline over time. Chub age proportions by year of tagging also suggest possible decline in relative abundance of young (< 7 year old) fish from 1991 to 1994 (Figure 7), especially when sample sizes are inflated by including all fish with time to recapture > 0.5 year.

Table 1 also reports independent estimates of natural mortality rate M from tagging studies during the 1990s. Note that for chub and bluehead sucker, the best fitting M is considerably lower than these independent estimates. Taken at face value, comparing these M estimates to the best fit Z values would indicate stability for flannelmouth sucker (or perhaps a slight annual decline), but possibly rapid decline for humpback chub and bluehead sucker. However, the Z estimates are close to estimates of M from the Pauly (1980) equation for all species.

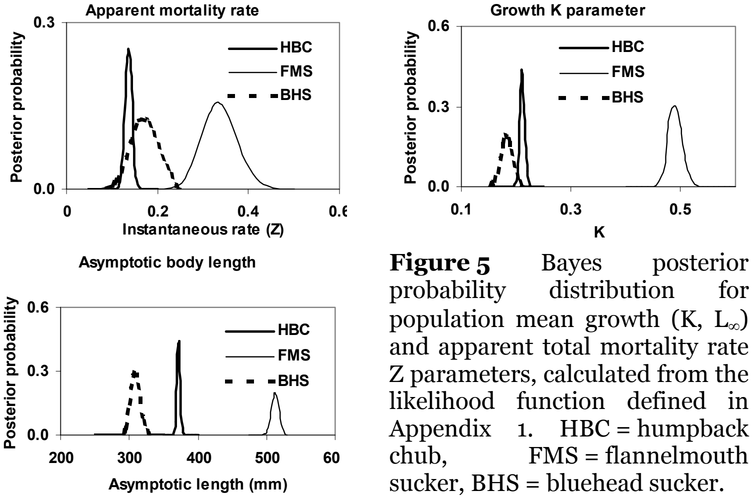

Figure 5 Bayes posterior probability distribution for population mean growth (K, L_∞) and apparent total mortality rate Z parameters, calculated from the likelihood function defined in Appendix 1. HBC = humpback chub, FMS = flannelmouth sucker, BHS = bluehead sucker.

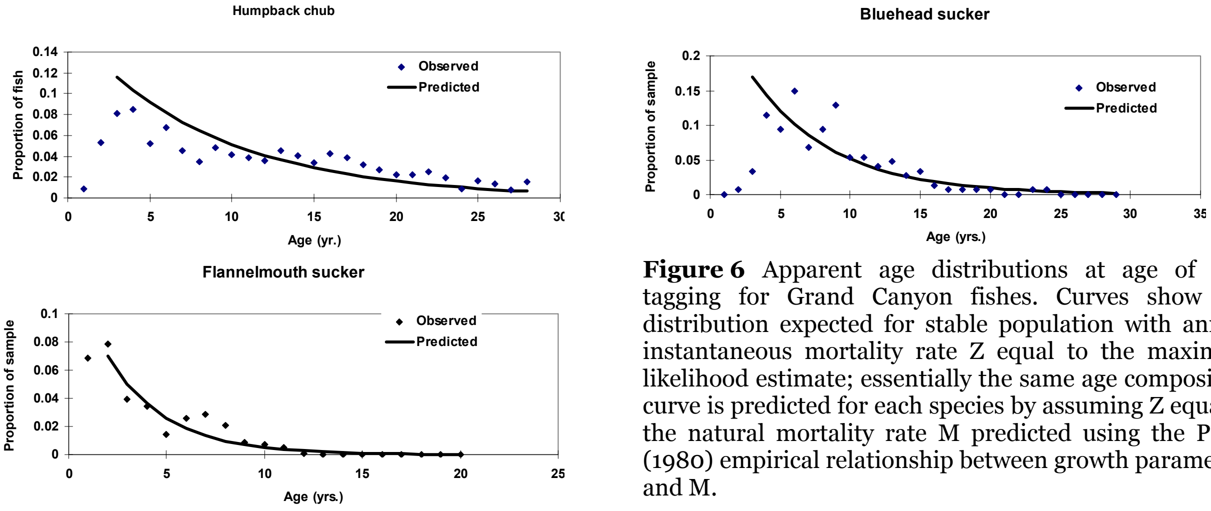

Figure 6 Apparent age distributions at age of first tagging for Grand Canyon fishes. Curves show age distribution expected for stable population with annual instantaneous mortality rate Z equal to the maximum likelihood estimate; essentially the same age composition curve is predicted for each species by assuming Z equal to the natural mortality rate M predicted using the Pauly (1980) empirical relationship between growth parameters and M.

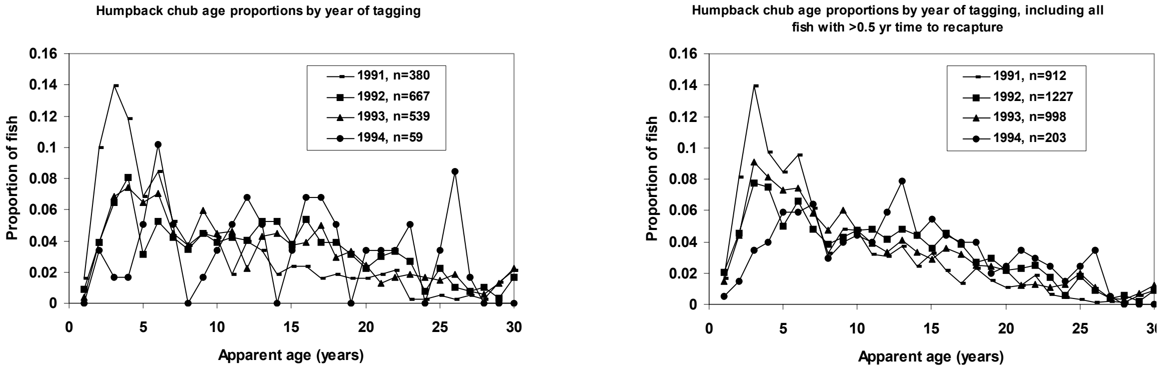

Figure 7 Apparent age distributions at age of first tagging for humpback chub, separated by year of tagging. Note apparent scarcity of younger fish after 1991, especially for larger sample created by including all fish with >0.5 year time to recapture (rather than 1 year to recapture).

DISCUSSION

Observed patterns of growth rate *vs*. length at tagging (Figure 3) leave little doubt that relatively large numbers of old fish were sampled for tagging. Far more old fish were tagged than would be expected from the low annual survival rates estimated by mark-recapture models (see Table 1), if the populations were stable. This means that the overall results of our analysis can be interpreted in at least three ways:

1. *Stable population hypothesis*: tagged fish were representative of population age composition, mortality rates are low as predicted from the Pauly (1980) relationship between mortality rate and K, L_∞, and the mark-recapture survival estimates have provided underestimates of survival for some reason;

2. *Nonrepresentative sampling hypothesis*: populations are stable, with higher mortality rates than predicted by the relationship of Pauly (1980), but younger fish were underrepresented in collecting fish for tagging due to ontogenetic differences in habitat preference;

3. *Declining populations hypothesis*: age composition sampling was representative and survival rates are low, but there are relatively few young fish in the populations due to declining recruitment.

We know of no other instance where the Pauly relationship has so grossly underestimated natural mortality rate for a species with low K as to lend credibility to hypotheses (2)-(3), and there is no evidence from analysis of length-frequency samples of smaller fish that growth rates (and hence K) are much higher than we have estimated. In fact the opposite appears to be the case for flannelmouth suckers; juveniles rearing in shoreline/backwater refuge areas appear to have lower first year growth rates than predicted by the von Bertalanffy model.

It is obviously frustrating to be unable to make a more definitive statement about population trends, but uncertainties about natural survival rates and age-selectivity in sampling make this impossible. However, it is clear from the distributions of apparent ages that all three populations were achieving at least some recruitment well after construction of GCD; most of the fish tagged were almost certainly less than 20 years. old, implying they were recruited well after construction of GCD. That is, growth of tagged fish implies that adult size distributions cannot be interpreted simply as closed cohorts of old fish left over from healthy populations prior to GCD, though such closed cohorts apparently still exist in a few locations.

It is understandable that Grand Canyon policy has been to avoid killing any native fishes for direct analysis of age and growth. There will likely be continued reliance on analysis methods based on tag recovery and size distribution data. But these methods cannot be tested and improved much without eventually: (1) killing a few fish for validation of age estimates based on eq. (3)-(4); (2) including more small fish (<200 mm) in the tagging programs even if tagging these fish causes a relatively high mortality risk; and (3) evaluation of possible reasons for underestimation of survival rate from mark-recapture methods.

The estimates of apparent age indicate that analysis of the adult size distribution alone will not provide a reliable index of changes in mortality and recruitment rates. Age estimates vary widely among individuals of any adult length interval, i.e., growth rates vary widely among individuals so that length alone is a very poor predictor of age. This means that length frequency distributions can appear stable on time scales of a decade or more, even if there were nearly complete recruitment failure. It is essential to continue gathering age composition information either by direct age sampling, or by methods like the tagging-based procedure described here. If tagging is continued, considerably more care should be taken to avoid the large measurement errors evident from comparing recorded lengths of fish recovered immediately after tagging (see Figure 2, top two panels).

A very interesting feature of the flannelmouth data is the discrepancy between first year growth rate measured from length-frequency sampling of shoreline habitats *vs.* the substantially higher predicted age 0-1 growth given growth, performance of older tagged fish. It appears that warmed shoreline-backwater areas are either not adequate to insure ‘normal’ first year growth in the face of the unnaturally cold waters that first year juveniles must often face (while dispersing to warm areas, and when such areas are flushed by flow changes), or that first year juveniles are driven to use relatively poor shoreline growth habitats by some other factor such as predation risk. Interestingly, rainbow trout (*Oncorhynchus mykiss*) just below GCD have similar, strong ontogenetic habitat shifts and also display lower first year growth than would be expected from growth rates of older fish. It is difficult to see why juvenile rainbows would concentrate in shoreline areas except to avoid predation risk, since there are large offshore areas of relatively slow water and shoreline areas have relatively low food concentrations due to diurnal water level fluctuation associated with operation of GCD.

It would not be necessary to seek indirect evidence of population trend from age composition data if reliable methods could be developed for direct assessment of changes in relative abundance over time. Unfortunately, past sampling and abundance index programs have specifically targeted sites where biologists expected to catch fish, and this could easily lead to ‘hyperstability’ (Hilborn and Walters, 1992) in catch rate indices (catch rates remaining high in preferred habitats despite population declines). It may be impractical with existing sampling methods to regularly visit enough additional sampling sites to avoid this problem in the future. If adaptive, experimental management programs are developed for GCD that involve comparing relative abundance trends under alternative water management regimes, a critical research investment prior to implementing such programs should be in development of better abundance indexing procedures for large, turbid rivers. For example, side-scan sonar now being used in the Canyon for geomorphology monitoring (sand accumulation on the river bottom) might be adapted to ‘count’ fish over long river reaches.

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APPENDIX 1. COMBINED LIKELIHOOD FUNCTIONS FOR GROWTH AND SURVIVAL PARAMETERS

Suppose a sample $i = 1 \ldots n$ fish of ages $a_i \geq a_{min}$ has been gathered from a population with a stable age distribution under population growth rate r and age-independent natural mortality rate M, hence displaying the apparent mortality rate $Z = M + r$. This population should have age proportions $P(a) = e^{-Z(a-amin)}(1 - e^{-Z})$ if ages are discrete, or $P(a) = e^{-Z(a - amin)} Z$ if ages are continuous (recruitment is a continuous process). These expected values for P(a) hold whether or not there has been historical random variation in recruitment. Assume each of these fish grows according to a von Bertalanffy growth curve with common K but individual asymptotic length $L^{(i)}_\infty = L_\infty + E_i$, where the E_i are normally distributed with mean 0 and variance σ^2: $p(E) = (2\Pi\sigma^2)^{-1/2}\exp(-E^2/2\sigma^2)$. For each fish, we observe the length at first capture L_S and growth $G = L_R - L_S$ over an arbitrary period T until it is next recaptured. To construct a likelihood function for these (L_S,G) observations, we need to express them in terms of the probability statements P(a) about age and p(E) about E. That is, we need to transform the probability distributions from (a, E) to (L_S, G). Assuming L_S and G are independent, this transformation gives the likelihood of a given observed combination. The transformation can be expressed as

$$l(L_S,G|\ L_\infty,K,M) = \Pi_i P(a_i)p(E_i)||J_i||^{-1} \qquad \text{... A1)}$$

In this likelihood function, each a_i is calculated as $a_i = -(1/K)\log(1 - L_S/L^{(i)}_\infty)$, i.e., by eqs. (3)-(4), and each E_i is calculated as $E_i = G_i/(1 - e^{-KT}) + L_S - L_\infty$. The term) $||J_i||^{-1}$ is the absolute value of the Jacobian of the transformation from (a,E) to (L_s,G), and it is given for each observation by $||J_i||^{-1} = KL^{(i)}_\infty\, e^{-K(ai - ao)}H_i$ where $H_i = 1 - e^{-KT}$. Note that $l(L_S,G|\ L_\infty, K, Z)$ depends on the parameters L_∞, K, and M in a complex, nonlinear way through the effect of the parameters on a_i and E_i, so we must expect to use numerical search procedures to find maximum likelihood estimators and/or posterior probability distributions for the parameters.

For maximum likelihood estimation it is generally easier to work with $\log(l)$. Taking the logarithm of $l(L_S,G|\ L_\infty, K, M)$ above, discarding constant terms that do not affect the maximization (or Bayesian analysis), and evaluating the nuisance parameter σ^2 at its maximum likelihood estimate $s^2 = \Sigma_i E^2_i/n$ conditional on the other parameters, we obtain the reduced log-likelihood function:

$$\log(l) = -(n/2)\log(s^2) - \Sigma_i \ln(H_i) + n\log(Z/K) - Z\Sigma_i(a_i - a_{min}) - \Sigma_i \log(L^{(i)}_\infty) + K\Sigma_i(a_i - a_o) \qquad \text{... A2)}$$

For analysis of growth data only (estimation of K and L_∞ without assuming that a random sample of the population age composition was obtained), the appropriate reduced log-likelihood function is just the first two terms of log(*l*); log(*l*) is actually quite simple to calculate in a spreadsheet format, and to maximize using spreadsheet functions like Excel's Solver: (1) enter the L_S, G, T data in columns and define cells for the parameters L_∞, K, Z; (2) calculate a column of E_i values (from $E_i = G_i/(1 - e^{-KT})+L_S - L_\infty$) and a column of $L^{(i)}{}_\infty = L_\infty+E_i$ values from the parameter values; (3) calculate the sum terms (s^2, etc.) of log(*l*) using the spreadsheet SUMPRODUCT function; and (4) assemble these terms into the log(*l*) formula.

K can be eliminated from the likelihood function above by assuming mean length at age 1, L_1 is measured exactly so $K = -\log(1 - L_1/L_\infty)$. But uncertainty in the independent estimate of L_1 can be easily incorporated in log(*l*), if it is assumed that the estimate has a normally distributed error with known standard deviation σ_1. Simply subtract the term $(L^*_1 - L_1)^2/(2\sigma_1{}^2)$ from log(*l*), where $L^*_1 = L_\infty(1 - e^{-K})$. Then assuming a very small σ_1 (L_1 known perfectly) becomes equivalent to removing K from the estimation by calculating it as $-\log(1 - L_1/L_\infty)$.

A 'pathology' can arise in maximization of log(*l*) when the number of young fish (just above age a_{min}) in the sample differs considerably by chance or age sampling bias from the number expected under exponential decline. In such cases, log(*l*) can be made larger just by increasing K so as to drive apparent ages a_i of such young fish below the cutoff age a_{min} for inclusion in the mortality components of the likelihood function.

APPENDIX 2. MONTE CARLO TESTS OF ESTIMATION METHODS

We conducted a variety of Monte Carlo simulation tests to evaluate possible biases in the estimation procedures. Each test consisted of generating 1000 samples of 300 fish each, doing the estimation procedures on each sample, and tabulating mean and variance of parameter estimates over the samples. Each fish was assigned an age at capture from a stable (exponential) age distribution with minimum capture age 4 years, and a normally distributed $L^{(i)}{}_\infty$ (most tests used a standard deviation of 60 mm, roughly what we estimated for the actual data). For some tests, each individual was also assigned a unique $K^{(i)}$, normally distributed around the population K for that test. Times to recapture were simulated as uniform over the interval 0-3 years. Simulated 'true' individual sizes at marking and recapture were calculated with the von Bertalanffy model from the assigned ages, $L^{(i)}{}_\infty$, and $K^{(i)}$, without measurement errors. Normally distributed random measurement errors were added to the true L_S and L_R values for each fish to generate 'observed' sizes.

The simulation tests revealed a number of potential biases. First, the maximum likelihood estimates of L_∞ are biased slightly (5%) downward, and K given L_1 is biased upward by the same relative amounts when age at first capture is high ($a_{min} = 4$). These biases can only be corrected by reducing the age at first capture and/or providing very precise values of L_1. Second, K is much more likely to be pathologically overestimated (see Appendix 1), and L_∞ underestimated, when independent information about L_1 is ignored, unless age at first capture is reduced to 1 year. This effect was also seen in the original data analysis, and reflects lack of information about K when only older fish are included in the sample. Third, estimates of Z are biased slightly upward (5%) so natural survival rate S is biased slightly downward (e.g., 0.76 when should be 0.78, 0.90 when should be 0.91). Since our main concern here is about apparent survival rates, this bias could tend to mask effects of negative population r values (i.e., make population appear stable when in fact it is actually declining slowly). Fourth, individual $K^{(i)}$ can vary with a standard deviation of up to 0.1 around a mean of 0.2 without causing bias in the growth and survival parameter estimates, though higher K variation of course causes increased variation in the parameter estimates (higher apparent variation in $L^{(i)}{}_\infty$, K, and S). Fifth, including Lee's phenomenon effects in the fake data (decreasing mean $L^{(i)}{}_\infty$ with increasing age) causes downward bias in $L^{(i)}{}_\infty$ and in estimated survival rate. Sixth, measurement errors of the magnitude apparent in the data can badly bias the estimates, unless the data are 'censored' to eliminate individuals with low T (<0.5 year.) and negative observed growth G. Censoring the data by eliminating such individuals does not cause any obvious bias in the estimated growth and mortality parameters, which is a bit surprising considering that older individuals are more likely to display negative apparent G and hence to be omitted from the analysis. Finally, distributions of L_∞ estimates have shapes and variances quite close to the posterior distributions calculated using Bayesian methods, though with slightly smaller variances due to not explicitly considering uncertainty about L_1.

EFFECTS OF LAKE AND POND AERATION ON FISH GROWTH AND RELATED PROCESSES[20]

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ABSTRACT

The basic principles of the growth of fish (and aquatic invertebrates) are recalled, with emphasis on the fact that oxygen, while continuously required for maintenance, cannot be stored for later use. Hence the rate at which oxygen is extracted via the gills and transported into the body of fish limits, at any time, their scope for activity, growth and food conversion efficiency. This is shown to be consistent with the increased growth and food conversion efficiency observed by aquaculturists who aerate their ponds. Some implications for aeration of larger water bodies, such as lakes and reservoirs, are presented.

INTRODUCTION

The following is a brief presentation of a theory, elaborated in more detail in Pauly (1979, 1981, 1984, 1986, 1998) and in Longhurst and Pauly (1987) of how fish grow. Emphasis is given to the fact that it explains some of the observed direct and indirect effects of pond aeration on fish growth and related processes (Loyacana, 1974; Hollerman and Boyd, 1980), and that it can be used to predict some of the effects of aerating larger water bodies such as lakes and reservoirs.

This theory applies to any submerged animal breathing through gill; the example presented below refers to fish in the narrow sense (i.e., to teleosts), although the principles it illustrates also apply to other fishes and aquatic invertebrates (see Pauly, 1998). We shall assume for simplicity's sake that fish consist of, and feed, only on proteins. The theory presented below can accommodate more realistic body composition and diets (van Dam and Pauly, 1995), but dealing with this does not change its main points.

THEORY OF FISH GROWTH

Fish are aerobic heterotrophs – with some exceptions, such as common carp (*Cyprinus carpio*), which may operate anaerobically at very low temperatures, a feature which is not a concern here.

As fish feed, their food is assimilated i.e., broken down into amino acids; part of the amino acid pool is oxidized, and the energy thus bound used to form ATP, used for activity (i.e., muscle contraction), and, along with building blocks drawn from the amino acid pool, used for synthesis of native protein.

This synthesis is required for net growth, but also, even more importantly, for replacing proteins that have spontaneously denatured (i.e., lost their quaternary and tertiary structures). Such spontaneous denaturation – a mildly exergonic reaction requiring neither O_2 nor ATP – is a characteristic of live proteins. Indeed, it expresses a basic feature of life itself: that living organisms will spontaneously decay, i.e., fail to maintain their structure integrity unless entropy is 'pumped out' (Schrödinger, 1944).

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[20] Cite as: Pauly, D., 2006. Effects of lake and pond aeration on fish growth and related processes. *In*: Palomares, M.L.D., Stergiou, K.I., Pauly, D. (eds.), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14(4), pp. 89-95. Fisheries Centre, University of British Columbia [ISSN 1198-6727].

Important here are:

- That the rate of spontaneous denaturation of proteins can be assumed proportional to protein mass (i.e., roughly proportional to body weight); and
- That this rate of spontaneous denaturation, being due to thermally-induced vibrations of protein molecules, increases with temperature, with a Q_{10} usually ranging from 2 to 4 (Winberg, 1971; Regier *et al.*, 1990).
- That the relation between the metabolic rate of fish and water temperature is reasonably well described by Krogh's 'normal curve' (Table 1).

Protein synthesis as mentioned above requires O_2 to be where needed (in cells' mitochondria); for this to be the case O_2 must have been brought in via the circulatory system, through the gills from the water surrounding a fish. Transfer of O_2 through the gills of fish follows Fick's Law:

$$Q = dP \cdot G \cdot U / WBD \qquad \ldots 1)$$

where Q is the O_2 uptake (e.g., $ml \cdot hour^{-1}$), dP is the O_2 pressure difference on either side of the gill membrane (in atm), G is the respiratory area of the gills (total area of respiratory lamellae), U is Krogh's diffusion constant, i.e., the quantity of O_2 (in ml) which diffuses through an area of 1 mm^2 in one minute for a given type of tissue when the pressure gradient is one atm O_2 μ^{-1}, and WBD is the water-blood distance, i.e., the thickness of the membrane separating water and blood, in μ (Hughes and Morgan, 1973; Hughes, 1984).

Table 1 Values of the temperature (t) correction factor (*q*) for converting respiratory rates to 20°C, according to the 'normal curve' of Krogh (1914) (from Winberg, 1971).

t	*q*	t	*q*	t	*q*	t	*q*
5	5.19	12	2.16	19	1.09	26	0.609
6	4.55	13	1.94	20	1.00	27	0.563
7	3.98	14	1.74	21	0.920	28	0.520
8	3.48	15	1.57	22	0.847	29	0.481
9	3.05	16	1.43	23	0.779	30	0.444
10	2.67	17	1.31	24	0.717	-	-
11	2.40	18	1.20	25	0.659	-	-

Of the four parameters which influence Q, only G varies with body weight (W), i.e.,

$$G = a \cdot W^d \qquad \ldots 2)$$

where 'a' is a multiplicative factor used here as 'gill area index', and 'd' is an exponent ranging in fish between 0.50 (in cyprinodonts, Winberg, 1961) and 0.95 (in tuna, Muir and Hughes, 1969), but never reaching unity, at least not in well-studied cases covering a wide range of body weight.

Thus, gill surface area can be expected to be a key variable when attempts are made to explain the wide difference of growth performance occurring among species of fishes.

This can be shown by using the parameters W_∞ and K of the von Bertalanffy growth function (VBGF), whose simplest version has, for weight, the form

$$W_t = W_\infty (1 - e^{-(K(t-t_o))})^3 \qquad \ldots 3)$$

where W_t is the weight at age t, W_∞ is the mean weight the fish would reach if they were to live indefinitely, K expresses the rate at which W_∞ is approached, and t_0 is the theoretical 'age' the fish would have at W = 0.

From W_∞ and K, a growth performance index Φ can be derived, i.e.,

$$\Phi = \log_{10}(K) + 2/3 \log_{10}(W_\infty) \qquad \ldots 4)$$

which takes similar values among different populations of the same species, and hence can be used to compare the growth performance of different fishes (Pauly, 1979; 1994).

Figure 1 shows that the gill area index of 37 species of teleosts, ranging from guppies to tunas, i.e., selected to cover a wide range of asymptotic sizes and ecologies, significantly and positively correlates with their growth performance index. It might be argued at this point that if gill size is limiting, then fish should, over evolutionary time, have developed larger gills. The answer to this is that they have: their gills are suitable for rapid growth up to the size at (first) reproduction, i.e., to the size which is crucial to their evolutionary fitness. It is only from that size that the limiting effect of low relative gill area manifests itself (Pauly, 1984; 1994). Moreover, a growth limitation would occur at some stages: whatever the initial endowment, gill area, being a *surface* cannot, for geometrical reasons, keep up with the growing *volume* it is supposed to supply with oxygen.

Given (2), we also have:

$$Q = a' \cdot W^{d} \qquad \dots 5)$$

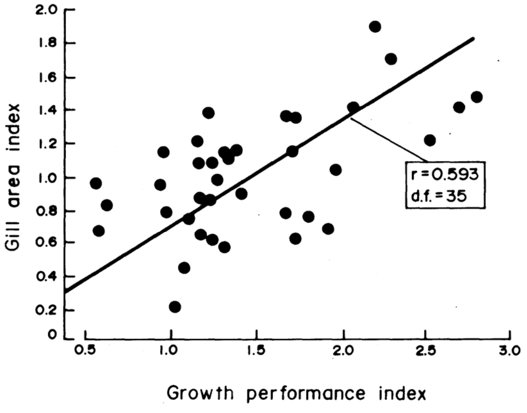

Figure 1 Relationships between an index of the gill area (a' in Equation 2) and the growth performance of 35 species of teleosts and two sharks as expressed by their value of Φ (see Equation 4; adapted from data in Pauly 1979).

in which Q is defined as in (1), W and d as in (2), and a' is a proportionality constant. Equation (5) implies that relative gill area, and hence the O2 available for growth and routine metabolism in fish, decline as size increases. This decline occurs in proportion to a power of weight equal to 1-d, down to a level where Q is, at W_∞, just enough for maintenance, i.e., that level of activity and of protein synthesis that is sufficient to compensate for spontaneous protein denaturation (Figure 2A). Thus the level of metabolism corresponding to W_∞ is, by definition, an estimate of maintenance metabolism, and any factor that increases maintenance metabolism (e.g., elevated temperature, or reduced food density, by increasing the level of activity required to secure the required food) will have the effect of reducing W_∞ (Figure 2B). This explains why, e.g., the fish of North American freshwaters tend to reach larger maximum sizes at their cold northern end than at the warm, southern ends of their range (see data in Carlander, 1969; 1977), or why Australian fishes have asymptotic sizes that are higher in the (cold) south than in the north of that country (Andersen and Pauly, 2006, this volume).

An important variable for managers of aquaculture ponds is food conversion ratio (FCR), defined as the amount of food required to produce a given amount of fish flesh. This is related to a concept commonly used in fisheries science, the food conversion efficiency (K_1) of Ivlev (1966) through 1/FCR = K_1, the latter being defined, for any time interval by:

$$K_1 = \text{growth increment/food consumption} \qquad \dots 6)$$

Various approaches exist to relate K_1 and growth (e.g., Paloheimo and Dickie, 1966), or more precisely equation (6), with the VBGF as represented in equation (3). One of these was presented by Temming (1994a), i.e.,

$$K_1 = A \cdot (1 - W/W_\infty)^{1-d} \qquad \dots 7)$$

where K_1 is the food conversion efficiency at weight W, W_∞ is as defined in equation (3), d is set at 2/3, as implied in the version of the VBGF presented here [there are other version of the VBGF, incorporating other, more realistic values of d, see Pauly, 1981; Temming, 1994b; and Essington *et al.*, 2001], and A is a factor constrained between zero and one, and expressing the fraction of the ingested food that is available for protein synthesis. It can be expected that A will be related to the nitrogen content of the food (Pandian and Marian, 1985).

APPLICATION OF THE THEORY TO AQUACULTURE POND AERATION

There is an extensive literature on pond aeration, which tends to emphasize its technological aspects (see e.g., Boyd *et al.*, 1988), and only one of its numerous biological effects: the reduction of mortality due to (early-morning) oxygen deficiency. However, aeration has numerous other biological effects, notably, beneficial effects on food conversion and growth (see Table 2). Strangely enough, these effects of aeration appear to date not to have been related to any theory of growth.

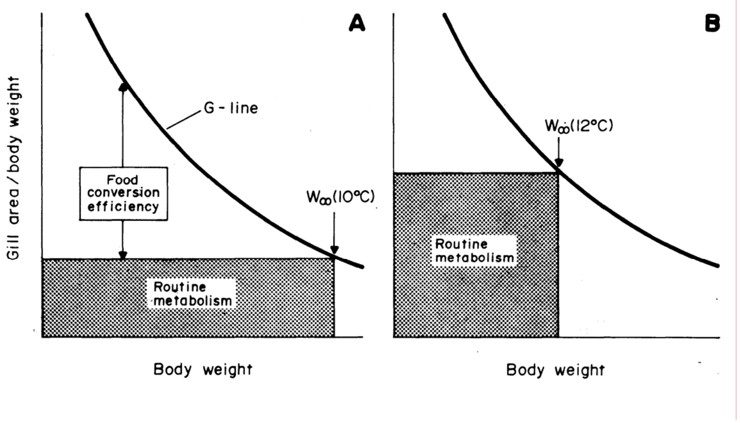

Figure 2 Illustrating how, given a certain G-line (determined by a' and d in Equation 5), maintenance metabolism determines asymptotic weight (W_∞), because relative gill area (and hence oxygen supply) *must* decline with body weight. **A.** Fish exposed to a low level of stress (e.g., environmental temperature, abundant food). **B.** Fish exposed to a higher level of stress (high temperature, causing rapid denaturation of body protein, and/or low food density, requiring O_2 to be diverted to foraging, rather than protein synthesis). Note that 'scope for growth' and food conversion efficiency can both be directly related to the difference, in these graphs, between the G-line and the level of routine metabolism.

The point here is that the observations in Table 2 are fully consistent with the theory presented above stating that fish growth is generally oxygen-limited. On the other hand, they flatly contradict conventional theories of fish growth, which tend to concentrate exclusively on *ad hoc* postulates of local food scarcity (see, e.g., Weatherley and Gill, 1987).

This suggests that quantitative predictions (i.e., hypotheses) concerning the response of fish to pond aeration made on the basis of that theory, represent 'strong inferences' *sensu* Platt (1964), the testing of which is likely to advance a field still dominated by empirical approaches.

APPLICATION OF THE THEORY TO LAKE AND RESERVOIR AERATION

One of the corollaries of the above theory is that destratifying a lake such that its overall oxygen content is increased (Fast and Hulquist, 1989) should result, other things being equal, in improved growth of the fish therein, both by directly facilitating respiration, and by increasing the size of those water layers that have both suitable temperature and food.

Table 2 Response to aeration of some cultivated fish species (√: increase explicitly noted; -: item not mentioned).

Common name	Scientific name	Location	Increase of:					
			Con^a	Growth	Survival	Harvest	Profits	Source
Common carp	*Cyprinus carpio*	Szarvas, Hungary	-	-	-	√	√	Abdul Amir (1988)
Silver carp	*Artistichthys nobilis*	Szarvas, Hungary	-	-	-	-	√	Abdul Amir (1988)
Bighead carp	*Hypophthalmichthys molitrix*	Szarvas, Hungary	-	-	-	-	√	Abdul Amir (1988)
Japanese eel	*Anguilla japonica*	Lukang, Taiwan	√	√	-	-	√	Anon. (1988a)
Tilapia	*Cichlidae*	Singapore	-	√	√	-	√	Anon. (1988b)
Channel catfish	*Ictalurus punctatus*	Alabama, USA	√	√	√	√	√	Hollerman and Boyd (1980)
Hybrid carp	*Ctenopharyngodon idella* X *Aristichthys nobilis*	Florida, USA	-	√	√	-	-	Shireman *et al.* (1983)

a) food *con*sumption and/or *con*version

This is illustrated here by a scheme in which stratification reduces the habitat of a fish population. Let us assume a lake with a warm epilimnion, a cool (10°), well-oxygenated mesolimnion and a small, oxygen-free hypolimnion (Figure 3). Let us further assume a population of cold-water fish, limited to the mesolimnion, feeding at 10°C, and having, for a value of d = 0.8, the VBGF parameters $W_{\infty(10°C)} = 1{,}000$g (Figure 3), and $K_{(10°C)} = 0.5$ year^{-1}.

Let us now imagine a change in the lake's stratification such that the O_2-free hypolimnion moves up, reducing the amount of benthos accessible in 10°C water. In such a case, the fish will have to undertake feeding forays into the warm epilimnion, and thus expose themselves to higher temperatures. Let us further assume that integrating time/temperature profiles of these forays suggests the fish to live, on the average, in a temperature of 12°C.

Other things being equal, and given Krogh's normal curve (Table 1), this will raise O_2 consumption by about 25%. Thus we have:

$$1.25 = (W_{\infty(10°C)}/W_{\infty(12°C)})^{1-d} \qquad \ldots 6)$$

from which $W_{\infty(12°C)} = 328$g.

Given equation (4) and the initial value of $K_{(10°C)} = 0.5$ year^{-1}, one can also estimate the value of K corresponding to $W_{\infty(12°C)}$, i.e., $K_{(12°C)} = 1.05$ year^{-1}.

Thus, given the above theory and ancillary field information, we can predict qualitatively and quantitatively how food conversion efficiency and growth (and hence also natural mortality, see Pauly 1980) will change, given changes in the thermal stratification of a lake (Figure 3).

Similar procedures can be applied to assess the impact of the distribution of O_2, and thus to reexamine as an example, the work of Coutant (1985, 1987, 1990), which documents a habitat – Chesapeake Bay – then in need of destratification, i.e., where striped bass – especially the large ones, for which oxygen supply was a problem – had become unable to grow and feed in certain areas of their original habitat.

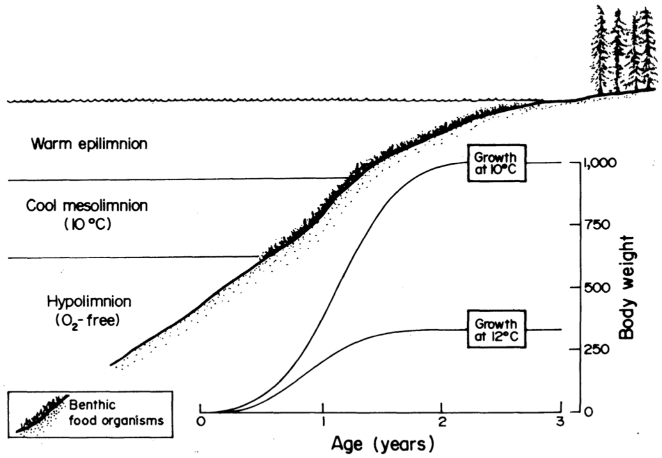

Figure 3 Schematic representation of a stratified lake, with each layer offering a different O_2/temperature combination to resident fishes. The insert in the lower right corner shows the growth curves resulting from the two scenarios in the text.

CONCLUSION

The theory presented above, based on first principles and easily verifiable assumptions, can be easily developed to provide a comprehensive framework both for interpreting aeration experiments and for predicting potential effects of aeration in various water bodies.

Without such development of the above theory, or of a modification thereof, the observed impacts of aeration on ponds and lakes will continue to be perceived as isolated facts, and not as elements of a well-articulated system of principles allowing strong inferences and rapid advances.

ACKNOWLEDGEMENTS

I thank Dr. R.S.V. Pullin for his most useful comments on the draft of this contribution, originally prepared in 1996, and which was intended as chapter in a book, to be edited by colleagues, on 'Lake and Pond Aeration'. The book project fell through, but this contribution was rescued and included here, only minimally updated (3 new references), as I feel it has not, 10 years later, lost any of its pertinence, notably for the interpretation of growth data in FishBase.

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