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Institute for the Oceans and Fisheries  
The University of British Columbia  
2202 Main Mall  
Vancouver, B.C., Canada V6T 1Z4

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Edited by  
Daniel Pauly, Lincoln Hood and Konstantinos I. Stergiou

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## PREFACE

This report, as indicated in its title, contains mainly contributions initially written several years or even decades ago, but not formally published. They are now, because they contained ideas and/or data that may still be valuable.

Two of the contributions in this volume are based on work conducted in the 1980s, a period during which manuscripts that remained unpublished could legitimately be cited, as exemplified by the unpublished essay on the effects of closing the Bering Strait on global climate, by the late Maxwell J. Dunbar. Currently, rules may be stricter, and it is thus appropriate to nudge unpublished essays from where they are, at the cusp of the transition from private knowledge to public knowledge. This accounts for the fact that, for scientists, it is act of publishing that counts; this is what connects them with other scientists, and opens the public debates that characterize science (besides establishing priority for any original idea).

Nowadays, the journals' guides to would-be-authors of scientific papers tend to stress that unpublished manuscripts (as opposed to material from the Internet, ephemeral or not) should not be listed in the 'literature cited' sections of papers. This can lead to the loss of valuable knowledge, and hence this compilation, through which we attempt to 'save', i.e., make more widely available what we could of some of the research that we, our graduate students and/or close colleagues have been conducting.

The majority of the contributions deal with various aspects of the growth of fish, a major structuring feature of their life histories, and the basis of their productivity when under exploitation. When editing these contributions, we linked them, where appropriate, with the theory elaborated by one of us (D.P.), on the limiting role of fish gills, and hence oxygen supply, for the growth of fish, which has begun to attract attention, given observed and/or anticipated effects of global warming on fish growth. This theory explains, among other things:

- Why fish (and aquatic invertebrates, as well) grow the way they do (asymptotically, predictably, temperature-dependent, etc.);
- Why fish reach maturity at a size that is a predictable fraction of their maximum size even when the latter varies due to environmental forcing, but sometimes 'skip' spawning;
- Why the food conversion efficiency of fish and aquatic invertebrates varies with size, temperature and dissolved oxygen;
- Why fish larvae have very discernable daily rings on their otoliths (and squid larvae on their statoliths), which are less visible in adults;
- Why visceral fat is abundant in cold temperate fish exhibiting strong seasonal growth oscillations, but not in tropical and polar fish exposed to narrow ranges of temperature; and
- Why fish and aquatic invertebrates are spatially distributed the way they are, and why they migrate as they do.

The other contributions in this report cover various topics in fisheries biology, marine ecology and ecosystem modelling, the last of which perhaps not being what it seems.

Daniel Pauly  
Lincoln Hood  
Konstantinos I. Stergiou



## MEDITERRANEAN SLIMEHEAD, *HOPLOSTETHUS MEDITERRANEUS* IN THE IONIAN SEA, GREECE: OTOLITH MORPHOMETRY, AGE AND GROWTH\*

Aikaterini Anastasopoulou<sup>1</sup>, Vasiliki Vassilopoulou<sup>1</sup>, Stelios Katsanevakis<sup>2</sup> and Paraskevi K. Karachle<sup>1</sup>

<sup>1</sup> Institute of Marine and Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Aghios Kosmas, Athens, Greece

<sup>2</sup> Department of Marine Sciences, University of the Aegean, University Hill, 81100 Mytilene, Greece  
[pkarachle@hcmr.gr](mailto:pkarachle@hcmr.gr)

### ABSTRACT

Age and growth of Mediterranean slimehead, *Hoplostethus mediterraneus* in the Ionian Sea, Greece, were studied and morphometric relationships of otolith morphological characteristics were established, based on samples collected in 1996-1997. The length-weight relationships were positively allometric (sexes separately and combined). A strong correlation was found between total length (TL) and otolith weight, with the morphological characteristics of the otoliths (i.e., length, diameter, width and perimeter). The maximum age recorded, based on otolith reading, was nine years, for a female individual of TL of 22.2 cm, while males reached a maximum age of six years (TL=19.9 cm). Five different growth models were compared: the von Bertalanffy growth function (VBGF), the generalized VBGF, the Gompertz model, the logistic model, and a power model. The VBGM and Gompertz had substantial support by the data of female growth, while Gompertz and the logistic model were substantially supported for the growth of males. With the combined sexes, three models had substantial support: VBGF, generalized VBGF, and Gompertz. The model-averaged asymptotic length of *H. mediterraneus* was estimated (point estimate and 95% confidence interval in parentheses): 22.5 cm (20.9 – 24.0), 22.0 cm (16.0 – 28.1) and 23.6 cm (21.4 – 25.8), for females, males, and combined sexes respectively. The estimated parameters of the von Bertalanffy equation for both sexes combined were:  $L_{\infty}$ =23.9 cm,  $K = 0.242 \text{ year}^{-1}$ , and  $t_0 = -1.39$  years, whereas for the two sexes separately were estimated as:  $L_{\infty}$ =24.2 cm,  $K = 0.241 \text{ year}^{-1}$ ,  $t_0 = -1.32$  years, and  $L_{\infty}$ =23.2 cm,  $K = 0.244 \text{ year}^{-1}$ ,  $t_0 = -1.52$  years, for females and males respectively.

### INTRODUCTION

Deep-sea fishes have been in the centre of scientific interest during the past few decades, as it is widely acknowledged that they comprise very sensitive stocks, mainly due to their high longevity, and low growth rates and reproduction outputs (e.g. Clark 2001). Their study has been made feasible due to technological enhancement related to sampling ability in greater depths, combined with economic aspects and the constant need to exploit new stocks (e.g. Merrett and Marshall 1981; Morato *et al.* 2006; Swartz *et al.* 2010).

Besides growth parameters, age determination is essential both for growth studies and for assessment purposes. Indeed, fish age distribution provides an accurate picture of the population dynamics (Shafer 1989), serves as basis for developing age-structured population models and is essential for effective fishery management (e.g. Kin 1995; Pauly and Binohlan 2000). Fish aging is being performed through a variety of different techniques (e.g. Jearld 1983; King 1995), with otolith reading being the most reliable (Williams and Bedford 1974). Otolith zone formation has been related to seasonal events, a fact also recorded in areas with stable temperatures throughout the year, as in the case of Mediterranean water bodies below the thermocline (see Morales-Nin 2001 and references therein).

However, age determination based on otolith reading is generally time consuming and expensive. Accordingly, there is a considerable interest in developing alternative more cost and time-effective methods for age determination. Numerous studies have demonstrated that there is a close relationship between otolith weight or size and age, suggesting that these parameters can be used as proxies for otolith ring counts in ageing fish (e.g. Pawson 1990; Worthington *et al.* 1995; Steward *et al.* 2009). Ontogenetic changes in otolith morphology have been noted (e.g. Fowler 1990; Newman *et al.* 1996), indicating that some otolith dimensions may be more useful than others for estimating fish age. Yet, the study of otolith morphometry

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may be useful for validating or estimating fish age, since the analysis of otolith shape can provide information related to genetic, ontogenetic, and environmental factors (Lombarte *et al.* 2003).

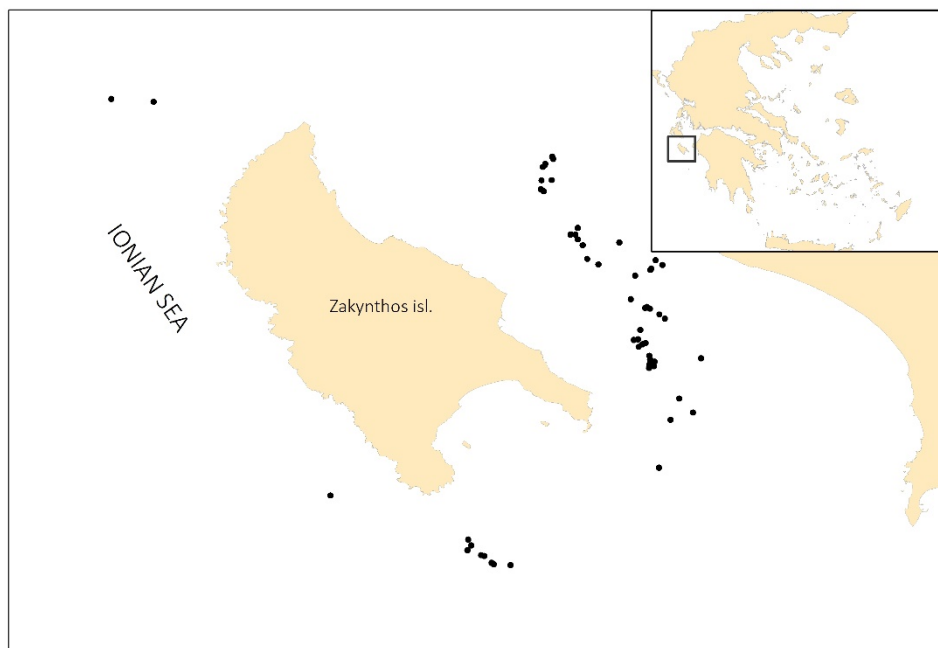
The Mediterranean slimehead, *Hoplostethus mediterraneus* (Cuvier, 1829), is a cosmopolitan bathypelagic fish species that dwells in relatively deep waters, down to 1175 m (Froese and Pauly 2016). Its main bathymetric distribution zone in the eastern Mediterranean is between 280 and 900 m (Katsanevakis and Maravelias 2009). The Mediterranean slimehead is traditionally caught in the shrimp fishery and almost exclusively discarded (e.g. Vitale *et al.* 2014). As it is of no commercial importance (Froese and Pauly 2016), the existing studies on its biology are limited and sporadic, while at the same time the existing life history parameters show great disparity (e.g. Vitale *et al.* 2014). With respect to the biology and the ecology of the species in the Mediterranean, information exists on the weight-length relationships (Merella *et al.* 1997; Filiz and Bilge 2004; Ismen *et al.* 2007; Öz and Ismen 2010), diet and feeding habits (Kabasakal 1999; Madurell and Labropoulou 2000; Madurell and Cartes 2005), and reproduction (Cau and Deiana 1982; Calabro *et al.* 2008). Analyses of the life history traits of the species, with information on its age and growth, are given by D'Onghia *et al.* (1998), Vitale *et al.* (2004) and Maiorano *et al.* (2010), all from Italian waters (NW Ionian Sea). Finally, Vitale *et al.* (2014) provide information on growth parameters of the species in various areas of the Mediterranean, based on length-frequency distributions.

The objectives of this study are to a) provide information on the morphometry of the otoliths of the species caught in the Greek part of the Eastern Ionian Sea; b) contribute to our knowledge of its age and growth; and c) investigate techniques to validate the growth in order to increase the accuracy.

## MATERIAL AND METHODS

Samples were collected during 4 experimental trawl surveys, from a network of 64 stations at depths ranging from 360 to 716 m, carried out during 1996 –1997 in the Ionian Sea (Figure 1). A commercial otter trawl was used with a cod- end liner of 16 mm stretched mesh size.

In the laboratory, each individual was measured to the nearest millimeter (total length, TL) and weighed to the nearest 0.01 g (total weight, W), and their sex was recorded. Length - weight relationships (LWR) were established for sexes separately and combined, using the allometric model  $W = a \cdot L^b$ . Differences between the b-values of the relationship were checked using the analysis of covariance (ANCOVA; Zar 1999). In addition, the von Bertalanffy growth equation was fitted to the raw age-at-length data, in order to estimate the asymptotic length ( $L_\infty$ ), and the parameters K and  $t_0$ , for each sex separately and for sexes combined.



**Figure 1.** Sampling sites of Mediterranean slimehead *Hoplostethus mediterraneus* in the Ionian Sea, with insert displaying Greece.

For the analyses regarding otoliths, both sagittae were removed, measured (maximum otolith length (OL)) and weighed (OW). Only undamaged, whole otoliths were used in the analysis. Relationships between

various morphometric characteristics [i.e., otolith diameter (OD), otolith width (OWd), otolith perimeter (OP), otolith radius (OR), OW], with TL and W, as well as amongst them, were explored using the classic model, i.e.,  $Y = aX^b$ , which is conceptually simple, with parameters that are easily estimated (Katsanevakis *et al.* 2007). Consequently, b-values of the regressions were tested for difference from 1 using t-test (Zar 1999). Otolith reading was performed using a binocular microscope fitted with a video camera. In order to obtain second readings of the otoliths, images were captured and a second aging using the Image Analysis Pro plus system was performed. Images were captured with a camera and analyzed using Image-Pro Plus, version 4.5.

An information theory approach was followed to model Mediterranean slimehead growth (Katsanevakis 2006; Katsanevakis and Maravelias 2008). According to the information theory approach, data analysis is taken to mean the integrated process of *a priori* specification of a set of candidate models (based on the science of the problem), model selection based on the principle of parsimony according to Akaike's information criterion or AIC (Akaike 1973), and the estimation of parameters and their precision. Rather than estimating parameters from only the 'best' growth model, parameter estimation was made from all the models that were supported by the data. This procedure is termed multi-model inference (MMI) and has several theoretical and practical advantages (Madigan and Raftery 1994; Hoeting *et al.* 1999; Burnham and Anderson 2002; Katsanevakis 2006; Katsanevakis and Maravelias 2008).

A set of five candidate models was used to model fish growth: von Bertalanffy growth function (VBGF; von Bertalanffy 1938), generalized VBGF (Pauly 1981), Gompertz (Gompertz 1825), Logistic (Ricker 1975), and several power models. The underlying principle of the VBGF is that the growth rate of fish tends to decrease linearly with size, as indicated in the equation  $dL/dt = K_i (L_\infty - L)$ , where  $K_i$  express the rate at which  $L_\infty$  is approached (of dimension  $\text{time}^{-1}$ , here  $\text{year}^{-1}$ ) and  $L_\infty$  is the asymptotic length ( $L_\infty$  has the same biological interpretation in all the models described below, i.e., the mean length the fish of a population would reach if they were to grow indefinitely). The most common parameterization of the solution to the above differential equation is  $L_t = L_\infty (1 - e^{-K(t-t_0)})$ , where  $t_0$  is interpreted as the age when an individual fish would have been of zero length assuming the equation to be valid at all ages. The generalized VBGF is given by the equation  $L_t = L_\infty (1 - e^{-KD(t-t_0)})^{1/D}$  (Pauly 1981)<sup>†</sup>. The parameters of the generalized VBGF are the same, except that D is added. While the VBGF has no inflection point for  $t > 0$  (its graph is concave downward), the generalized VBGF is sigmoidal having an inflection point ( $t_i$ ) at  $t_i = t_0 - \ln(D/KD)$ .

The Gompertz growth model (Gompertz 1825) is a sigmoidal growth curve that assumes exponential decrease of the growth rate with size and is given by the differential equation  $dL/dt = \lambda e^{-kL}$ , where  $\lambda$  is the theoretical initial relative growth rate at zero age (unit:  $\text{year}^{-1}$ ) and  $k$  is the rate of exponential decrease of the relative growth rate with age (with units  $\text{year}^{-1}$ ). The inflection point of the Gompertz model appears at  $t = k^{-1} \ln(\lambda/k)$ .

The logistic model, given by the equation  $L(t) = L_\infty (1 + e^{-k(t-t_0)})^{-1}$ , is an alternative sigmoidal curve that has also been used for modelling the growth of fish (Ricker 1975). Here, the parameter  $k$  is a relative growth rate parameter (with units  $\text{year}^{-1}$ ), while  $t_i$  corresponds to the inflection point of the sigmoidal curve. The power model has the form  $L_t = a_0 + a_1 t^b$  and has no asymptote; it is concave downwards for  $b < 1$  and concave upwards for  $b > 1$ .

The five candidate models  $g_i$  ( $i = 1$  to 5) were fitted to each dataset, with non-linear least squares (nl-LS) with iterations by means of Marquardt's algorithm, assuming additive error structure.

The small-sample, bias-corrected form  $AIC_c$  (Hurvich and Tsai 1989; Shono 2000) of the AIC (Akaike 1973; Burnham and Anderson 2002) was used for model selection. The model with the smallest  $AIC_c$  value ( $AIC_{c,min}$ ) was selected as the 'best' among the models tested. The  $AIC_c$  differences,  $\Delta_i = AIC_{c,i} - AIC_{c,min}$  were computed over all candidate models  $g_i$ . To quantify the plausibility of each model, given the data and the set of five models, the 'Akaike weight'  $w_i$  of each model was calculated, where  $w_i = \exp(-0.5\Delta_i) / \sum_{k=1}^5 \exp(-0.5\Delta_k)$ . The 'Akaike weight' is considered as the weight of evidence in favor of model  $i$  being the actual best model of the available set of models (Akaike 1983; Buckland *et al.* 1997; Burnham and Anderson 2002). 'Average' models were determined by averaging the predicted response variable  $L_{(t)}$  across models, using the corresponding  $w_i$ 's as weights (Burnham and Anderson 2002). Following the MMI approach, the model averaged asymptotic length  $L_\infty$  was estimated as a weighted average using all four models ( $g_1 - g_4$ ) that assume asymptotic growth with the prediction of each model weighted by  $w_i$ , where  $w_i^* = w_i / (w_1 + w_2 + w_3 + w_4)^{-1}$ .

<sup>†</sup> The parameter D, which is related to the growth of fish gills and/or metabolic rate, is usually provided externally rather than estimated from the data, as was done here (Pauly, 1981).

are the rescaled Akaike weight ignoring the weight of the power model (Katsanevakis and Maravelias 2008). The unconditional standard error of  $L_{\infty}$  was estimated as (Burnham and Anderson 2002):

$$se(\bar{L}_{\infty}) = \sum_{i=1}^4 w_i^* (\text{var}(\hat{L}_{\infty,i} | g_i) + (\hat{L}_{\infty,i} - \bar{L}_{\infty})^2)^{1/2}$$

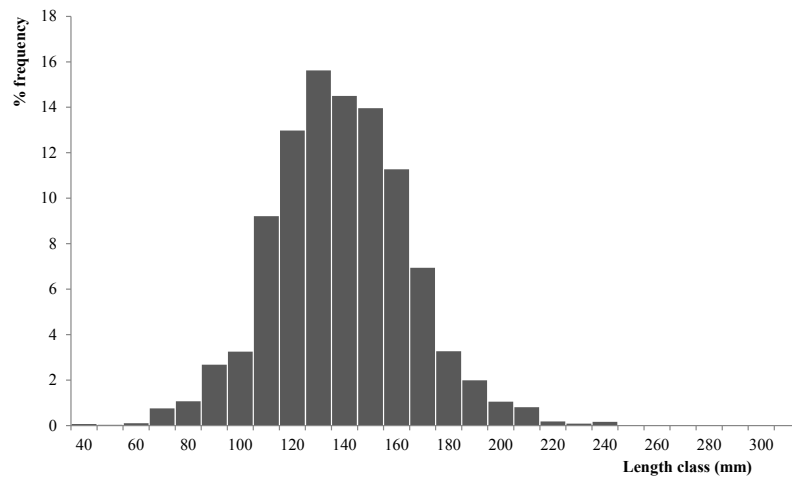
where  $\text{var}(\hat{L}_{\infty,i} | g_i)$  is the variance of the estimated asymptotic length according to model  $g_i$ , conditional on the model.

## RESULTS

A total of 3716 Mediterranean slimehead were caught in the study area, with a TL ranging from 4.3 to 31.6 cm. The length-frequency distribution was unimodal (Figure 2) with a dominant mode of 12-16 cm. The length-weight relationships (WLR; W in g, TL in cm) were established using a subsample of 1541 Mediterranean slimehead individuals and were the following:

*males:*  $W = 0.0036TL^{3.265}$ ,  $N = 746$ ,  $TL = 7.0-19.9$  cm,  $R^2 = 0.96$ , standard error of b ( $SE_b$ ) = 0.0497,  
*females:*  $W = 0.0027TL^{3.327}$ ,  $N = 617$ ,  $TL = 7.4-22.2$  cm,  $R^2 = 0.94$ ,  $SE_b = 0.0645$ , and  
*combined:*  $W = 0.0020TL^{3.380}$ ,  $N = 1541$ ,  $TL = 7.0-22.2$  cm,  $R^2 = 0.96$ ,  $SE_b = 0.0398$ .

All relationships were positively allometric, and there was a significant difference between sexes (ANCOVA:  $F = 4.13$ ,  $p < 0.05$ ).

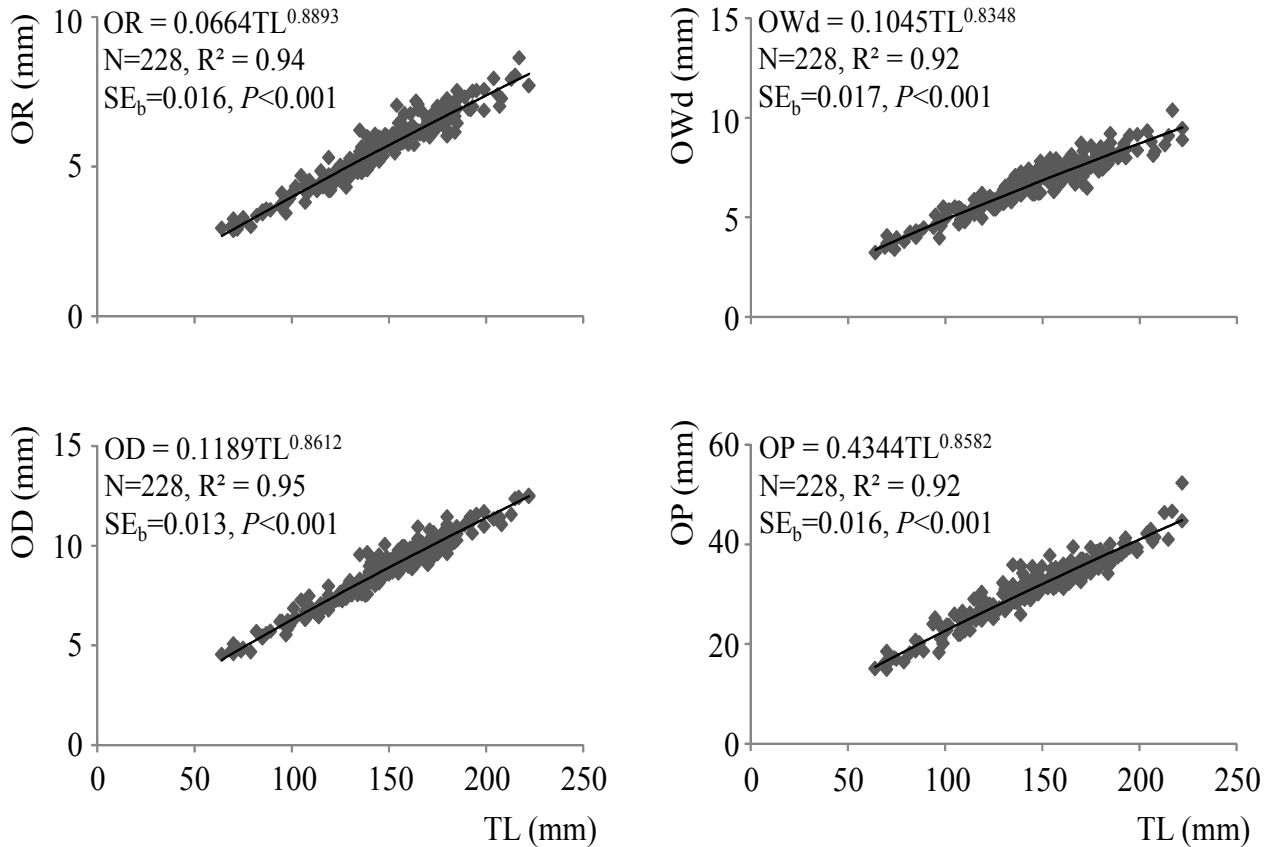


**Figure 2.** Length frequency distribution of Mediterranean slimehead *Hoplostethus mediterraneus* in the Ionian Sea.

Measurements of Mediterranean slimehead otoliths were taken from 228 individuals. No significant difference in otolith weight was found between the left and the right otolith (t-test;  $t = 1.404$ ,  $p = 0.161$ ) from the same fish, and hence only left otoliths were used for subsequent analyses. Additionally, no statistical differences were found on OW between sexes (t-test;  $t = 1.782$ ,  $p = 0.076$ ). Therefore, sexes were merged to increase sample size and power.

The relationships between the morphometric characteristics of the otoliths are given in Figures 3 and 4. There was a strong correlation between TL and OR, OD, OWd and OP ( $p < 0.001$ ; Figure 3). In all cases values of the slope b differed statistically from 1 (t-test:  $p < 0.001$ ), thus indicating an allometric relationship of the above mentioned morphometric characteristics with TL. Additionally, since in all cases  $b < 1$  (Figure 3), all relationships were negative allometric. Likewise, OW was strongly related with the other morphometric measurements of the otoliths and with TL, with a negative allometric type of relationship ( $p < 0.001$ ; Figure 4).

Otolith ageing and weighing was performed on a total of 233 individuals of Mediterranean slimehead (Table 1). Two distinct types of rings were observed: opaque rings appeared white and translucent rings appeared dark. Translucent rings continuing around the entire circumference of the otolith were considered annual growth zones (annuli). Ages fluctuated between 0 and 9 years, with the bulk of the collected stock comprised of two and three year's old specimens ranging between 2-4 years. Fish aging 1 and 4 years displayed limited abundance, whereas 0-group Mediterranean slimehead and those older than 4 years were rarely encountered. Females ( $TL = 6.66-22.2$  cm) covered all age classes, whereas males ( $TL = 6.6-19.9$  cm) reached a maximum age of 6 years. The mean OW showed an increasing trend with age (Table 1), yet OW overlapped among age classes.



**Figure 3.** Relationships of various morphometric characteristics of the otoliths with total body length (TL) of Mediterranean slimehead *Hoplostethus mediterraneus* in the Ionian Sea. OR=otolith radius; OD=otolith diameter; OWd=otolith width; OP=otolith perimeter; N=number of individuals;  $R^2$ =coefficient of determination;  $SE_b$ =standard error of slope b.

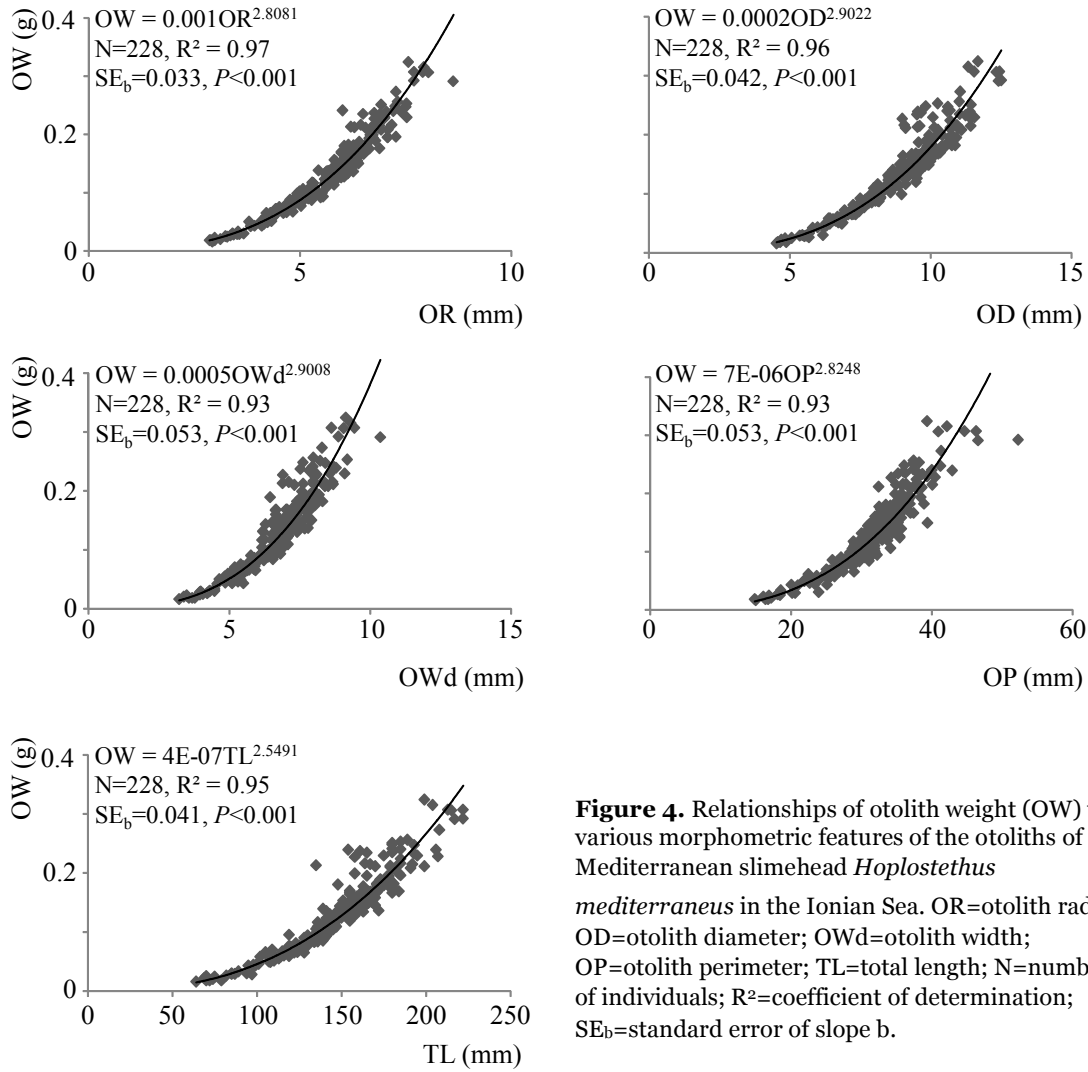
A GLM ANOVA analysis was carried out to evaluate the relation between the otolith parameters and age, showing that otolith weight, otolith perimeter and radius were significantly related to age ( $p < 0.05$ ). Having identified otolith weight as the best variable for predicting age, a predictive equation was established:

$$AGE = 0.1414 + 20.095 * OW \quad (F=780.32, p < 0.001, R^2=77.31).$$

With respect to the growth of the slimehead, a set of five candidate models was used. The estimated values of  $AIC_c$ ,  $\Delta i$ ,  $w_i$ ,  $L_{\infty,i}$ ,  $se(L_{\infty,i})$ , and 95% confidence limits of  $L_{\infty,i}$  are given in Table 2, as well as the values of  $L_{\infty}$ ,  $se(\bar{L}_{\infty})$ , and 95% confidence limits of  $L_{\infty}$ , separately for females, males, and combined sexes. The VBGF and Gompertz had substantial support ( $\Delta i < 2$ ) from the data of female growth, Gompertz and the logistic model were substantially supported for the growth of males, while with combined sexes, three models had substantial support (VBGF, generalized VBGF, and Gompertz) (Table 2). The growth curves of the average models for the two sexes were very close in the range of sampled ages (Figure 5). A comparison of female and male lengths at age (at ages 2–4 years, for which both males and females were satisfactorily sampled) revealed non-significant differences at 95% significance level (Mann-Whitney test,  $p$ -values 0.406, 0.224, and 0.076 for ages 2, 3, and 4 years respectively).

Although the VBGF was not always the best supported model, we provide its estimated parameters ( $\pm$ standard error (SE)) for comparison reasons with previous studies:

*males:*  $L_{\infty}=23.2 (\pm 1.9)$  cm,  $K= 0.244 (\pm 0.049)$  year<sup>-1</sup>,  $t_0= -1.52 (\pm 0.24)$  years,  
*females:*  $L_{\infty}=24.2 (\pm 0.8)$  cm,  $K= 0.241 (\pm 0.022)$  year<sup>-1</sup>,  $t_0= -1.32 (\pm 0.14)$  years, and  
*combined:*  $L_{\infty}=23.9 (\pm 0.8)$  cm,  $K= 0.242 (\pm 0.022)$  year<sup>-1</sup>,  $t_0= -1.39 (\pm 0.14)$  years.



**Figure 4.** Relationships of otolith weight (OW) to various morphometric features of the otoliths of Mediterranean slimehead *Hoplostethus mediterraneus* in the Ionian Sea. OR=otolith radius; OD=otolith diameter; OWd=otolith width; OP=otolith perimeter; TL=total length; N=number of individuals; R<sup>2</sup>=coefficient of determination; SE<sub>b</sub>=standard error of slope b.

## DISCUSSION

In this study, various morphometric relationships, and aging of the Mediterranean slimehead caught in the Ionian Sea was performed by otolith reading. Moreover, growth parameters of the species in the study area were estimated, and different growth models were compared.

Previously reported b-values of the length-weight relationship for this species range from 2.95 (North Aegean Sea, Turkey; Filiz and Bilge 2004) to 3.364 (Gulf of Cadiz, Spain; Torres *et al.* 2012). The estimated values in the present study fall within the above-mentioned range, when sexes examined separately (b-values for males=3.265; females=3.327), yet slightly higher when sexes were combined (b-value combined=3.38).

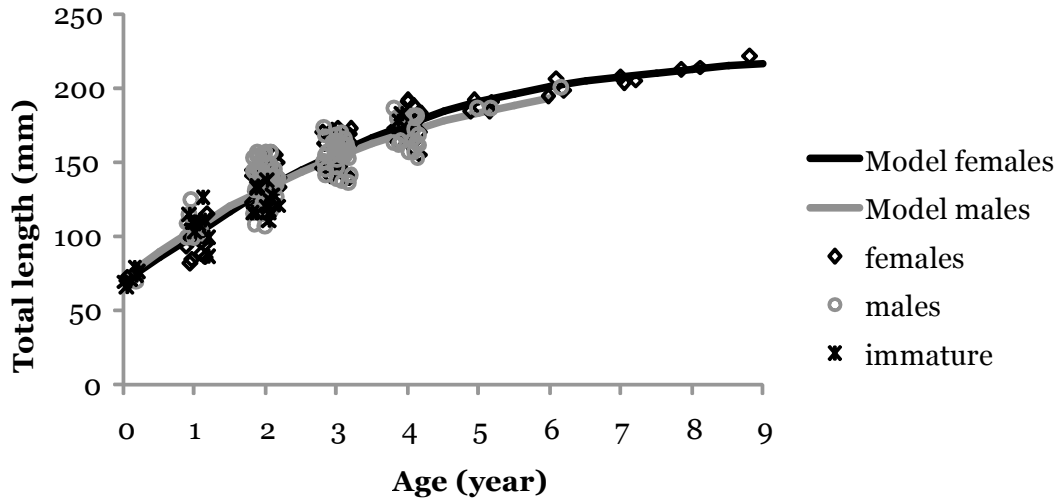
The estimates of the asymptotic length were lower than those reported by D'Onghia *et al.* (1998) and Vitale *et al.* (2014) in the Mediterranean Sea. This could indicate differences in the growth performance among the different populations, although the different modelling approaches could also have caused the divergence of the estimates. The von Bertalanffy model tends to give higher estimates of asymptotic length than the Gompertz and logistic models (Katsanevakis and Maravelias 2008). Hence, if previous studies had also applied a multi-model approach, their asymptotic length estimates would have been lower. When the data support evidence of more than one model as was the case here, model averaging the predicted response variable across models is advantageous in reaching a robust inference that is not conditional on a single model (Katsanevakis and Maravelias 2008). The information theory approach frees the researcher from the limiting concept that the correct growth model is somehow 'given'. *A priori* selection of the von Bertalanffy model would result to an underestimation of the uncertainty in the estimates, as model selection uncertainty

**Table 1.** Age-length key for Mediterranean slimehead *Hoplostethus mediterraneus* from the Ionian Sea: N= number of individuals; TL = total length (in cm); OW = otolith weight (in g); SE = standard error

Midrange (TL; cm)	Age (years)									
	0	1	2	3	4	5	6	7	8	9
6.5	2									
7.5	6									
8.5		5								
9.5		7								
10.5		10	2							
11.5		4	11							
12.5		2	10							
13.5			28	3						
14.5			18	13						
15.5			10	15	5					
16.5				14	9					
17.5				9	16					
18.5					14	4				
19.5					2	2	3			
20.5							1	3		
21.5									2	1
22.5										2
N	8	28	79	54	46	6	4	3	2	3
Mean TL	71.63	102.25	134.61	156.76	173.48	187.50	200.00	206.00	214.00	220.33
TL SE	±1.59	±2.09	±2.44	±1.46	±1.47	±1.59	±2.53	±1.15	±1.00	±1.67
Mean OW	0.020	0.046	0.100	0.147	0.184	0.230	0.248	0.276	0.306	0.297
OW SE	±0.001	±0.003	±0.004	±0.005	±0.006	±0.006	±0.026	±0.022	±0.005	±0.005

**Table 2.** Growth model comparisons; for each candidate model, the small-sample bias corrected form of Akaike's information criterion  $AIC_c$ , Akaike differences  $\Delta_i$ , Akaike weights  $w_i$ , and the estimation of asymptotic length ( $L_\infty$ ) with the corresponding conditional asymptotic standard error (SE), and 95% conditional confidence limits (CL). Point estimates, SE, and 95% CL for the model-averaged asymptotic length are also given (unconditional estimations). VBGF: von Bertalanffy Growth Function;  $n$  = total number of estimated regression parameters in the model.

Models	n	AICc	$\Delta_i$	$w_i$ (%)	$w_i^*$ (%)	Asymptotic length (mm); 95% CL			
						Point estimates	SE	lower	upper
Females									
VBGF	4	955.1	4.5	6.2	6.2	242.2	8.2	225.7	258.6
Gen. VBGF	5	954.0	3.4	10.8	10.8	231.6	10.6	210.4	252.7
Gompertz	4	950.6	0.0	60.1	60.1	224.5	5.2	214.1	235.0
Logistic	4	952.5	1.9	22.9	22.9	216.6	4.2	208.2	225.0
Power	4	992.4	41.8	0.0					
Model-averaged						224.6	7.8	209.0	240.2
Males									
VBGM	4	1061.2	0.0	37.1	42.3	231.7	19.4	193.1	270.3
Gen. VBGF	5	1063.3	2.1	12.8	14.6	241.9	78.0	86.4	397.5
Gompertz	4	1061.9	0.7	25.6	29.2	205.6	10.2	185.2	226.0
Logistic	4	1063.4	2.2	12.2	13.9	194.0	7.3	179.5	208.5
Power	4	1063.4	2.2	12.3					
Model-averaged						220.3	30.3	159.8	280.8
Combined sexes									
VBGF	4	1782.6	0.0	56.5	56.5	238.62	7.9	222.8	254.4
Gen.VBGF	5	1784.4	1.8	22.4	22.4	233.18	12.1	209.0	257.3
Gompertz	4	1784.6	2.0	20.5	20.5	221.58	5.3	211.0	232.2
Logistic	4	1791.8	9.2	0.6	0.6	213.66	4.4	205.1	222.2
Power	4	1814.9	32.3	0.0		-	-	-	-
Model-averaged						236.0	11.1	213.9	258.2



**Figure 5.** Average models of the absolute growth of females, males and all individuals (combined sexes), for Mediterranean slimehead *Hoplostethus mediterraneus* from the Ionian Sea. Data points were jittered horizontally to enhance clarity.



would result and would be ignored (Katsanevakis 2006). Nevertheless, we herein reported the VBGF estimated parameters, if mainly to enable comparisons with previous studies, e.g., via FishBase ([www.fishbase.org](http://www.fishbase.org)).

The age of Mediterranean slimehead was estimated in the Ionian Sea by otolith reading. Growth ring formation has been reported for many deep-water fish (Morales-Nin 2001). The otoliths of the species showed clearly discernible annuli. Ten age groups were determined, but 2 and 3 year old individuals dominated the population. Our results were similar to those presented by D'Onghia *et al.* (1998) for the species in the north-western Ionian Sea where 11 age groups were identified, the latter being the maximum reported age for the species (Froese and Pauly 2016).

The fish size showed a high correlation with the various otolith morphometric characteristics examined in the present study, which could be mainly attributed to the fact that they are controlled by the same metabolic processes (Gauldie 1988). Of the otolith morphologic characteristics measured here, otolith weight and radius were most highly correlated with age and thus the most useful predictors of age. Additionally, the otolith weight was a satisfactory predictor of age according to the GLM model. Otolith weight has been reported to be correlated with the age of some fish (Reznick *et al.* 1989; Secor and Dean 1989; Pino *et al.* 2004). However, in some studies, the increased variability of otolith weight in older fish suggests that such a predictor variable might produce less-reliable age estimates in older fish (Tuset *et al.* 2003). In the present study, although an increasing mean otolith weight was observed in relation to age, the small sample size of individuals aged >4 years did not allow to corroborate the above hypothesis. Including otolith morphometrics in the aging process reduces human-induced age determination errors and makes the age estimation more reliable. Yet, it is essential that the accuracy of age composition in the population is further explored (Doering-Arjes *et al.* 2008). This could be achieved with additional scientific efforts on age validation, especially for deep-water fishes whose mechanism of ring formation is not fully elucidated (Morales-Nin 2001).

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## INTERACTIONS BETWEEN GROWTH, SEX, REPRODUCTION, AND ACTIVITY LEVELS IN CONTROL AND FAST-GROWING STRAINS OF NILE TILAPIA, *OREOCHROMIS NILOTICUS*

Chantelle C. Bozynski<sup>1</sup> and Daniel Pauly<sup>2</sup>

<sup>1)</sup> Zoology Department, University of British Columbia, Vancouver, Canada

<sup>2)</sup> Sea Around Us, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, Canada  
[d.pauly@oceans.ubc.ca](mailto:d.pauly@oceans.ubc.ca)

### ABSTRACT

This study examined the relationship between growth, behavioral activity, and sexual maturation in control strains of Nile tilapia, *Oreochromis niloticus* (Family Cichlidae) and in strains resulting from a project devoted to the Genetic Improvement of Farmed Tilapias (GIFT). Locomotor and agonistic activity of fish groups was video recorded each month of the three-month study period. Under laboratory conditions, the fast-growing GIFT fish performed less locomotor and agonistic activity than the slow-growing control fish. Mirror image stimulation tests performed on individual males supported the finding that controls are more aggressive than GIFT fish. Nesting behavior, which is often the first indication of sexual maturity, was observed only in males; also the slow-growing control fish became sexually mature sooner, and at a smaller size than the fast-growing GIFT fish. These results are thus fully compatible with the hypothesis that oxygen supply limits the growth of fish, that calm behavior allows reallocation of oxygen to somatic growth, and that, in contrast, high activity levels reduce growth and lead to earlier maturation, at smaller sizes.

### INTRODUCTION

One important production trait of farmed fish is its size at first sexual maturation. Fish strains that possess a high growth rate and reach harvestable size before attaining sexual maturation are sought by fish culturists because sexual maturation and spawning complicate production operations and/or affect product quality. This is especially important for the tilapias (mainly *Oreochromis* and *Tilapia*, Fam. Cichlidae), fish of African origin, which is now farmed for local and export markets in over 80 countries (e.g., Philippines, Taiwan, Israel, and the United States). When tilapia are stocked in an unpopulated pond or another aquaculture facility, the fish often shift towards a more altricial life style, characterized by a shorter period of somatic growth, an earlier onset of reproductive maturity, and more numerous, smaller eggs (Fryer and Iles 1972; Noakes and Balon 1982). The fish become “stunted,” in that they are smaller than other adults of the same species. These stunted individuals are unsuitable for the market, thus causing problems in the fish industry. This provides the overall background for the work presented here.

### Wild vs. hatchery-reared fish

Growth rate comparisons have been made between wild and hatchery-reared fish. Vincent (1960), and Flick and Webster (1964) observed in the brook trout, *Salvelinus fontinalis*, that under hatchery conditions, farmed fish grew faster than wild stocks. Einum and Fleming (1997), and Fleming and Einum (1997) also observed, under hatchery conditions, faster growth in farmed Atlantic salmon, *Salmo salar*, than in wild stock. Even under natural conditions, wild stock had a lower growth rate than farmed fish (Einum and Fleming 1997). Furthermore, Davis and Fenderson (1971) observed in Atlantic salmon that, even though hatchery and wild parr were matched for size when introduced to a divided outdoor stream aquarium, hatchery parr were on average larger in size than wild parr as the study progressed. Overall, hatchery-reared fish seem to have a growth advantage over wild fish stocks.

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Wild and hatchery-reared fish differ not only in growth rates, but also in their behavioral activity. Bachman (1984) observed in the brown trout (*Salmo trutta*) that hatchery-reared fish fed less than wild fish. A similar feeding pattern was observed in Atlantic salmon (Fenderson *et al.* 1968; Sosiak *et al.* 1979). Sosiak (1978) also observed in Atlantic salmon that hatchery parr were less shelter-oriented and more mobile than wild parr, and exhibited higher frequencies of agonistic behaviors. Norman (1987), in contrast, found Atlantic salmon fry of the hatchery stocks to be less aggressive.

Holm and Fernö (1978) went a step further in their study, by examining the connection between aggressive activity and growth rate. They observed that aggressive Atlantic salmon parr grew less rapidly, while parr with the most rapid growth performed aggressive actions less frequently (Holm and Fernö 1978). These results imply a negative relationship between aggressive activity and growth. Furthermore, Robinson and Doyle (1990) found a negative correlation between aggression and growth in the tilapia hybrid, *Oreochromis mossambicus* x *O. hornorum*. Unfortunately, there is little information on the relationship between activity and growth in farmed-reared and wild fish stocks. Thus, more research is needed to examine these relationships to see to what extent growth differences between farmed-reared and wild fish can be attributed to differences in locomotor and/or aggressive activity levels of fish stocks.

### Sexual dimorphism

As information has accumulated on growth rates of various fish species, it has become apparent that either a) the males and females of a given species grow at the same rate and have similar maximum sizes (e.g., herrings); b) the females have faster growth rates and reach larger size than the males (e.g., codfishes), or c) the males have faster growth rates and become larger than the females (e.g., cichlids) (Fryer and Iles 1972). The sex-related growth differences in cichlids, including Nile tilapia, are well established (van Someren and Whitehead 1959; Mabaye 1971; Fryer and Iles 1972; Lowe-McConnell 1975, 1982; Balarin and Hatton 1979; Palada-de Vera and Eknath 1993; Toguyéni *et al.* 1996, 1997).

The causes of male growth superiority in cichlids have been examined; however, no single explanation of sexual dimorphism in size has been widely accepted. One hypothesis is that tilapia females put so much more energy into egg production, producing eggs at very frequent intervals, which may result in costs to growth<sup>3</sup>; also the females almost cease to feed while mouthbrooding their eggs and young (Lowe-McConnell 1975). Another is that male sex hormones have an anabolic or growth promoting effect, which could result in the higher growth of males (Donaldson *et al.* 1979; Ufodike and Madu 1986). In addition, thyroid hormones ( $T_3$  and  $T_4$ ) also participate in regulating growth and development. Toguyéni *et al.* (1996, 1997) observed, in Nile tilapia, that plasma  $T_3$  levels were higher in males than females, which could account for the males' growth advantage. It was also suggested that the difference in growth may be related to a sex-linked genetic characteristic which gives the male an advantage either through efficiency of food conversion, or through aggressive feeding behavior (Mabaye 1971). Behavioral activity and its association with larger-sized males compared to females is an area that remains to be explored. Toguyéni *et al.* (1997) observed, in mixed sex groups of Nile tilapia, an increase in activity and a decrease in growth; however, no connection was made between the higher growth of males and their activity level. Therefore, more experimentation is needed to study the relationship between growth and activity level in both sexes.

### Nile tilapia (*Oreochromis niloticus*)

Nile tilapia has dominated global tilapia culture since the 1980s, and its share of total tilapia production has increased dramatically from 33% or 66,000 t in 1984 to 72% or 474,000 t in 1995 (Rana 1997). However, Pullin and Capili (1988) found that little attention had been given to the genetic improvement of farmed Nile tilapia and that more investment in research for the in genetic improvement was needed. Based upon these findings, the International Center for Living Aquatic Resources Management (ICLARM) and its collaborators initiated the Genetic Improvement of Farmed Tilapias (GIFT) project in the Philippines. Four new wild founder populations of Nile tilapia (from Egypt, Ghana, Kenya, and Senegal) and populations of four strains of Nile tilapia in current use by farmers in Asia ('Israel', Singapore, Taiwan, and Thailand) were assembled. The genetic material from the best families of all strains were incorporated, according to their performance

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<sup>3</sup> Note that this should result in female fish of other species also being smaller than the males. However, females are larger than males in about 70% of all species of fishes (Pauly, 1994)



rankings, into a synthetic strain termed 'GIFT' strain. This synthetic strain has since been subjected to selective breeding for good growth (Pullin 1998), which resulted in the GIFT strain having a higher growth potential than that of some of the strains farmed in Asia (ICLARM-ADB 1998; Pullin 1998).

### Objective of the study

In culture ponds of the Philippines, fish of the GIFT strain of Nile tilapia were observed to grow faster than control fish (Pullin 1998). To examine these growth differences in Nile tilapia, the following questions were addressed through a first set of experimental studies: Do the differences in the growth rate of GIFT and control fish persist under controlled laboratory conditions? Does the difference apply to both male and female? Can any growth differences be related to a difference in behavioral activity, and the onset of sexual maturity? To examine the relationship between growth rate and the onset of sexual maturity in both strains of Nile tilapia, nesting activity, a behavior that is often the first indication of the sexual maturity of fish, was studied.

The second set of experiments examined, in more details, the differences in the offensive aggression between male fish of both strains. In a first experiment, male control fish were observed to perform more agonistic behaviors than male GIFT fish. However, the effect that social interactions in mixed sexed groups have on behavioral measures (see Toguyéni *et al.* 1997) may have complicated the results of the first experimental study. Therefore, offensive aggression was quantified using the mirror image stimulation (MIS) tests (Gallup 1968). In juvenile coho and chinook salmon, the reactions to mirror images have been correlated with the reactions to conspecifics (Rosenau 1984; Taylor and Larkin 1986; Rosenau and McPhail 1987; Taylor 1988; Swain and Holtby 1989). Fish that spend more time performing mirror-elicited agonistic behaviors were also found to be more aggressive in social interactions under more natural circumstances. These tests have the advantage that individuals are tested against 'opponents' of exactly the same size and motivational state and that adequate replication is practical (Swain and Riddell 1990). Male fish were only examined in this MIS test because female fish were observed to perform relatively little agonistic behavior in mixed sexed groups (Experiment 1), and in all-female stock aquaria (Boyzynski pers. obs.).

## MATERIALS AND METHODS

### Experimental animals

The two strains of Nile tilapia (*Oreochromis niloticus*), a fish of African origin, were imported into Vancouver, Canada in early 1997 from the National Freshwater Fisheries Technology Research Center (NFFTRC), Muñoz, Nueva Ecija, then jointly operated by ICLARM and the Bureau of Fisheries and Aquatic Resources (BFAR) of the Philippines. The two strains were 4th generation of GIFT fish (see Introduction for background on Nile tilapia) and 'control' Nile tilapia from Bulacan Province, Philippines, typical of those fish farmed in Asian countries where selective breeding had not been widely applied.

### Holding and experimental facilities

On arrival at the University of British Columbia, the fish were placed in 55 and 102 liter (L) stock tanks with similar fish densities (approximately 5.5 L of water per fish) for a five week period to acclimatize the fish to the laboratory conditions; the fish were then transferred to the experimental aquaria. All experimental aquaria were maintained at  $24.0 \pm 0.5^\circ\text{C}$ ; the water temperature was similar to both pond sources in the Philippines (i.e.,  $24\text{--}25^\circ\text{C}$ ). The temperature of the water in the experimental tanks was maintained by the use of a room heater which kept the room temperature at approximately  $27^\circ\text{C}$ . Each experimental tank, with dimensions of 61.0 cm x 30.5 cm x 30.5 cm, was provided with a layer of gravel (depth of 2.5 cm), and a box charcoal filter. All four sides of the tanks were covered with beige paper to prevent visual interaction between neighboring fish. Illumination was provided, over a 12-h photoperiod, by fluorescent lights mounted 2 m above each row of tanks. The light strips were positioned upwards to minimize light reflection from the water surface from entering lens of the video camera during recording. A color pro843 RCA video camera was supported by a 4-wheeled aluminum stand that enabled it to be positioned lens down approximately 75 cm above the rim of each experimental tank. During behavioral recording, two extra light strips, housed in a wooden frame, were placed on either side of the row of aquaria to allow the fish to be seen clearly. These two extra light strips were turned on 30 min prior to the observation sessions to acclimatize the fish to the higher light intensity. The

fish were fed commercially prepared catfish feed (Otter Co-op, Aldergrove, British Columbia) at 3% wet weight of fish daily. The quantity of feed given was adjusted monthly following the recording of standard length and weight of each fish.

### **Fish identification**

The fish were marked by attaching a colored bead to each individual. The beads were attached 10 days prior to the start of the behavioral recordings. The fish were anaesthetized by being immersed in a buffered 0.03% w/v solution of methane tricaine sulfonate (MS 222, Syndel Laboratories, Vancouver). When a fish was nearly motionless, on its side, and respiring slowly, the fish was removed from the solution and placed on a moist sponge. A 0.25 mm diameter nylon monofilament, with one bead tied onto one end, was sewn through the musculature at the front end of the dorsal fin using a sewing needle. The bead was secured onto the fish as described in Kroon (1997). The fish was returned to the freshwater and allowed to recover. Five light-colored beads were used: yellow, white, blue, green, and pink. These bead colors were chosen because they were in sharp contrast to the dark surroundings (i.e., dark body coloration and sand).

The presence of brightly colored beads on the fish apparently did not change the motivational state of the neighboring fish: there appeared to be no increase in the frequency of agonistic acts directed towards beaded fish (Boyzynski pers. obs.). It was important to resolve this issue because body color patterns are important in the visual communication of cichlids and the pattern of coloration changes according to the motivational state of the fish (Billy 1982; Nelissen 1991). For a more detailed description of color patterns in tilapias see Billy (1982).

### **Determination of sex**

The sex of the fish was initially determined by the external examination of the genital papilla (Afonso and Lebouté 1993) and then verified later by the dissection of the gonads. The distinctive features of the genital papilla of the male and female tilapia are described by Maar *et al.* (1966). Briefly, the male has two orifices situated just forward of the anal fin. One is the vent, the other is the urogenital aperture which usually forms into a small papilla. The female, in contrast, has three orifices, namely the vent, a transverse genital opening and a microscopic urinary orifice, which is scarcely visible to the naked eye (Balarin and Hatton 1979). The anaesthetized fish was placed belly-up on a moist sponge and a dye (potassium permanganate) was applied onto the genital papilla with a Q-tip, as suggested by L.O.B. Afonso (pers. comm. to the first author). This dye was used to highlight a slit (genital opening) present only in the females (Afonso and Lebouté 1993). The anaesthetized fish was then placed under a dissecting microscope (magnification: 7-10X) to inspect the genital papilla. A fish was considered to be a female when the slit was observed. The sex determination procedure commenced on May 19, 1997 and was repeated and thereby verified during the monthly recordings of the weight and length measurements.

### **Behavioral measures**

Detailed descriptions of cichlid behavior can be found in Baerends and Baerends-van Roon (1950), Billy (1982), and Fryer and Iles (1972). For the purpose of this experiment, the activity was measured on the basis of the following twelve behaviors.

- 1) Swimming: a movement of the fish in any direction in the water column without any interactions with other fish;
- 2) Resting: a fish stays in the same position, either in the water column or on the gravel bottom, long enough for the computer key used to encode resting behavior to be pressed by the observer;
- 3) Chasing/Escaping: a fish swimming after another fish at a high velocity is described as chasing, while escape behavior is carried out by the fish swimming away from the aggressor;
- 4) Tail-beating: a fish presents the lateral aspect of its body to an opponent, head to tail, and uses its caudal fin to beat the water sideways over the head of its opponent (Baerends and Baerends-van Roon 1950; Billy 1982; Fryer and Iles 1972). The tail-beating individual does not actually touch the opponent. Tail-beating is used as a threat signal by a territorial male towards an intruding male (Billy 1982); presumably, this act communicates the animal's strength (Baerends and Baerends-van Roon 1950). Tail-beating also serves as a courtship signal by a territorial male towards a female entering his territory (Billy 1982);

- 5) Nipping: a bite directed towards a fin and/or the body of a neighbouring fish. Occasionally, nipping results in fin amputation and body scarring (Billy 1982);
- 6) Confronting: occurs between territorial males during boundary disputes. Opposing males rush at each other ending their charges at the common boundary (nest rim). The males then oscillate back and forth in synchrony, with one male (fins collapsed) retreating while its opponent (fins raised) advances a few centimetres. This back and forth motion is completed several times in rapid succession, after which the males separate or attack (e.g., jaw lock) (Billy 1982);
- 7) Jaw lock: the fish grip each other's mouth, and start pushing and pulling each other to and fro (Fryer and Iles 1972);
- 8) Opercular flare: a fish erects the operculae and branchiostegal membrane, and reveals its dorsally-situated black opercular spots;
- 9) Gulping: a fish swims to the water surface and takes in surface water with its mouth. This behavior increases oxygen uptake, i.e., complements gill breathing (Weber and Kramer 1983);
- 10) Feeding: a fish picks up sand with its mouth, sifts (i.e., separates food particles from sand), and then drops sand indiscriminately;
- 11) Nesting: a fish swims head down into the substrate, secures a mouthful of sand, swims a short distance from the centre of the pit, and spits out the substrate. In contrast to feeding, no sifting is performed. The displaced substrate is deposited on the edge of a territory, where it accumulates and forms a raised rim around the nest. This raised rim defines territorial boundaries. Localized digging produces a pit which a male occupies and defends from intruders while attempting to attract spawning partners. Nesting is used to maintain the nest rim and to remove debris from the pit. Each male digs throughout its residency in a territory, with the frequency of digging at a peak when the territory is being established. The female fish also nest, but only in the later stages of courtship prior to spawning (Billy 1982).

The total duration of swimming and resting was recorded, while the number of bouts of chasing, escaping, tail-beating, nipping, confronting, jaw-locking, opercular flaring, gulping, feeding, and nesting were recorded. The data on locomotor and agonistic behaviors were then analysed using The Observer version 3.0 computer software (Noldus Information Technology, Wageningen, Netherlands).

### **Experimental procedures**

Small mixed sex groups (5 fish per tank) of GIFT and control strains were established in 55 L aquaria on March 7, 1997. At this time, the mean weight and standard length of the mixed sex GIFT and control fish were  $5.3 \pm 1.6$  g and  $5.3 \pm 0.6$  cm, and  $4.8 \pm 1.8$  g and  $5.1 \pm 0.7$  cm, respectively. Initially, the fish could not be sexed, and hence the mixed sex design. However, as the experiment progressed and the fish grew, sex determination became possible.

At the start of the experiment (April 19th), each aquarium contained five fish. However, as the experiment progressed, some aquaria had less than five fish present as a result of mortality. The aquaria with four fish were retained in the experiment. Groups with fewer than four fish were excluded. Preliminary observations showed that the fish in aquaria with four or five fish had similar activity levels, while the surviving fish in the tanks with less than four fish were very aggressive. This resulted, in most cases, in only one fish remaining in the tank.

On day 1, the weight and standard length measurements were recorded. The locomotor and aggressive activities of the control and GIFT fish were video recorded on day 10 and day 12 (trials #1 and 2, respectively) during a 300 second observation period. On day 31, length and weight measurements were repeated. This experimental schedule was repeated three times over the three-month study period (April-June). The mean growth and behavioral measurements of all fish in an experimental group were compared, instead of individual measures because growth and behavior of individual fish in each aquarium were not independent of the behavior of other members of the group. Due to the fact that individual fish in the video recordings of the first trial in April could not be identified, only trial #2 could be used to compare activity levels between the female and male fish of each strain. Furthermore, size-specific mortality in male and female fish could only be examined in May and June because, in April, the sex of the fish could be determined neither by the external examination of the genital papilla due to the small size of fish, nor by the dissection of the gonads, due to the cannibalistic practice of live tank mates towards dead fish.



Aggressive behavior of males from the control and GIFT strains in response to a mirror image was also examined. Biting and tail-beating behaviors were distinguished in the MIS tests. These two behaviors are similar to the nipping and tail-beating behaviors previously mentioned, except that they are directed towards a mirror instead of a conspecific.

Small groups (5 fish per tank) of mixed sex GIFT and control strains were re-established in 55 L aquaria on November 15, 1997. These fish had been previously used in the growth experiment approximately four and a half months earlier. On day 1 (Nov. 19th), the weight and standard length measurements of all male fish were recorded; during the two week study period, the mean weight and standard length of the male control and GIFT fish were  $26.2 \pm 9.8$  g and  $9.5 \pm 1.3$  cm, and  $34.0 \pm 10.6$  g and  $10.2 \pm 1.2$  cm, respectively. On day 3, one day prior to the start of behavioral observations, male control and GIFT fish were individually placed in 55 L aquaria; the mean water temperature of the experimental aquaria was  $23.7 \pm 0.3^\circ\text{C}$  during the two week study period. Each experimental aquarium was divided in two by an opaque partition; the fish was placed on the left side with a boxed filter, while the mirror was positioned on the right side behind the partition.

On day 4, at the start of each behavioral session, the partition was lifted exposing the mirror to the fish. A 300 second observation period began when the male fish was observed, on the video monitor, swimming towards the mirror and performing either biting or tail-beating behaviors. At the end of the day when all behavioral sessions were recorded, the fish were returned to their appropriate stock tanks and new fish were transferred to the experimental aquaria for the next day. Each male was tested twice about a week apart between the two trials, so the data provided is a mean of the two trials.

### Statistical analyses

Linear regressions were used to test for significant differences in the growth curves (weight and length). The Mann-Whitney U-test was used in the comparison of independent measures of fish from the GIFT and control strain. These tests were one-tailed unless otherwise stated. The chi-square goodness of fit test was used to determine if there were significant differences between the actual number of fish from four experimental groups (i.e., female control, male control, female GIFT and male GIFT) that performed behavioral activities, and a theoretically even distribution. If the chi-square analysis detected significant departures from the even distribution, it was subdivided to determine whether the significant difference between observed and expected frequencies was concentrated in certain of the experimental groups, or whether the difference was due to the effects of the data in all of the four experimental groups (Zar 1996). When the observed frequencies were small, the use of the two-tailed Fisher exact test was preferred over the chi-square analysis. The level of significance was set at  $p = 0.05$  for all statistical analyses.

## RESULTS

### Growth, activities and sexual maturation in the control and GIFT strains of Nile tilapia

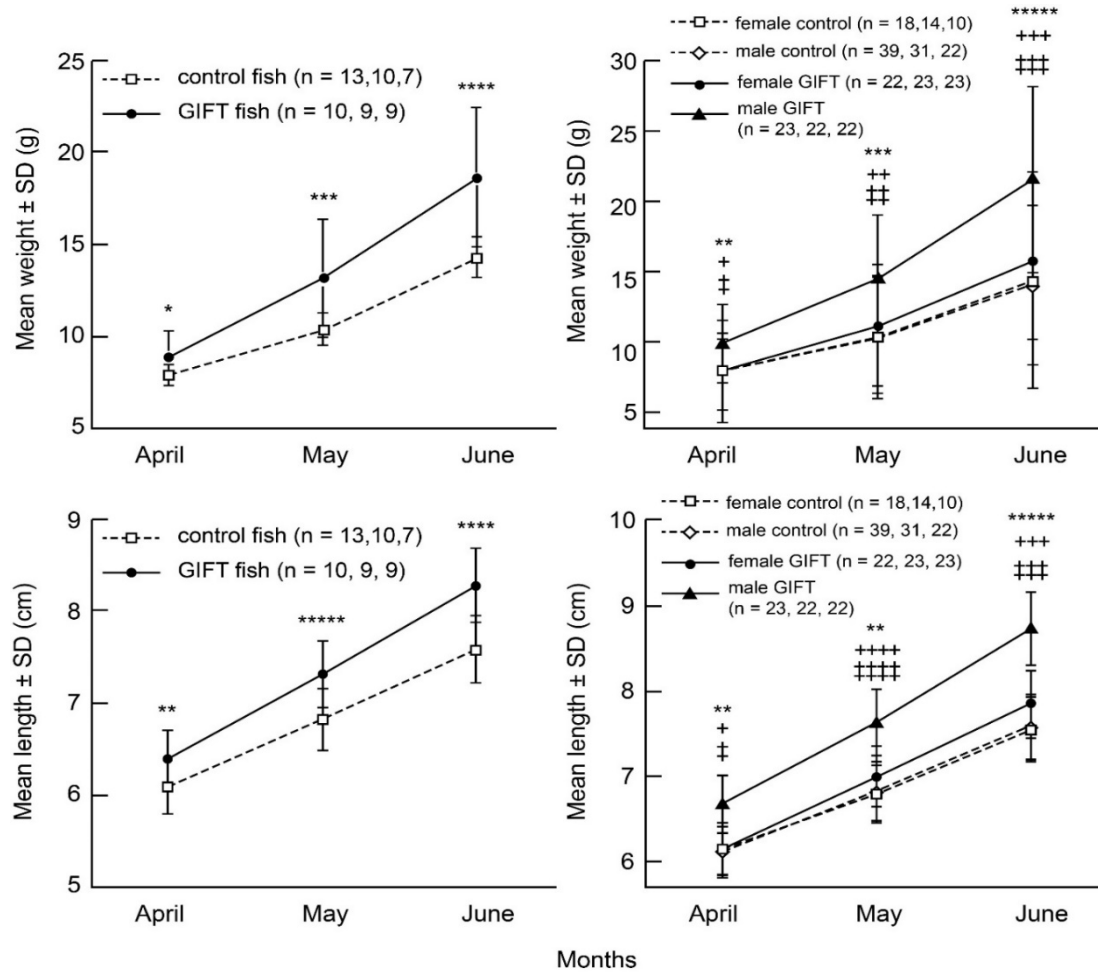
During the three-month study period (April-June), the GIFT fish were observed to have significantly faster growth rates than the control fish (one-tailed comparison of simple linear regression equations; weight:  $p < 0.05$ , length:  $p < 0.005$ ) (Figure 1). GIFT fish gained  $4.9 \text{ g} \cdot \text{month}^{-1}$  and increased in length by  $0.9 \text{ cm} \cdot \text{month}^{-1}$ , while the values for the control fish were  $3.2 \text{ g} \cdot \text{month}^{-1}$  and  $0.7 \text{ cm} \cdot \text{month}^{-1}$ , respectively. Furthermore, the weight and length of the GIFT fish were found to be significantly greater than the control fish at each measurement (Figure 1).

**Table 1.** Total time (mean  $\pm$  SD) two strains of juvenile Nile tilapia (control and GIFT) performed swimming and resting acts each month of the three-month study. Each month two 300 second behavioural trials were recorded one day apart. All experimental aquaria had four or five fish present and the number of aquaria used is represented by the n-values (data from the aquaria with less than four fish present were not used). The Mann-Whitney U-test (one-tailed) was used to test for significant differences in the total time the control and GIFT fish allotted to swimming and resting acts each month. \*  $p < 0.025$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.005$ , \*\*\*\*  $p = 0.0025$ .

MONTH	STRAINS OF NILE TILAPIA	TOTAL TIME (SEC) SPENT PERFORMING BEHAVIOURS PER 300 SECOND TRIAL (MEAN $\pm$ SD)	
		Swimming	Resting
April	control (n=13)	$76.4 \pm 81.0^{***}$	$213.4 \pm 85.3^{****}$
	GIFT (n=10)	$19.3 \pm 33.0$	$279.8 \pm 33.2$
May	control (n=10)	$51.9 \pm 45.8^*$	$233.3 \pm 60.4^{**}$
	GIFT (n=9)	$10.7 \pm 12.6$	$287.8 \pm 15.3$
June	control (n=7)	$41.4 \pm 46.1$	$252.2 \pm 57.7$
	GIFT (n=9)	$19.1 \pm 27.1$	$280.1 \pm 29.0$

The GIFT fish also spent less time swimming and more time resting than the control fish (Table 1). The differences in swimming/resting behaviors between the control and GIFT fish were significant in April and May, but not in June (Table 1). The time the control fish spent swimming decreased by 46% during the three-month period, while the level of swimming activity for the GIFT fish remained relatively constant (Table 1). In contrast, the control fish increased the time spent resting by 18% during the study, while the resting values for the GIFT fish again remained relatively constant (Table 1).

Moreover, control fish performed more chasing and escaping behaviors than the GIFT fish (Table 2). The differences were significant in April and May, but not in June (Table 2). The frequency of chasing and escaping exhibited by control fish increased in May by 23% and 10% of April values, respectively, and then declined in June by 55% and 52%, respectively (Table 2). In the GIFT fish, the frequency of chasing increased by 29% during the study, while escaping increased in May by 20% of April values, and then declined in June



**Figure 1.** Upper left: Weight (mean ± SD) and Lower left: Length (mean ± SD) of fish from two strains of Nile tilapia (control and GIFT). All experimental aquaria had four or five fish present and the number of aquaria used during the study period is represented by the n-values (data from aquaria with less than four fish present were not used in the mean weight calculations). The Mann-Whitney U-test (one-tailed) was used to test for significant differences in the weight and length, respectively, of fish of both strains. (\* $p < 0.05$ , \*\* $p < 0.025$ , \*\*\* $p < 0.01$ , \*\*\*\* $p = 0.005$ , \*\*\*\*\* $p < 0.0025$ ). Upper right: Weight (mean ± SD) and Lower right: Length of females and males from two strains of Nile tilapia (control and GIFT). The numbers of males and females from both strains used during the three-month study is represented by the n-values. The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the weight of females and males of the same strain (GIFT: \* $p < 0.05$ , \*\* $p < 0.025$ , \*\*\* $p < 0.01$ , \*\*\*\* $p = 0.005$ , \*\*\*\*\* $p < 0.0025$ ), females or males of different strains (males: +  $p < 0.01$ , ++  $p < 0.001$ , +++  $p < 0.0005$ , ++++ $p < 0.0025$ ), and females and males of different strains (GIFT male vs control female: †  $p < 0.025$ , ††  $p < 0.01$ , †††  $p < 0.0025$ , ††††  $p < 0.0005$ )

by 37% (Table 2). A higher frequency of tail-beating was characteristic of the control fish compared to the GIFT fish; the differences were only significant in April (Table 2). Tail-beating frequency of control fish increased by 61% during the study while, in GIFT fish, the frequency increased in May by 327% of April values, and then declined by 70% in June (Table 2). Furthermore, nipping frequency was found to be significantly higher in the control fish than the GIFT fish during the three-month study period. The nipping frequency of control and GIFT fish increased in May by 169% and 129% of April values, respectively, and then declined in June by 73% and 94%, respectively (Table 2). Only the control fish performed confronting and jaw-locking behaviors and the frequency of confronting declined by 73% during the study, while jaw-locking remained relatively constant (Table 2). No opercular flares were performed during the behavioral trials so this behavior was excluded from analyses.

Gulping was also found to be mostly performed by the control fish (Table 2). An increase (114%) in the frequency of gulping was observed in May, and then dropped to zero in the behavioral sessions of June (Table 2). Feeding behavior was performed more often by control fish than GIFT fish especially in May, but the differences were not significant (Table 2). The feeding frequency of control fish increased in May by 150% of April values while, in the GIFT fish, the frequency remained relatively constant (Table 2). In the behavioral sessions of June, no feeding behavior was recorded by either control or GIFT fish (Table 2).

As the experiment progressed and the sex of each fish could be determined, the weight and length, and activity levels of male and female fish of both strains were compared. During the three-month study period, the male GIFT fish were observed to have a faster growth than the female GIFT fish (Figure 1). The difference was significant only for growth in length (one-tailed comparison of simple linear regression equations;  $p < 0.05$ ). The male GIFT fish gained 5.8 g·month<sup>-1</sup> and increased in length by 1.0 cm·month<sup>-1</sup>, while the corresponding values for the female GIFT were 3.9 g·month<sup>-1</sup> and 0.9 cm·month<sup>-1</sup>, respectively. In contrast, the growth rates of the male and female control fish were similar (Figure 1). The male control fish gained 3.1 g·month<sup>-1</sup> and increased in length by 0.7 cm·month<sup>-1</sup>, and the values for the female control fish were 3.2 g·month<sup>-1</sup> and 0.7 cm·month<sup>-1</sup>, respectively. The growth rate in weight of female GIFT was slightly higher than the male and female control fish (Figure 1). However, in the male GIFT, the growth rate in weight was found to be significantly higher (one-tailed comparison of simple linear regression equations; comparison of female and male control to male GIFT fish:  $p < 0.05$ ,  $p < 0.05$ , respectively). Furthermore, the growth rates in length of the female and male GIFT were significantly different than that of the male and female control fish (one-tailed comparison of simple linear regression equations; comparison of female and male control to female GIFT fish:  $p < 0.025$ ,  $p < 0.005$ , respectively; comparison of female and male control to male GIFT fish:  $p < 0.025$ ,  $p < 0.025$ , respectively).

The weight and length of the male GIFT were significantly higher than the female GIFT during the three-month study period. In contrast, the weight of the male control was slightly lower than the female control during the study. The length of the male control also was slightly lower than the female control fish in April, but then increased slightly above length values of female control in May and June (Figure 1). Furthermore, the weight and length of male GIFT fish were significantly greater than either the male or female controls, while the measurements of the female GIFT fish were slightly higher than either the female or male controls (Figure 1). The only exception was in April where the weight of the female GIFT fish was found to be slightly lower than in the female controls.

The male control fish also spent more time swimming and less time resting than the female control fish. However, a significant difference in the allotment of time to swimming and resting was only found in May (Table 3). In contrast, the male GIFT fish spent less time swimming and more time resting than the female GIFT fish, except in April (Table 3). The differences in swimming and resting behaviors were significant only in June (Table 3). Furthermore, the male control fish spent significantly more time swimming and less time resting than either female or male GIFT fish (Table 3). The female control fish also spent more time swimming and less time resting than either female (except in June) or male GIFT fish (Table 3). The differences in swimming and resting behaviors between the female control and male GIFT fish were significant throughout the three-month study. The differences in swimming behavior between the female control and GIFT fish were only significant in April, while the differences in resting behaviors were significant in both April and May (Table 3).

**Table 2.** Number of bouts of locomotory and agonistic behaviours (mean  $\pm$  SD) the control and GIFT strains of juvenile Nile tilapia performed each month of the three-month study. Each month two 300 second behavioral trials were recorded one day apart. The number of control and GIFT aquaria used each month is represented by the n-values. The Mann-Whitney U-test (one-tailed test, except for gulping and feeding behaviours) was employed to test for significant differences between the number of acts performed by the fish from the control and GIFT aquaria for each month. \*  $p=0.05$ , \*\*  $p<0.025$ , \*\*\*  $p<0.01$ , \*\*\*\*  $p<0.005$ , \*\*\*\*\*  $p<0.0025$ .

MONTH	STRAINS OF NILE TILAPIA	NUMBER OF BOUTS OF LOCOMOTORY AND AGONISTIC BEHAVIORS (MEAN $\pm$ SD)								
		Chasing	Escaping	Tail-beat.	Nipping	Confront.	Jaw-lock.	Gulping	Feeding	Nesting
April	control (n=13)	1.2 $\pm$ 1.3***	1.7 $\pm$ 1.8*****	0.6 $\pm$ 0.8**	0.3 $\pm$ 0.3*	0.1 $\pm$ 0.3	0.01 $\pm$ 0.03	1.0 $\pm$ 3.1	0.2 $\pm$ 0.4	0.1 $\pm$ 0.3
	GIFT (n=10)	0.2 $\pm$ 0.4	0.3 $\pm$ 0.5	0.1 $\pm$ 0.4	0.1 $\pm$ 0.1	0	0	0	0.1 $\pm$ 0.3	0
May	control (n=10)	1.5 $\pm$ 1.4***	1.9 $\pm$ 1.7****	0.9 $\pm$ 1.2	0.7 $\pm$ 0.6****	0.1 $\pm$ 0.2	0.02 $\pm$ 0.06	2.1 $\pm$ 5.3	0.4 $\pm$ 1.0	0.2 $\pm$ 0.5
	GIFT (n=9)	0.2 $\pm$ 0.5	0.3 $\pm$ 0.8	0.5 $\pm$ 1.4	0.2 $\pm$ 0.2	0	0	0.01 $\pm$ 0.03	0.1 $\pm$ 0.3	0.01 $\pm$ 0.03
June	control (n=7)	0.7 $\pm$ 0.9	0.9 $\pm$ 1.4	1.0 $\pm$ 2.1	0.2 $\pm$ 0.3**	0.03 $\pm$ 0.05	0	0	0	0.4 $\pm$ 0.8
	GIFT (n=9)	0.2 $\pm$ 0.6	0.2 $\pm$ 0.5	0.1 $\pm$ 0.3	0.01 $\pm$ 0.03	0	0	0	0	0.03 $\pm$ 0.10

**Table 3.** Total time in seconds (mean  $\pm$  SD) performing swimming and resting acts and number of bouts of agonistic and escape behaviours (mean  $\pm$  SD) performed by the female and male juvenile Nile tilapia (control and GIFT strains) each month of the three-month study. Each month two 300 second behavioral trials were recorded one day apart. The five behaviors included under the agonistic category are chasing, tail-beating, nipping, confronting, and jaw-locking. Due to unforeseen circumstances, only data from the behavioral trial #2 in April were tabulated. The number of female and male fish of both strains used each month is represented by the n-values (i.e., # of fish in April, May, June, respectively). In each table cell, the top values represent the sex/strain of Nile tilapia of the column heading, while the bottom values represent the sex/strain of Nile tilapia of the row. The Mann-Whitney U-test (one-tailed) was employed to test for significant differences in the total time the female and male fish of both strains allotted to swimming and resting acts each month. \*  $p < 0.05$ , +  $p < 0.025$ , \*\*  $p = 0.01$ , ++  $p < 0.01$ , \*\*\*  $p < 0.005$ , ‡  $p < 0.025$ , +++  $p < 0.001$ , \*\*\*\*  $p < 0.0005$ .

SEXES/STRAINS OF NILE TILAPIA		female control (n=18, 14, 10)			male control (n=39, 31, 22)			male GIFT (n=23, 22, 22)		
		April	May	June	April	May	June	April	May	June
female GIFT (n=22, 23, 23)	Swimming	70.3 $\pm$ 79.8 *	35.1 $\pm$ 43.2	19.2 $\pm$ 16.5	84.7 $\pm$ 99.7 ***	62.9 $\pm$ 51.4 ****	55.5 $\pm$ 56.7 *	35.3 $\pm$ 64.3	10.0 $\pm$ 18.3	12.8 $\pm$ 24.6 +
		35.1 $\pm$ 55.1	11.5 $\pm$ 12.7	25.1 $\pm$ 27.6	35.1 $\pm$ 55.1	11.5 $\pm$ 12.7	25.1 $\pm$ 27.6	35.1 $\pm$ 55.1	11.5 $\pm$ 12.7	25.1 $\pm$ 27.6
	Resting	221.0 $\pm$ 81.1 *	256.5 $\pm$ 52.3 *	279.7 $\pm$ 18.2	202.4 $\pm$ 97.6 +++	218.0 $\pm$ 69.7 ****	234.8 $\pm$ 71.4 +	261.2 $\pm$ 65.3	288.3 $\pm$ 23.7	286.0 $\pm$ 28.4 +
		264.0 $\pm$ 55.2	287.3 $\pm$ 13.9	274.6 $\pm$ 28.3	264.0 $\pm$ 55.2	287.3 $\pm$ 13.9	274.6 $\pm$ 28.3	264.0 $\pm$ 55.2	287.3 $\pm$ 13.9	274.6 $\pm$ 28.3
	Agonistic	0.1 $\pm$ 0.1	0.1 $\pm$ 0.3	0.2 $\pm$ 0.6	0.5 $\pm$ 1.4 *	0.9 $\pm$ 1.4 ***	0.6 $\pm$ 1.6 ***	0.3 $\pm$ 0.9	0.3 $\pm$ 1.1	0.1 $\pm$ 0.5
		0.03 $\pm$ 0.09	0.1 $\pm$ 0.1	0.04 $\pm$ 0.13	0.03 $\pm$ 0.09	0.1 $\pm$ 0.1	0.04 $\pm$ 0.13	0.03 $\pm$ 0.09	0.1 $\pm$ 0.1	0.04 $\pm$ 0.13
	Escaping	3.0 $\pm$ 3.7 ‡	1.6 $\pm$ 1.9	0.6 $\pm$ 1.0	2.2 $\pm$ 3.9 +	2.1 $\pm$ 3.0	1.2 $\pm$ 2.1 *	0.7 $\pm$ 1.6	0.2 $\pm$ 0.8	0.1 $\pm$ 0.6
		0.4 $\pm$ 1.0	0.4 $\pm$ 1.4	0.2 $\pm$ 0.6	0.4 $\pm$ 1.0	0.4 $\pm$ 1.4	0.2 $\pm$ 0.6	0.4 $\pm$ 1.0	0.4 $\pm$ 1.4	0.2 $\pm$ 0.6
male GIFT (n=23, 22, 22)	Swimming	70.3 $\pm$ 79.8 +	35.1 $\pm$ 43.2 ++	19.2 $\pm$ 16.5 **	84.7 $\pm$ 99.7 ***	62.9 $\pm$ 51.4 ****	55.5 $\pm$ 56.7 ****	-----	-----	-----
		35.3 $\pm$ 64.3	10.0 $\pm$ 18.3	12.8 $\pm$ 24.6	35.3 $\pm$ 64.3	10.0 $\pm$ 18.3	12.8 $\pm$ 24.6	-----	-----	-----
	Resting	221.0 $\pm$ 81.1 +	256.5 $\pm$ 52.3 ***	279.7 $\pm$ 18.2 **	202.4 $\pm$ 97.6 +++	218.0 $\pm$ 69.7 ****	234.8 $\pm$ 71.4 ****	-----	-----	-----
		261.2 $\pm$ 65.3	288.3 $\pm$ 23.7	286.0 $\pm$ 28.4	261.2 $\pm$ 65.3	288.3 $\pm$ 23.7	286.0 $\pm$ 28.4	-----	-----	-----
	Agonistic	0.1 $\pm$ 0.1	0.1 $\pm$ 0.3	0.2 $\pm$ 0.6	0.5 $\pm$ 1.4	0.9 $\pm$ 1.4 ***	0.6 $\pm$ 1.6 ***	-----	-----	-----
		0.3 $\pm$ 0.9	0.3 $\pm$ 1.1	0.1 $\pm$ 0.5	0.3 $\pm$ 0.9	0.3 $\pm$ 1.1	0.1 $\pm$ 0.5	-----	-----	-----
	Escaping	3.0 $\pm$ 3.7 ++	1.6 $\pm$ 1.9 ***	0.6 $\pm$ 1.0	2.2 $\pm$ 3.9	2.1 $\pm$ 3.0 ****	1.2 $\pm$ 2.1 ***	-----	-----	-----
		0.7 $\pm$ 1.58	0.2 $\pm$ 0.8	0.1 $\pm$ 0.6	0.7 $\pm$ 1.6	0.2 $\pm$ 0.8	0.1 $\pm$ 0.6	-----	-----	-----
male control (n=39, 31, 22)	Swimming	70.3 $\pm$ 79.8	35.1 $\pm$ 43.2 *	19.2 $\pm$ 16.5	-----	-----	-----	-----	-----	-----
		84.7 $\pm$ 99.7	62.9 $\pm$ 51.4	55.5 $\pm$ 56.7	-----	-----	-----	-----	-----	-----
	Resting	221.0 $\pm$ 81.1	256.5 $\pm$ 52.3 *	279.7 $\pm$ 18.2	-----	-----	-----	-----	-----	-----
		202.4 $\pm$ 97.6	218.0 $\pm$ 69.7	234.8 $\pm$ 71.4	-----	-----	-----	-----	-----	-----
	Agonistic	0.1 $\pm$ 0.1	0.1 $\pm$ 0.3	0.2 $\pm$ 0.6	-----	-----	-----	-----	-----	-----
		0.5 $\pm$ 1.4	0.9 $\pm$ 1.4	0.6 $\pm$ 1.6	-----	-----	-----	-----	-----	-----
	Escaping	3.0 $\pm$ 3.7	1.6 $\pm$ 1.9	0.6 $\pm$ 1.0	-----	-----	-----	-----	-----	-----
		2.2 $\pm$ 3.9	2.1 $\pm$ 3.0	1.2 $\pm$ 2.1	-----	-----	-----	-----	-----	-----

During the three month study, the total time male and female control fish spent swimming declined by 35% and 73% of starting (April) values, respectively, while the time spent resting increased by 16% and 27%, respectively (Table 3). In contrast, the amount of time the male and female GIFT fish spent swimming declined in May by 72% and 67% of the April values, respectively, but then increased in June by 29% and 119%, respectively (Table 3). Moreover, the total time male and female GIFT fish spent resting increased from April to May by 10% and 9%, respectively, but then declined slightly (i.e., by 1% and 4%, respectively) in June (Table 3).

Male fish performed more agonistic behaviors than the female fish (except in June between male GIFT and female control). However, only the differences between the male control and female GIFT fish were significant (Table 3). When males of both fish strains were compared, the male control performed more agonistic behavior than the male GIFT fish (Table 3). The differences were significant in May and June, but not in April. When the females were compared, the control also performed more agonistic behavior than the GIFT fish, but the differences were not significant (Table 3). The frequency of agonistic behavior exhibited by male control, and female and male GIFT fish increased in May by 65%, 100% and 4% of the April values, respectively, then declined in June by 27%, 33% and 48%, respectively, while the frequency of agonistic behavior exhibited by female control increased by 243% during the study. The number of male control fish performing agonistic behaviors was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: April,  $p < 0.01$ ; May,  $p < 0.001$ ; June,  $p < 0.005$ ).

Escape behavior was performed by both female and male fish (Table 3). Both the male and female control fish performed more escape behavior than the male and female GIFT fish (Table 3). The differences in escape behavior between the female control and GIFT fish were only significant in April, while the differences between female control and male GIFT were significant in both April and May (Table 3). In the comparison of the male control to the female and male GIFT, significant differences were found in April and June, and May and June, respectively (Table 3). When female and male control fish were compared, male fish exhibited less escape behavior in April than female fish, but in May and June, male fish performed more escape behavior than female fish. In

**Table 4.** Number of bouts of locomotory behaviors (mean  $\pm$  SD) performed by the female and male juvenile Nile tilapia (control and GIFT strains) each month of the three-month study. Each month two 300 second behavioral trials were recorded one day apart. Due to unforeseen circumstances, only data from the behavioral trial #2 in April were tabulated. The number of female and male fish of both strains used each month is represented by the n-values. The Mann-Whitney U-test (two-tailed test, except for nesting behaviour) was employed to test for significant differences between the number of acts performed by the female and male fish from the control and GIFT aquaria for each month.

Month	Sexes/strains of Nile tilapia	Number of bouts of locomotory behaviors (mean $\pm$ SD)		
		Gulping	Feeding	Nesting
April	female control (n=18)	0	0	0
	male control (n=39)	2.7 $\pm$ 13.4	0.5 $\pm$ 1.9	0
	female GIFT (n=22)	0	0.1 $\pm$ 0.5	0
	male GIFT (n=23)	0	0.3 $\pm$ 1.1	0
May	female control (n=14)	1.3 $\pm$ 4.7	0.2 $\pm$ 0.8	0
	male control (n=31)	2.8 $\pm$ 9.7	0.4 $\pm$ 1.2	0.3 $\pm$ 1.3
	female GIFT (n=23)	0	0.1 $\pm$ 0.2	0
	male GIFT (n=22)	0.02 $\pm$ 0.11	0.1 $\pm$ 0.5	0.02 $\pm$ 0.11
June	female control (n=10)	0	0	0
	male control (n=22)	0	0	0.4 $\pm$ 1.7
	female GIFT (n=23)	0	0	0
	male GIFT (n=22)	0	0	0.1 $\pm$ 0.3

contrast, male GIFT fish exhibited more escape behavior in April, but performed less escape behavior than female GIFT fish in May and June. No significant difference in escape behavior was found between female and male of either the control or GIFT strain. The frequency of escape behavior exhibited by the female and male control, and the female and male GIFT fish declined during the study by 82%, 47%, 42%, and 80% of the April values, respectively. The number of male control fish performing escape behavior was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: April,  $p < 0.025$ ; May,  $p < 0.001$ ; June,  $p < 0.025$ ).

Gulping was mostly performed by the male control fish; however, in May, the female control fish also performed gulping behavior (Table 4). A slight increase in the gulping frequency of male control and GIFT fish was observed in May, but it dropped to zero in June. The number of male control fish gulping was greater than either the number of female control, male GIFT or female GIFT fish; however, the differences were not significant.

A greater number of feeding bouts were performed by the male control and GIFT fish than the female fish; however, in May, the feeding frequency of the female control was higher than male GIFT. The feeding frequency of male control fish also was greater than male GIFT fish; the difference was significant only in May (Table 4). In contrast, female GIFT performed more feeding bouts than female control in April, while female control performed more feeding bouts than female GIFT in May. The feeding frequency of male controls and of female and male GIFT fish declined in May by 4%, 50%, and 63% of April values, and then dropped to zero in June. The number of male control fish feeding during the behavioral trials was significantly greater than the number of female control, and male and female GIFT fish combined (corrected chi-square analyses: May,  $p < 0.01$ ).

To assess the sexual maturity of fish, nesting behaviors, and the number of nests present in both the control and GIFT aquaria were recorded during the three-month study period. Nests were first observed on April 1st in three of the control tanks; and by the eve of the first behavioral trial in April, nests were present in 11 of the 13 control tanks compared to only 1 GIFT tank out of a total of 10. During the three-month study period, nesting behavior was performed more frequently by the control fish than the GIFT fish, but the differences were not significant (Table 2). A large increase (236%) in nesting frequency of control fish was observed during the study, while the nesting frequency of GIFT fish increased slightly (Table 2). Only males of both the GIFT and control strains were observed to perform nesting behavior. The nesting frequency of male control increased from May to June by 45%, while the frequency of male GIFT increased slightly (Table 4). The number of male control fish nesting was greater than either the number of female control, male GIFT or female GIFT fish; however, the differences were not significant. Furthermore, significantly more nests were present in the control aquaria than GIFT aquaria during the three-month study (Figure 2). Control fish also built more nests earlier in study (i.e., April) than GIFT fish; it took the GIFT fish until June to reach the number of nests found in the control aquaria in April (Figure 2).

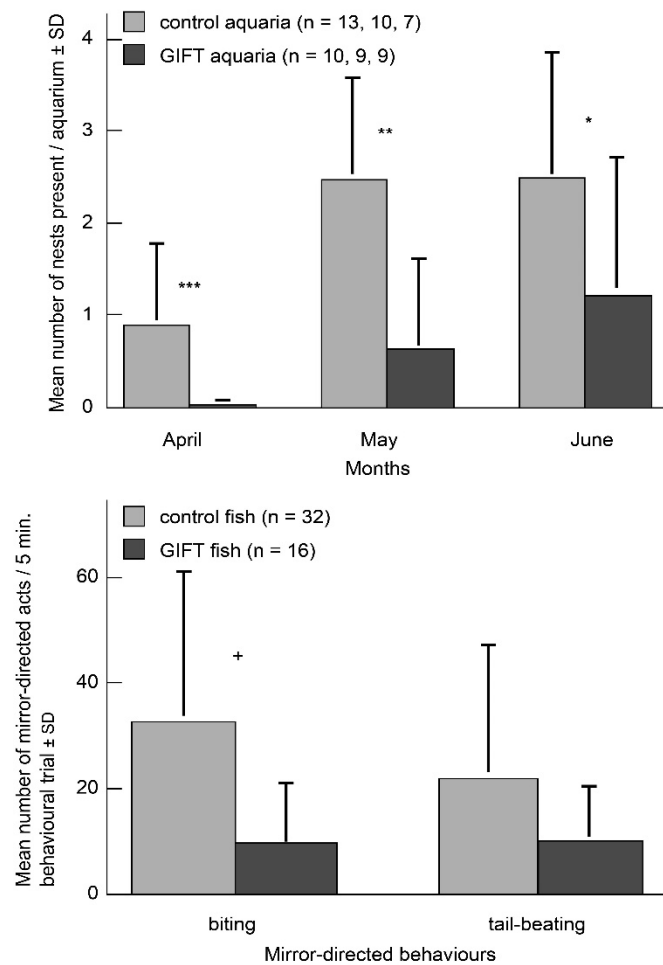


Figure 2. Upper panel: Number of nests (mean  $\pm$  SD) present in the experimental aquaria (control and GIFT strain of Nile tilapia). All experimental aquaria had four or five fish present and the number of aquaria used during the three-month study is represented by the n-values (data from aquaria with less than four fish present were not employed in the mean calculations). The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the number of nets present in the control and GIFT aquaria for each month. \* $p = 0.05$ , \*\* $p < 0.005$ , \*\*\* $p < 0.0005$ . Lower panel: Number of mirror-directed biting and tail-beating (mean  $\pm$  SD) performed by the male fish from two strains of Nile tilapia (control and GIFT) during the two behavioral trials. Each behavioral trial was five minutes in duration and the two trials were spread out over a one-week period. The Mann-Whitney U-test (one-tailed) was used to test for significant differences between the number of mirror-directed acts performed by the male control and GIFT fish during the behavioral trials. + $p < 0.001$

Size-specific mortality was observed in both strains (Table 5). The dead control fish had lower weights and lengths than the live fish present in the same experimental aquaria; the differences were significant in May and June, but not in April (Table 5). The dead GIFT fish also had smaller weight and length measurements than the live fish in the same experimental aquaria; however, no rigorous analyses could be performed due to the low number of dead fish (Table 5). The weight and length of dead and live male control fish were significantly different in both May and June, while the dead and live female fish were similar (Table 6). Therefore, size-specific mortality occurred only in male fish.

### **Aggressive behavior of males from the control and GIFT strains of Nile tilapia in response to a mirror image**

During the two-week study period, the male control fish performed a higher number of bouts of mirror-directed biting and tail-beating than the male GIFT fish (Figure 2). Only the differences in mirror-directed biting were significant (Figure 2).

## **DISCUSSION**

Under laboratory conditions, the GIFT fish grew faster than the fish from the control strain. It was not surprising that growth performance was higher in the GIFT than control fish, as the former had been subjected to intentional selection for that trait (Pullin, 1998 and see Introduction for background on Nile tilapia). The results from the behavioral experiment on Nile tilapia suggest that behavioral activity contributes to this effect on growth.

The fast growth of GIFT fish was associated with a lower activity level compared to control fish. GIFT fish performed less swimming and more resting behavior than control fish. These findings are similar to the study by Koebele (1985) on juvenile *Tilapia zillii*, which suggested that an increase in activity such as swimming may have resulted in a slight decrease in their mean growth. The fast-growing GIFT fish also exhibited a lower frequency of agonistic behavior than the slow-growing control fish. This connection between growth and aggression has been previously documented. Ruzzante and Doyle (1991) observed in the medaka, *Oryzias latipes*, that fish 'indifferent' to other neighboring fish (i.e., not involved in aggressive behavior) grew the fastest. In addition, a negative correlation between aggression and growth was found in the tilapia hybrid, *Oreochromis mossambicus* x *O. hornorum* (Robinson and Doyle 1990) and Atlantic salmon (Holm and Fernö 1986). Swimming activity, and especially agonistic interactions are energetically costly, and thus passive (i.e., GIFT) fish, with a relatively lower metabolic expenditure, should gain a growth advantage over active (i.e., control) fish. Increased demand for energy during exercise has been confirmed in several studies on oxygen consumption, which reflect behavioral activities in fish (Beamish 1980; Nahhas *et al.* 1982; Butler 1985).

The fact that the more active control fish have reduced compared with GIFT fish is well explained by the oxygen-limitation hypothesis proposed by Pauly (1981; see also Pauly 1984, 1994; 2010). It has been observed by Stewart *et al.* (1967), that largemouth bass held in hypoxic waters usually had a lower percent dry weight than fish held at concentrations near the air-saturation level. Balarin and Hatton (1979) found, in tilapia, that at low oxygen levels, growth decreased; Kolding *et al.* (2008) obtained similar results. Thus, anything, in a given population, that causes a higher metabolic expenditure (e.g., high activity level), will result in a reduced fish size.

Gulping was mostly performed by the active, slow-growing control fish. It has been observed that aquatic surface respiration (i.e., gulping) is initiated at higher oxygen concentrations than necessary for survival, and thus this behavior can provide an energetic advantage to fish (Weber and Kramer 1983). The fish approaching the water surface and aerating their gills with oxygen-saturated water increase oxygen uptake rate and/or decrease the work required for ventilation, as compared to subsurface respiration (Weber and Kramer 1983). An increase in the oxygen uptake rate of fish would permit greater food intake (Weber and Kramer 1983; Pauly 2010). The control fish was also observed to perform more feeding behavior than the GIFT fish. Intraspecific comparisons between wild and hatchery-reared Atlantic salmon have shown that wild fish generally feed more than hatchery fish (Fenderson *et al.* 1968; Sosiak *et al.* 1979).



A likely explanation for the higher gulping of control fish in April and May is that their higher oxygen requirements were due to their high activity and feeding frequency compared to GIFT strain. However, in June, no gulping was performed by the control fish during the behavioral recordings, which may be the result of a decline in their locomotor and agonistic activity. It is probable that, as the active control fish became larger, less oxygen per body weight was available for performing behavioral activity. However, the quieter GIFT fish, required less oxygen, so their lower activity level remained relatively unchanged.

The divergence in locomotor and agonistic behavior of the GIFT and control fish is not surprising, because behavioral traits are among the first traits to respond to domestication; it is usually the frequency or intensity with which a particular behavior is expressed that is affected by domestication (Price 1984). In the Philippines, both fish strains tested were reared under similar hatchery conditions (e.g., pH, salinity, temperature). Thus, the difference in activity level between GIFT and control fish must have been due to a genetic difference between the two types or to pre-fertilization environmental differences (environmental maternal effects) rather than a phenotypic/environmental effect (Swain and Riddell 1990). A genetic basis has been demonstrated for behavioral differences among families (Bakker 1986), populations (Rosenau and McPhail 1987), and closely-related species of fish (Ferguson and Noakes 1982, 1983), but no scientific studies have indicated an effect of the pre-fertilization, maternal environment on behavior (Swain and Riddell 1990). Thus, it is likely that the behavioral differences reported between GIFT and control fish are the result of the selection program described by Pullin (1998) that, by selecting for fast growth, actually selected for calm behavior.

In the comparison of female and male GIFT fish, the growth performance of males was higher than females. The growth advantage experienced by male GIFT fish was connected with a lower activity level. Male GIFT performed less swimming and escaping, and more resting behavior than female GIFT. Even though a higher frequency of agonistic behavior (excluding escape behavior) was exhibited by the fast-growing male GIFT fish, the difference in male and female frequencies was not significant, and the number of bouts of agonistic behavior performed by the male GIFT fish was up to 4.5 times less than male control values. The mirror image stimulation tests supported the finding that male control fish are more aggressive than male GIFT fish. When female and male fish of the GIFT and control strains were compared, the connection between growth and activity level was still observed, suggesting that differences in growth between sexes may be to some extent mediated by behavioral differences. However, in the control fish, the growth rates, and size of male and female fish were similar even though the male control fish performed more swimming and escaping behavior, and less resting than the female control fish. The male controls also exhibited a higher frequency of agonistic activity than the female controls.

In the comparison of female and male fish, low growth of fish was also associated with a high activity level; however, a few experimental observations seemed to deviate from this relationship. For example, the fast-growing male GIFT exhibited a higher frequency of agonistic activity (excluding escape behavior) compared to slow-growing female GIFT, and in the control fish, growth of male and female fish was relatively similar even though, the male control fish performed more locomotor and agonistic acts than the female control fish.

Conventional explanations of the higher growth in males have involved androgens or male sex hormones (Donaldson *et al.* 1979; Ufodike and Madu 1986). The anabolism-enhancing effect of androgens has been observed in Nile tilapia (Ufodike and Madu 1986), goldfish (Yamazaki 1976), and all salmonids (see Donaldson *et al.* 1979). Varadaraj and Pandian (1988) suggested, in 'normal' (phenotypic and genetic), and phenotypic males *Oreochromis mossambicus*, that androgens stimulated growth by increasing food intake or food conversion efficiency. Thyroid hormones ( $T_3$  and  $T_4$ ) are also involved in controlling growth and development of fish (see Donaldson *et al.* 1979). Toguyéni *et al.* (1996, 1997) observed, in the Nile tilapia, that plasma  $T_3$  levels were higher in males than females, and thus could account for the males' growth advantage over females. It was suggested that  $T_3$  increases the efficiency of food utilization by males, and thus their growth as well (Toguyéni *et al.* 1997). Eales and Shostak (1985) also observed, in a population of Arctic charr, that plasma  $T_3$  levels are strongly correlated with both food ration and growth. However, the behavioral differences, and their effects of oxygen availability for growth provide a more parsimonious explanation for the findings reported here.

Nesting behavior, which is often the first indication of the sexual maturity of fish, was observed only in males. Billy (1982) observed, in *Oreochromis mossambicus*, a species closely related to Nile tilapia, that both female

and male fish performed nesting behavior, but female fish only performed nesting behavior immediately prior to spawning. Male controls performed more nesting behavior than male GIFT fish. A significantly higher number of nests were also present in the control than GIFT aquaria. Aggression, as observed mostly in the male control fish, appears to be the prevalent mechanism of establishing and maintaining nesting sites (Fenderson *et al.* 1968; Mabaye 1971; Koebele 1985), and thus attracting mates (Oliveira *et al.* 1996). The control fish also built more nests earlier in the study (i.e., April) than the GIFT fish; it took the GIFT fish till June to reach the level of nesting activity observed in the control aquaria in April. These findings indicate, at least in males, that the slow-growing control fish became sexually mature sooner, and at a smaller size than the fast-growing GIFT fish. Siddiqui *et al.* (1997) also observed that in male and female hybrid tilapia, *Oreochromis niloticus* x *O. aureus*, fast-growing fish matured at larger sizes, whereas slow-growing fish matured at smaller sizes. These findings were confirmed by Kolding *et al.* (2008), who found that in Nile tilapia kept at different dissolved oxygen concentrations, the fish held under low oxygen not only grew more slowly, but also matured at small sizes, as predicted by Pauly (1984).

Size-related mortality was found in both strains of Nile tilapia: dead fish were smaller than the survivors (i.e., live fish). On examination of the bodies of the dead fish, many fish had frayed fins (i.e., pectoral, tail). Christiansen and Jobling (1990), Christiansen *et al.* (1991), and Siikavuopio *et al.* (1996) used the incidence of caudal fin damage as an indirect indication of aggressive interactions. If this interpretation is correct, most fish seem to have died from an aggressive encounter with a tank mate or the consequence of the aggression rather than from natural causes. It was suggested that high mortality in small fish may result from starvation as a consequence of the aggression of a few large individuals (Saclauso 1985). This behavior could have elicited inhibitory effects (e.g., small fish become less mobile) which denied the smaller conspecifics access to the food even if it was given in excess (Saclauso 1985).

In the control strain, it was observed that only male control fish experienced size-related mortality. The male control fish could have experienced size-related mortality because they performed more agonistic behavior than females, and the subordinate males, as suggested by Saclauso (1985), were probably unable to evade damaging and potentially lethal attacks of the dominant fish in closely confined aquaria.

Furthermore, control fish suffered a higher mortality than GIFT fish. The higher mortality of control fish could be correlated with their higher bouts of agonistic behavior compared to GIFT fish. Similarly, high mortality rates have been attributed to increase aggressiveness of fish (Saclauso 1985). Siikavuopio *et al.* (1996) observed a high mortality and incidence of caudal fin damage amongst wild-caught Arctic charr, while amongst hatchery-reared fish, mortalities were low and little evidence of fin damage was found. In all, these results add further support to the conclusion that the slow-growing control fish were more aggressive than the fast-growing GIFT fish during the three-month study period.

## CONCLUSIONS

The rearing of cultured fish has become an increasingly important industry. Fish culturists seek fish strains that possess high growth rates and reach harvestable size before attaining sexual maturation. Sexual maturation of fish can complicate production operations and/or affect product quality. This is especially important for the tilapia which, when they mature precociously, can overpopulate waters with small, stunted fish. Aggressiveness in the form of attacking and fin-nipping, also associated with breeding behavior, is an undesirable habit for farmed fish (Balarin and Hatton 1979) and one for important consideration when choosing a tilapiine strain for culture practices. It has been argued that in competitive environments, artificial selection for fast growth may lead to higher levels of overall aggression, and therefore would result in no net gain in assimilation efficiency or growth in the populations (Kinghorn 1983).

However, considering the oxygen demand of various behaviors of fish under domestication, such as in Nile tilapia, could be used in their selective breeding. The results of behavioral studies are likely to be of more direct utility to breeders than most physiological and biochemical measures such as food conversion efficiency, and protein, lipid and water contents of body tissues, which are indirect results of the underlying scarcity of oxygen available for growth in fish exhibiting, e.g., aggressive, oxygen-demanding behaviors (Pauly 1981, 2010).

The main focus of many breeders is on genetic improvement of farmed fish. If indeed quiet behavior reflects an underlying genetic variation and thus amenable to selection (as the GIFT fish demonstrate), then it could be incorporated into or even become the primary criterion of fish breeding programs. Quiet behavior could also be correlated with other desirable traits (e.g., high survival, disease resistance). The domestication of livestock (notably cattle) has involved a similar selection strategy.

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## INDICES FOR THE COMPARATIVE STUDY OF FISH GROWTH, WITH EMPHASIS ON RED BANDFISH *CEPOLA MACROPHTHALMA*<sup>\*</sup>

Konstantinos I. Stergiou<sup>1,2\*</sup> and Yong Chen<sup>3</sup>

<sup>1)</sup> *Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Aghios Kosmas, Athens, Greece*

<sup>2)</sup> *Laboratory of Ichthyology, Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece*

<sup>3)</sup> *School of Marine Sciences, University of Maine, 218 Libby Hall, University of Maine, Orono, ME, USA*

[kstergio@bio.auth.gr](mailto:kstergio@bio.auth.gr), [kstergio@hcmr.gr](mailto:kstergio@hcmr.gr), [yuchen@maine.edu](mailto:yuchen@maine.edu)

### ABSTRACT

Fish growth is one of the most basic elements of the life history and dynamics of fish populations. Quantification of growth patterns and comparisons of growth among different species/populations, based on various indices, are the focus of many studies of fish growth. In this study, we identify the necessary features of accurate indices for growth quantification and comparisons, and suggest that single von Bertalanffy parameters (notably K) should not be used for comparisons of growth rates and life-history studies. On the other hand, we suggest that combining K and asymptotic size yields a usable index, and illustrate this by comparing growth in two population of red bandfish *Cepola macrophthalma*, with reference to the temperature regime of their habitat.

### INTRODUCTION

In fisheries research, growth can mean change in size and/or change in number. The former is often referred to as change in a specified dimension of fish body over a certain period of time, and the latter is referred to as change in the total number of fish within a fish population or stock over a defined time period. Although different, these two growth processes together are the most important factors that result in an increase in the biomass of a fish stock. The focus of this study is the change in fish size.

Many indices have been developed to quantify and then compare growth rates of different fish species or populations of the same species. Because these indices tend to have different biological implications, the use of different indices may lead to different conclusions in growth comparison studies. Such an index-based conclusion in fish growth comparison studies may lead to different interpretations of the same data (Francis 1996; Pauly 2010), resulting in erroneous conclusions.

In this study, we evaluate some indices commonly used to quantify and compare growth in fisheries, as well as their impacts on fish growth comparisons and life history studies, and propose a general approach for describing and comparing fish growth.

### MATERIAL AND METHODS

#### Classification of growth indices

In general, there are two groups of indices that can be used to describe the process of change in size of fish: *absolute* growth rate and *relative* growth rate (e.g., Wootton 1990). Absolute growth rate refers to changes in one of the dimensions that can be used to measure a fish, e.g., its length or weight over a specified time period.

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Relative growth rate is a more complex rate of change, but also involves measurements of a dimension of fish related to time, an example being an increase of the length or weight of a fish increase per unit of total length or weight, respectively.

These two groups of growth rate are usually defined instantaneously, i.e., at a single point in time (or fish age). Although such definition provides exact values, it is often necessary to perform their computation in the form of mean values over a stated time interval. Thus, two methods exist to describe absolute and relative growth rates: instantaneous rate and average (mean) rate. In mathematical terms, the instantaneous growth rate can be written as  $r_R = \lim_{\Delta t \rightarrow 0} (\frac{\Delta L}{\Delta t})$  for absolute growth rate, and  $r_R = \lim_{\Delta t \rightarrow 0} (\frac{\Delta L}{L \Delta t})$  for relative growth rate, where  $\Delta L$  is the change in size in the time period of  $\Delta t$ , and  $L$  is the size measured at time (or age)  $t$ . The average growth rate can be described by the following formula  $\bar{r}_A = [(L_2 - L_1) / (t_2 - t_1)]$  for absolute growth rate, and by the formula  $\bar{r}_R = [\ln(L_2) - \ln(L_1) / (t_2 - t_1)]$  for relative growth rate, where  $L_1$  and  $L_2$  are sizes measured at time  $t_1$  and  $t_2$ , respectively. Either absolute or relative growth rate can be used in comparing the growth of different fish species or different populations of the same species in a specified life stage. Although the implication may differ, the outcomes of comparisons using these two types of indices should be consistent. A limitation of these indices is that they can only consider changes in sizes of two specific marks on the time scale.

A more sophisticated approach can be used to describe growth patterns of fish in their life spans when there are size estimates for fish in different periods of time. The most commonly used equation for describing fish growth data is the von Bertalanffy growth function (VBGF; Bertalanffy 1938), which can be written as:  $L_t = L_\infty(1 - e^{-K(t-t_0)})$ , where  $L_t$  is the length of fish at age  $t$ ,  $L_\infty$  is the asymptotic length (i.e., the mean length a fish would reach if it was to grow indefinitely),  $K$  the rate at which  $L_\infty$  is approached, and  $t_0$  the hypothetical age at size of 0.

### Growth comparisons using growth indices

Francis (1996) discusses six different methods for comparing the mean growth of two fish species or populations, and concludes that, to some extent, it does not matter which method is used as long as this is clearly stated. Also, Francis (1996) writes that the use of the  $K$  values of the VBGF is ‘... the most “natural” method of growth comparison, in the sense that it produces common-sense results.’ This conclusion is misleading, and might lead to erroneous results in comparisons of changes in fish sizes. In the VBGF,  $K$  has the dimension of time<sup>-1</sup> (usually year). Hence,  $K$  may be seen as a relative growth rate.

The first derivative of the VBGF is  $dL_t/dt = KL_\infty e^{-K(t-t_0)} = K(L_\infty - L_t)$ , which can be rewritten as  $dL_t/(L_\infty - L_t) = K dt$ . Integrating, we have  $\int_{t_1}^{t_2} \frac{d(L_\infty - L_t)}{(L_\infty - L_t)} = \int_{t_1}^{t_2} K dt$ . Solving this, we get  $K = \frac{\ln(L_\infty - L_{t_1}) - \ln(L_\infty - L_{t_2})}{t_2 - t_1}$  for a given time period from  $t_1$  to  $t_2$ .

The value of  $K$  is thus not only a function of the change in size during the period from  $t_1$  to  $t_2$ , but also of the asymptotic size  $L_\infty$ . This is the main reason for the discrepancy in using  $K$  for comparisons of growth of fish among populations/species with different  $L_\infty$  values (also noted by Francis (1996)).

Because neither  $K$  nor  $L$  (which has the dimension of size only) are adequate descriptors of growth, various indices that combine these two parameters have been proposed for the comparison of growth between/among different fish species or populations of the same species. These include the  $\omega$  index [=  $K \cdot L$ ; sometimes as  $\omega = \log(K \cdot L_\infty)$ ] of Gallucci and Quinn (1979), and the widely used  $\Phi'$  index (=  $\log K + 2 \log L$ ) of Munro and Pauly (1983) and Pauly and Munro (1984). Although both indices are derived from the VBGF, they have different implications, and conclusions may differ greatly for a growth comparison study if they are based on different indices. The  $\Phi'$  index has the dimension of length<sup>2</sup> time<sup>-1</sup>, which is not a dimension of growth. The  $\omega$  index has the dimension of absolute growth rate (length time<sup>-1</sup>). From the derivative of the VBGF (see above), we can see that  $\omega$  represents absolute growth rate at the hypothetical age  $t_0$ . For a well-estimated VBGF (i.e., based on correct absolute ages),  $t_0$  tends to be a small negative value (mainly because newly hatched fish larvae have a non-zero size, and also because the VBGF does not describe well the growth of larvae and early juveniles,



which grow faster than predicted by that equation; Pauly 2010). Thus,  $\omega$  is a growth rate that does not exist in reality, and is certainly not appropriate for representing the growth of fish of any age.

Here, we also present two more indices, using the first derivative of the VBGF, to describe growth rates. Both absolute and relative growth rates, calculated as instantaneous rates, can be estimated from this derivative. The instantaneous rate of absolute growth can be calculated as:  $r_A = dL_t/dt = KL_\infty e^{-K(t-t_0)} = K(L_\infty - L_t)$  and the instantaneous rate of relative growth can be calculated as:  $r_R = (dL_t/L_t dt) = K(L_\infty/L_t) e^{-K(t-t_0)} = K[(L_\infty/L_t) - 1]$ .

The values of  $r_A$  and  $r_R$  both decrease with an increase in  $L_t$  and approach 0 when  $L_t$  approaches  $L_\infty$ , a realistic description of the changes in fish growth rate with sizes.

## RESULTS AND DISCUSSION

### Application

The effect of the use of different indices presented here is evaluated considering the growth of two populations of red bandfish, *Cepola macrophthalmia* (Linnaeus, 1758), in two adjacent gulfs of the western Aegean Sea (Table 1) differing greatly in their productivity and temperatures. The study of its age, growth, and mortality (Stergiou *et al.* 1992; Stergiou 1993; Stergiou and Papaconstantinou 1993) show that the southern population, when compared with the northern one, is stunted; it is characterized by smaller mean length-at-age, smaller asymptotic length and weight, lower longevity and higher adult natural mortality. In addition, the mean length-at-age of red bandfish is smaller in the southern area and the differences in the mean length-at-ages for ages > 2 years are statistically significant (t-test,  $p < 0.05$ ) (Stergiou *et al.* 1992). The values of  $K$  and  $\omega$  in the southern area are larger than those in the northern one, whereas the opposite is true of the values of  $\Phi'$  and  $r_A$  and  $r_R$  at age 3 years (Table 1).

**Table 1.** VBGF growth parameters and derived growth indices red bandfish *Cepola macrophthalmia* at two locations in Evoikos Gulf, Greece (data from Stergiou *et al.* 1992).

	North	South
$L_\infty$ (cm)	67.2	42.5
$K$ (year <sup>-1</sup> )	0.21	0.38
$\Phi$ (length <sup>2</sup> time <sup>-1</sup> )	2.98	2.83
$\omega$ (length time <sup>-1</sup> )	14.2	16.2
$r_A$ (length time <sup>-1</sup> )	7.56	5.16
$r_R$ (length time <sup>-1</sup> )	0.24	0.18

### Life-history theory and growth rates

The various growth rate indices may have different implications, and conclusions may differ greatly for life-history studies also if they are based on different index. Life-history theory is based on the concept of trade-off constraints between alternative energy-consuming functions, and the resulting balance between life-history traits tends to maximise fitness, i.e., total reproductive output (Wootton 1990; Stearns 1992; Roff 1992). Evidence of such a trade-off could be the identification of a negative correlation between various measures of fitness, such as current reproduction, parental growth, parental mortality, and number, size, and survival of offspring (e.g. Stearns 1992; Roff 1992). Several empirical studies on fishes (e.g., Adams 1980; Pauly 1980; Gunderson and Dygert 1988; Jennings and Beverton 1991) show relationships between age and/or length at maturity, adult natural mortality, and growth rate consistent with the trade-off concept. Yet, other empirical studies (e.g. Alm 1959; Myers and Hutchings 1987; Wootton 1990) reveal no relationship or relationships that are not consistent with life-history theory.

To show that the use of certain growth rate indices may be also misleading in terms of life-history theory and modelling, we used published data of the von Bertalanffy (1938) parameters  $K$ ,  $L_\infty$  and  $t_0$  as well as adult natural mortality rates,  $M$ , for a total of 419 fish stocks. These data were extracted from The PopGrowth Table of FishBase ([www.fishbase.org](http://www.fishbase.org); Binohlan and Pauly 1998), whose data are linked to the reference from which the parameter values were extracted (Froese and Pauly 1998). For these stocks, we estimated the length at age 3 year (hereafter  $L_3$ ) from the von Bertalanffy (1938) equation and the corresponding growth parameters. At the time the study was conducted the median age at maturity of the 338 stocks for which such information was available was 3 years. Thus,  $L_3$  is here considered to refer to pre-mature growth.

Correlation analysis revealed that  $M$  and  $K$  are positively correlated ( $r = 0.76$ ,  $n = 419$ ,  $p < 0.001$ ). Such a positive relationship between  $M$  and  $K$  is well known and recognised (e.g. Beverton and Holt 1956; Pauly 1980, 1994, 1998; Roff 1992; Charnov 1993; and see [www.fishbase.org](http://www.fishbase.org)). Although  $\omega$  was positively correlated with  $M$  ( $r = 0.24$ ,  $p < 0.05$ ,  $n = 419$ ),  $L_3$  and  $M$  were negatively correlated ( $r = -0.30$ ,  $p < 0.05$ ,  $n = 419$ ) as were  $\Phi'$  ( $r = -0.27$ ,  $p < 0.05$ ,  $n = 419$ ),  $r_A$  ( $r = -0.78$ ,  $p < 0.05$ ,  $n = 419$ ), and  $r_R$  ( $r = -0.67$ ,  $p < 0.05$ ,  $n = 419$ ), with the latter two indices

proposed here being characterized by considerably higher  $r$  values than those for  $L_3$  and  $\Phi'$ . In addition,  $\Phi'$ ,  $\omega$ ,  $r_A$  and  $r_R$  were all positively correlated with  $L_3$  (logged;  $r = 0.95, 0.74, 0.58$  and  $0.22$ , respectively; for all cases  $p < 0.05$ ,  $n=419$ ). Finally,  $r_A$  and  $r_R$  were positively correlated (logged;  $r = 0.92$ ,  $p < 0.05$ ,  $n=419$ ).

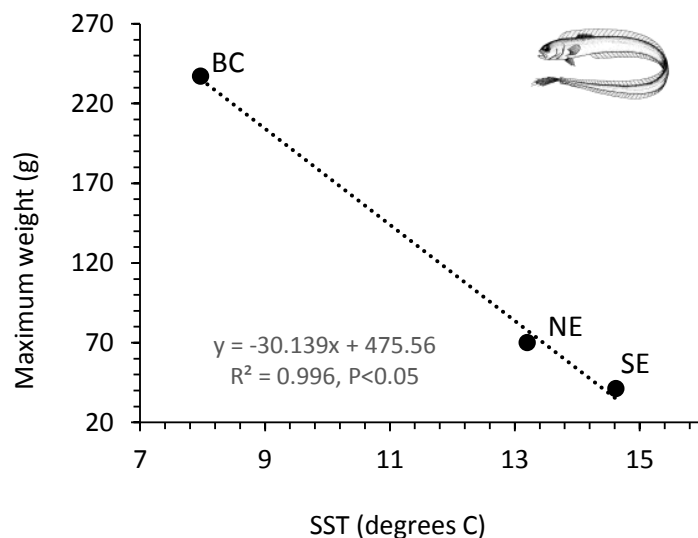
Should we consider  $K$  as an index of growth rate, then the positive relationship between  $M$  and  $K$  may imply that fast-growing species (or populations) suffer from higher adult natural mortality (and possibly smaller length at first maturity). The same is also true of the positive relationship between  $M$  and  $\omega$ . In contrast, the negative relationships between  $M$  and  $\Phi'$ ,  $r_A$  and  $r_R$  may imply that fast-growing species (or populations) suffer from lower adult natural mortality (and possibly larger length at first maturity). The latter seems to be consistent with life history theory and implies that fast-growing species attain fast a large threshold size that ensures predator avoidance (Peterson and Wroblewski 1984; Roff 1992; Pauly 1998). In such a case, fast-growing species may suffer from lower adult natural mortality, the major part of which is attributed to predation (Pauly 1980).

### An alternative interpretation

An alternative interpretation of the data in Table 1, based on Pauly (1981, 2010), and on D. Pauly (pers. comm.), is based on the fact that higher environmental temperatures force the fish of a given species to remain smaller, because their oxygen demand increases with temperature, while their gill surface area, which determines the supply of oxygen to their body, does not.

Previous studies show that the southern end of Evoikos Gulf is 2-3 degrees C warmer than its northern end (Friligos and Gotsis-Skreta 1987; Balopoulos and Papageorgiou 1991; Stergiou 1993). Similarly, the analysis of AVHRR satellite data (processed by S. Kavadas, IMASFISH database) shows that the mean (1984-2008) January-February sea surface temperature in North Evoikos is by 1.47 degrees C colder than that of the South Evoikos Gulf. Such temperature difference is large enough to explain the decrease in asymptotic length and the increase in  $K$  in Table 1 (Pauly 2010; Cheung *et al.* 2013), thus rendering superfluous the detailed argument about the north of this Gulf being more biologically productive than the south. It is worth noting here that red bandfish attains its maximum observed weight in Bristol Channel (237 g as opposed to <100 g in the Mediterranean; Stergiou 1993), an area where the mean January-February sea surface temperature is 7.97 degrees C, i.e., 5.2 and 6.7 degrees C colder than in North and South Evoikos respectively (Figure 1).

Moreover, the hypothesis that higher temperature reduces the growth of fish is compatible with the values of  $\Phi'$  in Table 1, which is higher in the north. Thus, while normally distributed when examined for a number of species (see, e.g., Longhurst and Pauly 1987),  $\Phi'$  may, because of its peculiar dimension (length<sup>2</sup>·time<sup>-1</sup>, i.e., surface·time<sup>-1</sup>), also roughly correspond to the very process that limits fish growth, i.e., gill surface area (which supplies O<sub>2</sub>) not keeping up with the growth of the O<sub>2</sub> demand emanating from the 3-dimensional body of a fish (Pauly 2010). Note also that the atypical length-weight relationship of red bandfish (in which the exponent  $b$  in  $W = a \cdot L^b$  has a value of about 2 instead of the more common  $b \approx 3$ ; see [www.fishbase.org](http://www.fishbase.org)) does not alter the fact that, in this species as well, gill surface area increase cannot keep up with body mass increase.



**Figure 1.** Relationship between the maximum observed weight of red bandfish, *Cepola macrophthalma*, in North Evoikos (NE), South Evoikos (SE) (data from Stergiou 1993) and Bristol Channel (BC; data from Atkinson *et al.* 1977) in relation to the mean January-February sea surface temperature (SST; data for NE and SE see text; data for BC from <http://www.watertemperature.org/Bristol-Channel--Geo.html>).

Finally, while  $r_A$  and  $r_R$  behave like  $\Phi'$  in Table 1, they would not if the arbitrary ages to which they pertain were different, e.g., to accommodate very short-lived fishes. Thus, indices such as  $r_A$  and  $r_R$  will remain inherently local, without general applicability.

Thus, overall, the  $O_2$ -is-limiting hypothesis, which has been corroborated for a vast number of species (Pauly 2010), would thus not only explain the difference in the indices of Table 1, but also provides a rationale for selecting one index over all others, very much contradicting the suggestion of Francis (1996) that they are, to some extent, equivalent if used consistently.

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## DIET AND FOOD INTAKE OF JUVENILE WHITE-SPOTTED SPINEFOOT, *SIGANUS FUSCESCENS* (SIGANIDAE)

Joselita T Salita-Espinosa<sup>1</sup> and Daniel Pauly<sup>2</sup>

<sup>1</sup> Marine Science Institute, College of Science, University of the Philippines, Diliman, Quezon City 1101, Philippines

<sup>2</sup> Sea Around Us, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, Canada  
[d.pauly@oceans.ubc.ca](mailto:d.pauly@oceans.ubc.ca)

### ABSTRACT

This paper investigates the feeding behavior and feeding rate of juvenile mottled spinefoot, *Siganus fuscescens* (Houttuyn 1782) (Siganidae: Teleostei), an important fishery component of the seagrass-dominated Bolinao reef-flat, in the northern Philippines. The feeding pattern of the fish was constant throughout the day and similar between seasons. Ingestion rates of 30–45 mm *S. fuscescens* were estimated for December 1990, representing the dry-cool season and April 1991, representing the dry-warm season. These estimates, of 0.223 and 0.289 g dry weight fish<sup>-1</sup> day<sup>-1</sup>, respectively, were not significantly different from each other. Ingestion rate estimates during the wet season, July 1991, for fish of 58 mm, was 0.336 g fish<sup>-1</sup> day<sup>-1</sup> by use of two methods were compared and likewise, statistically not different. Examination of the fish diet ranging from 34 to 130 mm revealed an increase the fraction of seagrass ingested, which gradually replaced epiphytic algae dominant in the diet of the juveniles.

### INTRODUCTION

Siganids (rabbitfishes or spinefoots) are widely distributed marine fishes in the Indo-Pacific region; their economic value together with their hardy nature make them interesting to mariculturists (Lam 1974; Carumbana and Luchavez, 1979.). It is, therefore, not surprising that a number of studies on their aquaculture potential have been done in the Philippines (Westernhagen 1973a, 1973b; Rosario 1974; Westernhagen 1974; Bryan 1975; Horstmann 1975; Westernhagen and Rosenthal 1975; Tahil 1978; Alcala and Alcazar 1979; Mangaoang 1982; Carumbana 1983; Ponce 1983) where siganids account for about 5% of the “coastal fishery” catches in the 1970s (Philippine Bureau of Agricultural Statistics 1988), and 0.3 to 0.5 % of the total catch in the Exclusive Zone of the Philippines from the 1980s to the early 2010 ([www.seaaroundus.org](http://www.seaaroundus.org)).

This study investigates the feeding behavior and feeding rate of the juveniles of *Siganus fuscescens* (Houttuyn 1782), previously known as *S. canaliculatus* (see [www.fishbase.org](http://www.fishbase.org)), which is by far the most common among the nine siganid species reported from Bolinao, Pangasinan Province, Philippines (McManus *et al.* 1992) and whose juveniles support a ‘*padas*’ industry in the same area (Aragones 1987). The paper also compares estimates from two independent methods of quantifying ingestion rates.

### MATERIALS AND METHODS

#### The area

Bolinao is located in the northern part of the Philippines (Figure 1), 16°23'N and 119°55'E. The substrate of its 24-km<sup>2</sup> reef flat is dominated by 4 species of seagrasses with an average density of 400 shoots m<sup>-2</sup> (Fortes 1989). The villagers of the area rely heavily on fishing for income-generation and sustenance; 40% of the total catch from the area in the 1980s was contributed by *Siganus fuscescens* (see McManus *et al.* 1992), whose population dynamics were studied by Del Norte and Pauly (1990).

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## The experiments

Most of the feeding experiments were done in the lab of the University of the Philippines Marine Science Institute, Bolinao Marine Laboratory. Three 500-liter tanks were maintained under natural light, salinity and temperature regimes, and running sea water conditions.

Every day, fresh shoots of four species of seagrasses (with their epiphytes) were placed in each tank, anchored in stones. The number of shoots per tank is given in parenthesis: *Cymodocea serrulata* (25), *Enhalus acoroides* (2), *Halodule uninervis* (36), and *Thalassia hemprichii* (5). The species type and shoot number closely parallel that of the fish collection site.

## Fish collection

Specimens of *Siganus fuscescens* ranging from 35-40 mm standard length (SL) and an equivalent average wet weight of 0.86 g were captured in fish corrals in a seagrass-dominated area in Bolinao in December 1990 and April 1991, representing the cool-dry and warm-dry seasons, respectively. In July 1991, during the wet season, *S. fuscescens* of about 58 mm (equivalent wet weight of 3.18 g) were collected from the same site in a similar manner. All fish collected were immediately transferred to the laboratory 500-liter tanks, at densities of 30 to 35 individuals per tank.

## Estimation of ingestion rates

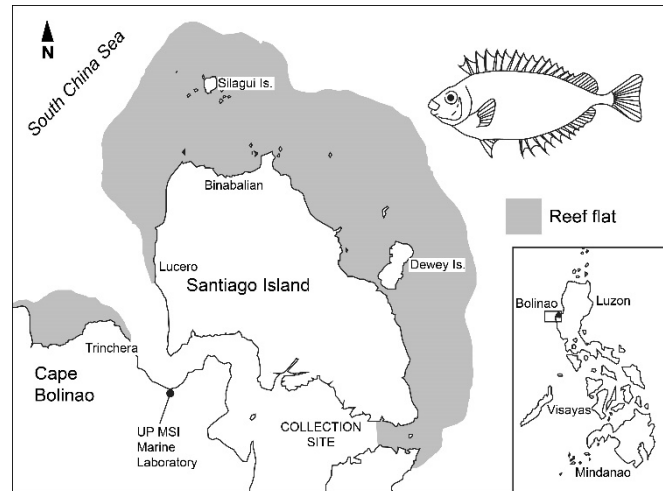
Two methods were used in estimating ingestion rates. Where it was possible to count fish bites, the gut-filling/feeding activity method presented by Polunin (1988), Polunin and Klumpp (1989), and Klumpp and Polunin (1989, 1990) was used. Where 24-hour collections of entire gut contents were made, ration estimations were performed using the approach proposed by Sainsbury (1986), as modified by Jarre *et al.* (1991) and implemented in the MAXIMS software of Jarre *et al.* (1990)<sup>4</sup>.

The gut-filling/feeding activity method is described by the equation  $I = T \cdot B$ , where  $I$  is the amount of food ingested per g fish per day ( $\text{g fish}^{-1} \text{day}^{-1}$ ) is the weight-specific daily ingestion,  $T$  is the total number of daily bites ( $\text{bite day}^{-1}$ ) and  $B$  is the bite size ( $\text{g fish}^{-1} \text{bite}^{-1}$ ).  $B$  is estimated as  $G/N$ , where  $G$  (gut fullness index ( $\text{g fish}^{-1}$ )) is the weight of the entire gut contents standardized to fish weight at a time when the gut is full. The time in question was predicted by a regression where the observed cumulative defecation frequencies per fish were plotted against time of the day and whose intercept estimated the time at which defecation began, i.e., the time a which the gut was filled;  $N$ , the number of bites needed to fill the gut, was also estimated from this. The total number of bites was estimated via the bite frequency, based on bites counted at random for several minutes during the feeding period, i.e., during daylight.

The MAXIMS software estimates daily ingestion rate (or daily ration) by fitting a 24-hour cycle of observed stomach or foregut contents to a stomach/foregut contents time trajectory predicted by the equations:

$$dS/dt = a - cS \text{ while feeding, and}$$

$$dS/dt = -cS \text{ while not feeding,}$$



**Figure 1.** Map of the Bolinao area, Pangasinan Province, Philippines, showing the reef flat (shaded) upon which seagrasses grow.

<sup>4</sup> The MAXIMS software, which was implemented in Microsoft BASIC, is not available any more. It would be good if it were reprogrammed in R. Readers interested in doing this are welcome to contact the second author for information.

where S	= stomach/foregut content
T	= time
A	= input rate of food (here % body weight, hr <sup>-1</sup> )
C	= instantaneous rate of stomach/foregut content evacuation (here: hr <sup>-1</sup> )

From 04:00 to 21:00, fish were sacrificed at variable intervals and the entire guts were removed, weighed and standardized by re-expression as % fish body weight. Gut content weights were obtained by subtracting the weight of an average empty gut from the weight of a gut at particular times. Note that this analysis of gut contents was based entire guts, and not on stomach or foregut contents only; we assumed this made no difference here, due to the important fraction that the full foregut contributes to the entire gut, and to the rapid passage of food, through the gut of *S. fuscescens*, see Discussion).

All dry weights mentioned below (gDWt) are constant weights of oven-dried samples (60°C). All observations from tanks were made after a 24-h acclimation period.

### Foregut content analyses

In July 1991, siganids of 35 to 130mm standard lengths were caught in the grass beds with a scissor net, immediately killed and kept in ice. In the lab, the fish were measured and dissected and the foregut contents taken and preserved in 10 ml 10% formalin-seawater solution. The contents were analyzed by either of the following:

- a) A subsample of foregut contents of fish (n=12) from the 30-50 mm size group was taken for identification of the plant material. The solution was centrifuged for 10 min at a speed of 150 rpm and a 3 ml concentrate was taken for analysis. From the 3 ml sample, three readings (replicates) each from a 50- $\mu$ l aliquot were taken. Plant materials were identified to the lowest possible taxonomic level. The relative frequency of occurrence of each plant for every 50- $\mu$ l aliquot was noted. The following levels of occurrence were used: 1 - found infrequently; 2 - found frequently, and; 3 - found very frequently. The average frequency of occurrence in the three readings/replicates was taken to obtain an estimate of the dominance index of a food type in the stomach of the fish, used for rankings.
- b) The rest of the sample (n=38) were used to determine the proportion of algae and seagrasses in the foreguts of siganid of different sizes.

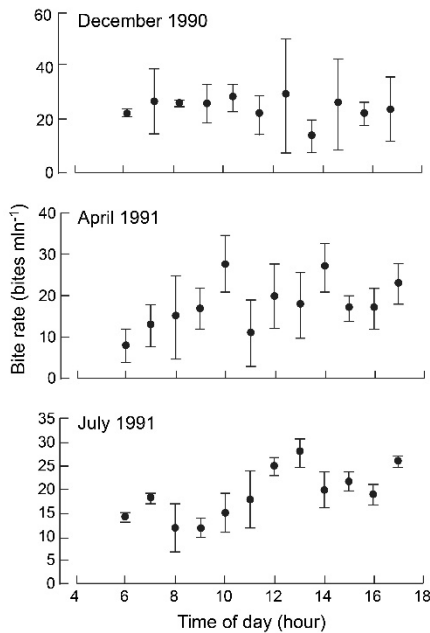
A 30-ml aliquot was taken and placed on a Petri dish with a grid composed of 10 x 10 squares. All algae found in the aliquot were grouped and the same was done with seagrasses and other materials. The number of squares occupied by the three components (algae, seagrasses, and animals) were counted to provide the relative percentage of each material.

### Statistical treatment

For every parameter (e.g., bite rate), the average observation for 5-10 fish represents a data point in one tank. A two-level nested ANOVA was performed to determine significant differences in bite rates among the seasons and hourly samples. The data were log-transformed to meet the requirements of normality and homoscedasticity. Simple linear regressions were established between time of day (x) and cumulative frequencies of defecations (y) to predict the time at which defecation commenced, thus, filling of the gut starts. Kruskal-Wallis tests were used to identify significant differences in ingestion rates between seasons and between the two methods of estimation (Sokal and Rohlf 1981).

## RESULTS

The length-weight relationship estimated from 53 carefully measured and weighed specimens wet weight =  $0.0163SL^3$  where the weight is in grams and the length in centimeters.



**Figure 2.** Bite rates of juvenile *Siganus fuscescens* plotted against time of day at different months (bars indicate standard errors of the means). The ANOVA was performed with data points from 08:00 to 16:00, to ensure that only data points referring to full guts were considered (see text and Table 1).

Thus feeding rate can be assumed to remain unaffected, as the small change in salinity is probably not enough to affect feeding especially as we are dealing here with a very euryhaline fish (Carumbana 1983).

The feeding rate estimates by use of the two methods are, likewise, not significantly different (see Table 2, computed  $H = 3.857$ ,  $df = 1$ ) lending credibility to the results obtained by both methods.

Examination of the foregut contents of *S. fuscescens* caught from the wild indicates that the algae ingested by juveniles are mainly seagrass epiphytes (Table 3), which are replaced by seagrasses as they grow (Figure 3). Further, ranking of the food items found in the foreguts of juvenile siganids in Table 3 shows that *Enhalus acoroides* is the most frequently ingested seagrass.

## DISCUSSION

### Feeding behavior and feeding rates

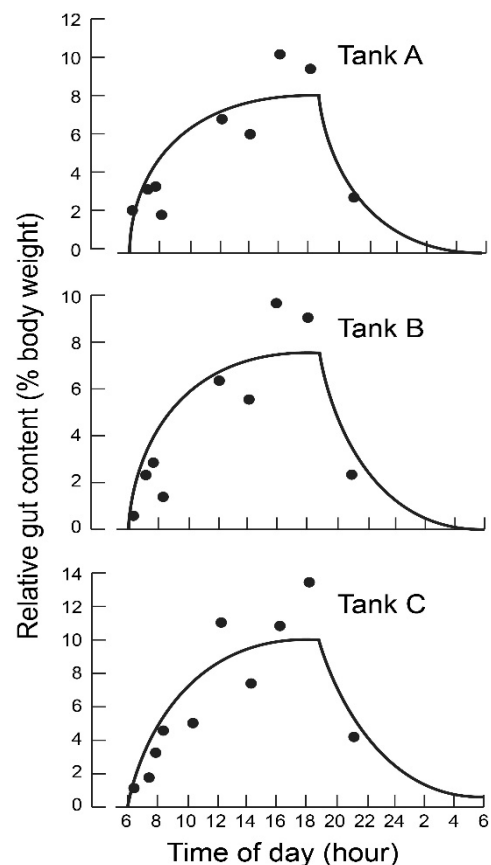
Herbivores, as compared to carnivores, are known to have high food intakes relative to their body weights (Brett and Groves 1979; Palomares and Pauly 1989, 1998; Polunin and Brothers 1989). In this study, a weight-specific daily food intake of 96% was estimated for fish of 0.27 g (DWt) body weight (30-45 mm), while for fish with an average of 0.73 g (DWt) body weight (58 mm) a smaller weight-specific ration of 52% was estimated. This is consistent with observations of other fishes whereby relative food intake declines as body weight increases (Pauly 1986).

Feeding by siganids shows a diurnal pattern, starting at sunrise (05:30 to 06:00), remaining more or less constant through the day and stopping near sunset (17:30 to 18:00) (Figure 2). This is confirmed by the analyses of the wet season (July) samples, performed with MAXIMS (Figure 3). Further, a nested ANOVA of bite rates (Table 1) shows no statistical difference among time of day and among the three seasons in the area (dry-cool, dry-warm and wet) suggesting that the feeding pattern is uniform throughout the year as well.

Table 2 shows a summary of the parameters used to estimate ingestion rate. Based on the gut-filling method, the onset of defecations (where  $y = 0$ , see Materials and Methods) is predicted to occur from late 07:00 till early 08:00 throughout the sampling period. These times may be similar, however, the cumulative number of bites taken at these periods varies highly and thus the differences in bite size (B). Gut weights (G) appear to be inversely related to bite size, and thus overall ingestion rate estimates between December and April were not significantly different (computed  $H = 3.857$ ,  $d.f. = 1$ ). It must be noted that only the results from December and April sampling were tested against each other as the samples from July were larger (see Materials and Methods). July is part of the wet season, but has the same temperature as in April (30 to 32°C).

Thus feeding rate can be assumed to remain unaffected, as the small change in salinity is probably not enough to affect feeding especially as we are dealing here with a very euryhaline fish (Carumbana 1983).

The feeding rate estimates by



**Figure 3.** Time trajectory, as estimated using MAXIMS, of the relative weights of the entire gut contents of *Siganus fuscescens* of 50-60 mm. (SL) sampled in July 1991 and kept in three laboratory tanks (see also Table 2).



## Comparison of two methods

Sainsbury (1986) summarized the broad categories of methods used for estimating food consumption of fish and discussed the advantages and disadvantages before presenting the approach upon which the MAXIMS software of Jarre *et al.* (1990) was later based. In this technique, the parameter necessary for the estimate is foregut/stomach contents for a 24-h period, which makes estimation of ingestion less difficult than the gut-filling method. The latter requires careful and tedious observations of bites and defecation frequencies of live fish that could be almost impossible when done in the wild on a fast-swimming and very active fish such as *S. fuscescens*. In addition, sacrifice of fish to obtain the weights of full guts also is necessary.

**Table 1.** Two-factor nested ANOVA of log-transformed bite rates of juvenile *Siganus fuscescens* for the three sampling months (December, 1990, April and July 1991), from 08.00 to 16.00.

Source of variation	Degrees of Freedom	Sum of squares	Mean sum of squares	Computed $F_s$	$F_{s(.05)}$
Among seasons	2	0.272	0.136	2.2423	3.1
Among hourly samples	24	1.455	0.606	0.1912	1.7
Within hourly samples	54	17.129	0.317	---	---
Total	80	18.856	---	---	---

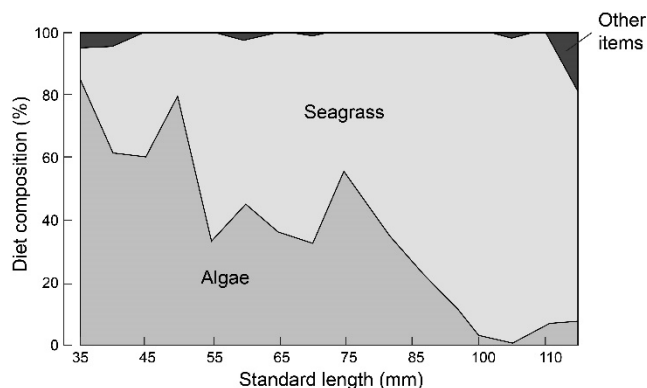
The key feature of the method of Jarre *et al.* (1991) as implemented in the MAXIMS software is that daily ration is estimated as the net result of feeding and foregut/stomach contents evacuation acting simultaneously. However, in our study we considered evacuation of the entire gut instead of the stomach/foregut because of the high observed evacuation rates. Feeding in *S. fuscescens* starts as early as 05:30 to 06:00 and defecation commences at 08:00 (see Table 2) and continues simultaneously with feeding until about 3 hours after feeding stops. This means that it takes only 2-2.5 hours for food to pass through the entire gut, which in *S. fuscescens* is about 3-4 times as long as the body. Therefore, gut passage rate is 49-62 mm hr<sup>-1</sup>, which is much less than in, e.g., the southern sea garfish *Hyporhamphus melanochir* fed with seagrass (Klumpp and Nichols 1983).

## Selection of food items

*Enhalus acoroides* is a tough-leaved seagrass and may not be a preferred food item of juvenile siganids. We surmise that *E. acoroides* leaves are incidentally ingested by the fish while it is feeding on its epiphytes, for which the broad and thick leaves of this seagrass provide an ideal substrate. Also its structure could provide protective cover for the fish while they are feeding.

For these reasons, it is likely that the juvenile siganids browse more frequently upon this seagrass in the wild. Westernhagen (1973b) also found *E. acoroides* more frequently than the other seagrasses in the stomachs of several species of siganids caught from Cebu (southern Philippines) and related this to the abundance of this seagrass in the area. He, however, reported that the siganid did not browse upon this seagrass in his lab experiments when seaweeds were provided as an alternative.

The higher proportion of epiphytic algae relative to seagrass material in the stomachs of the young, and the decreasing trend for larger, older fishes allows for two alternative interpretations (Figure 4). One is that only juveniles prefer epiphytic algae, due to their nutritional quality and digestibility relative to seagrasses. Klumpp *et al.* (1989) suggested that, in general, algae are more nutritious than seagrasses. For instance, C:N for seagrasses is 20:1 (Duarte 1990) against 9:1 to 18:1 for epiphytes in Bolinao (Klumpp *et al.* 1992). Digestibility also appears to be an



**Figure 4.** Percentage of algae, seagrass, and other items in the stomach of *Siganus fuscescens* caught in the Bolinao area, Philippines, July 1991.

**Table 2.** Summary of parameter values used to estimate the ingestion rate of young *Siganus fuscescens*, December 1990 to July 1991; A, B and C are replicates. T: Total number of bites day<sup>-1</sup>; G: Gut fullness index (% of body weight); C: Intercept of regressions of time of day vs. cumulative defecation frequencies; D: Slope of same regressions; F: Predicted time at which guts become full, and defecation stats (h:min); N: Number of bites needed to fill guts; B: Relative bite size (% of body weight); I: Ingestion rate (%weight day<sup>-1</sup>); \* MAXIMS results (see also Figure 3)

Month	Tank	Mean fish weight (g ± s.d.)		T	G	C	D	F	N	B	I
Dec	A	0.274	0.070	19,961	18.7	-3.475	0.434	0.800	3826	.0048	97.6
	B	0.270	0.081	12,527	12.3	-2.992	0.385	07.46	2338	.0052	65.9
	C	0.283	0.081	15,744	13.7	-3.234	0.397	08.09	2736	.0050	78.8
April	A	0.234	0.154	12,920	9.8	-2.983	0.363	08.12	901	.0108	140.5
	B	0.220	0.158	13,510	10.0	-2.368	0.296	08.00	1285	.0077	105.1
	C	0.301	0.284	12,153	15.8	-2.504	0.313	08.00	1875	.0084	102.4
July	A	0.743	0.144	14,208	6.8	-3.811	0.477	07.54	2093	.0032	46.2
	B	0.722	0.184	14,208	6.9	-4.904	0.519	07.54	2087	.0033	47.0
	C	0.757	0.201	13,559	7.9	-2.857	0.378	07.54	1700	.0046	63.0
July*	A	0.743	0.144	---	---	---	---	---	---		40.5
	B	0.722	0.184	---	---	---	---	---	---		36.0
	C	0.757	0.210	---	---	---	---	---	---		39.6

**Table 3.** Comparisons of *Siganus fuscescens* foregut contents (n=12) with the epiphytes of the seagrass *Enhalus acoroides* sampled in the same area. The members under ‘foregut contents’ are dominance rankings (see “Foregut Contents Analyses” in text); the x and - under ‘Epiphytes’ refer to presence and absence, respectively, while n.a. (not applicable) refers to food items that cannot be epiphyte.

Taxon	Foregut contents <sup>a)</sup>	Found as:epiphyte on <i>E. acoroides</i> <sup>b)</sup>
<b>Animals</b>		
Amphipods	11	n.a.
Copepods	11	n.a.
Foraminiferans	11	n.a.
<b>Algae</b>		
Cyanophyta (bluegreens)		
<i>Brachytrichia</i> sp.	3	--
<i>Calothrix</i> sp.	8	X
<i>Lyngbya</i> sp.	10	X
<i>Oscillatoria</i> sp.	6	--
Chlorophyta (greens)		
<i>Cladophora</i> sp.	7	X
<i>Enteromorpha</i> sp.	4	X
Rhodophyta (reds)		
<i>Asterocystis</i> sp.	10	--
<i>Centroceras</i> sp.	9	X
<i>Ceramium</i> sp.	7	X
<i>Goniotrichium</i> sp.	9	--
<i>Polysiphonia</i> sp.	2	X
Phaeophyta (browns)		
<i>Sphacelaria</i> sp.	6	X
<b>Diatoms</b>		
pennate forms	1	--
centric forms	6	--
<b>Vascular plants</b>		
<i>Cymodocea serrulata</i>	6	n.a.
<i>Enhalus acoroides</i>	5	n.a.
<i>Halodule ninervis</i>	10	n.a.
<i>Thalassia empirichii</i>	6	n.a.

<sup>a)</sup> This study

<sup>b)</sup> Klumpp *et al.* (1992)

important factor in the feeding preference of siganids (Westernhagen 1973a; 1974; Tsuda and Bryan 1973; and Bryan 1975). Similarly, Lobel and Ogden (1981) showed that the parrotfish *Sparisoma radians* prefers to feed on *Thalassia testudinum* covered with epiphytes rather than on clean *T. testudinum* because the former increased digestibility of the seagrass by a factor of five.

The other interpretation for this is that adult *S. fuscescens* prefer epiphytes to seagrasses as much as the juveniles do, but the trend in Figure 3 may be due to differences in feeding modes. Thus, the juveniles have small mouths and less powerful jaws, which may prevent them from directly biting off chunks of seagrass. Rather, in the feeding process, they browse the epiphytes from seagrass leaf surface, whereby some seagrass is ingested. The adult siganids, on the other hand, have bigger and stronger mouthparts enabling them to feed on epiphytes by biting off and ingesting chunks of the seagrass to which epiphytes are attached.

Whichever alternative is correct, and whether one deals with adults or juveniles, the high daily food requirement of *S. fuscescens* may have a strong impact on the seagrass communities in the area. Further

investigation should determine whether the grazing pressure exerted by *S. fuscescens* on seagrass beds such as those of Bolinao may in fact be beneficial, through strand rejuvenation and nutrient cycling.

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## THE WORLD DISTRIBUTION OF CAPELIN (*MALLOTUS VILLOSUS*): VIEWS AND REVIEW

Konstantinos I. Stergiou<sup>1,2</sup>

<sup>1</sup>*Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Aghios Kosmas, Athens, Greece*

<sup>2</sup>*Laboratory of Ichthyology, Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece*

[kstergio@bio.auth.gr](mailto:kstergio@bio.auth.gr), [kstergio@hcmr.gr](mailto:kstergio@hcmr.gr)

### ABSTRACT

In this work I review the written account and historical information (for the period 1850s- 1982) on the distribution (excluding the seasonal one) of capelin, *Mallotus villosus* (Müller 1776), in the world ocean. Capelin occupy different climatic zones in the North Atlantic and North Pacific Oceans, namely, the marine subarctic in the former, the cool temperate in the latter. Its distribution in the Arctic is discontinuous, and, quite likely, Arctic populations are relicts from preceding warm periods following glaciations.

### INTRODUCTION

The work presented below was undertaken within the framework of my MSc thesis that was conducted during 1981-1984 at the then Institute of Oceanography of the McGill University, under the guidance of Professor Maxwell J. Dunbar (Stergiou 2005). The paper presented here was part of my thesis that was submitted to the journal 'Arctic' sometime in the early 1990s. The submitted paper was tentatively accepted, subject to minor revision; one of the main comment was that the data on the distribution of capelin (which covered the period 1850- 1982) had to be updated so that to also cover the years up to the early 1990s. However, by that time I was back in Greece, working in the then National Centre for Marine Research (now Hellenic Centre of Marine Research), without access to the excellent library of McGill University in order to update the distribution of capelin *Mallotus villosus* (Müller 1776). Thus, I never completed the revision. Yet, it remained on my desk, and thought about it every now and then. Undoubtedly the publication of a special volume on belated or 'relict' papers is an excellent opportunity to present it. Naturally again the distribution of capelin has not been updated and readers should perceive it as a historical essay with a value (if any) for the period described.

Capelin, *Mallotus villosus* (Müller 1776), is a small, short-lived migratory pelagic fish with high reproductive potential, feeding on plankton (e.g., Stergiou 1989). It plays a key role in the North Atlantic ecosystem (e.g. Stergiou 1989; Vilhjálmsson 2002; Rose 2005). It ranks in the world's top ten most important pelagic species in terms of catches, with landings reaching more than 6.5 million t in the late 1980s sharply declining thereafter (FAO 2011). According to the literature, capelin has a boreal to arctic distribution (e.g. McAllister 1963; Winters 1969; Jangaard 1974; McAllister 1984; Rose 2005; Froese and Pauly 2016, [www.fishbase.org](http://www.fishbase.org)). In general, capelin most probably originated in the North Pacific from where it entered the Northwest Atlantic during past interglacial periods and then spread to the Northeast Atlantic (Stergiou 1989; Rose 2005). Stergiou (1984) shows that its distribution in the Barents Sea is closely associated with the distribution of the subarctic zone, *sensu* Dunbar (1968, 1972), and maintains that the same may also be true of other areas of the North Atlantic. There is a question on whether the distribution of capelin is circumpolar or not. For instance McAllister (1963) believes that capelin is a circumpolar species with probable Arctic populations existing at least across the Canadian Arctic. FishBase ([www.fishbase.org](http://www.fishbase.org)) also presents capelin as circumpolar. In contrast, Dunbar (1976, 1983) proposes that capelin in the Canadian arctic are climatic relicts from a warm period (e.g. 1880s) persisting locally because of the high summer sea temperatures. In addition, Lutsik *et al.* (1981) mentions that it is not known whether the occurrences of capelin in the former Soviet Arctic waters are of a permanent or intermittent nature.

In this work, I review the available historical accounts and information (for 1850s-1982) on the distribution of capelin in the world ocean (Figure 1). The seasonal changes in the distribution of capelin over its entire range are outside the scope of the present work (for reviews see e.g. Jangaard 1974; Vilhjálmsson 2002)

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## NORTH ATLANTIC OCEAN

### Labrador, Newfoundland, Gulf of St. Lawrence

In the western Atlantic capelin occur from the northernmost Labrador Peninsula to Newfoundland and the northern part of the Gulf of St. Lawrence (north coast, Anticosti Island, estuary of the St. Lawrence River, Gaspé Peninsula), reaching as far up the St. Lawrence estuary as Trois Pistoles (Bell 1859; Hardy 1867; Jordan and Evermann 1896; Kendall 1909; Templeman 1948, 1968; Backus 1957; Leim and Scott 1966; Bigelow 1963; Winters 1969; Jaangard 1974; Parent and Brunel 1976). It has also been reported as rare from the Northwest River and Lake Melville, Labrador (Kendall 1909; Backus 1957). Capelin is abundant, however, south of Cape Harrison, Labrador, around Newfoundland and Grand Banks (Kendall 1909; Sleggs 1933; Templeman 1948, 1968; Pitt 1958; Bigelow 1963; Dunbar 1970). Capelin were rare (or even absent in some years) from the south and southwestern parts of the Newfoundland coasts during 1929-1938 (Templeman 1948; Templeman and Fleming 1953).

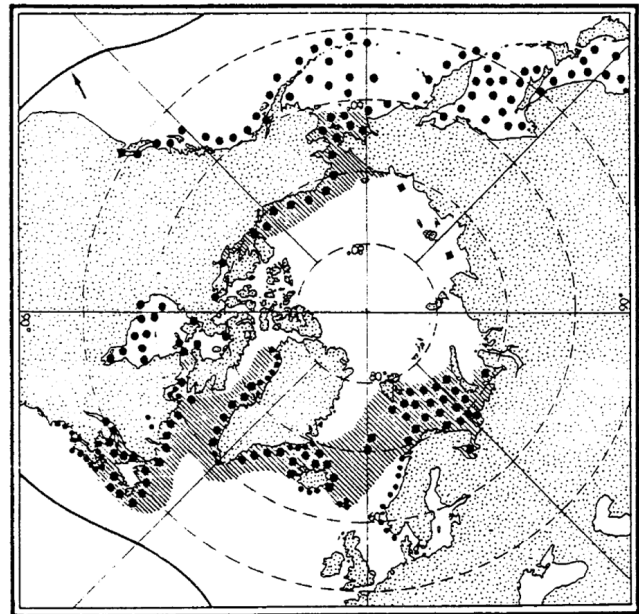
Capelin have been sporadically reported from the southern part of the Gulf of St. Lawrence. They were present in the Miscou-Chaleur Bay sometime in the mid 19th century given that Perley (1859) writes that the cod fishery there "... does not fairly commence until the arrival of capelin..." In 1917 capelin were found at Cheticamp and Magdalen Islands (Cox 1921) and reported again from the southern Gulf of St. Lawrence in 1948 (Dunbar *et al.* 1980). Investigations by Leim and Day (1959), on the other hand, during 1950-1958 in the southern part of the Gulf did not reveal any capelin. Leim (1960), however, reports that capelin were found frequently in cod stomachs in the Miscou-Chaleur Bay during the summer of 1959. Capelin occurred again in St. Georges Bay during the 1970s: a few larvae were caught in 1973 with their number increasing in 1974-1976, the abundance of adult capelin peaked in 1977, some individuals were also caught in 1978, but not during 1979-early 1980s (Lambert *et al.* 1982; Lambert 1984).

### Eastern coast of Nova Scotia

Capelin occasionally visit the eastern coast of Nova Scotia. They were present in the waters around the Gut of Canso in the summer of 1849 (Storer 1850), appeared again near Halifax in 1916 and 1919, whereas in 1917 they were abundant off the southeastern corner of Cape Breton (Bigelow and Welsh 1924; Bigelow and Schroeder 1953; Bigelow 1963). Pitt (1958), however, did not find any capelin, either from nets or from cod stomachs, in 1950 around Cape Breton Island, and in the waters off the eastern coast of Nova Scotia and Sable Island Bank. Nevertheless, spawning capelin were abundant at the Cabarus and Fourchu beaches (Cape Breton) in 1958-1959 and local fishers had not seen capelin for many years (Leim 1960). There were no registered catches of capelin in the ICNAF/NAFO Statistical Bulletins in Subarea 4W (northeastern Nova Scotia and southeastern Cape Breton Island) during 1961-1982 whereas 1 t of capelin was registered in 1975 in Subarea 4V (northeastern Cape Breton and Cabot Strait).

### Bay of Fundy, Gulf of Maine

Capelin occasionally visit the Bay of Fundy and Gulf of Maine. They were found at various localities in the Saint John, New Brunswick, district during the mid-19th century (Huntsman 1922; Bigelow and Welsh 1924; Bigelow and Schroeder 1953; Bigelow 1963). They occurred again in the Bay of Fundy in 1903 and in 1915-1918 (Bigelow and Welsh 1924; Bigelow and Schroeder 1953). "...This was the prelude to a period of local abundance..." write Bigelow and Welsh (1924), since capelin were found in great numbers at various localities in the Bay of Fundy and Gulf of Maine (Minas Basin, Passamaquoddy Bay, Dennysville River, Winter Port, Penobscot River) (Kendall



**Figure 1.** Illustrating the Ortmann line (heavy line marked with an arrow), the marine subarctic zone (hatched area, as defined by Dunbar 1968) and the distribution of capelin. For the distribution of capelin small black dots indicate areas visited occasionally, large black dots indicate areas permanently inhabited and black squares indicate areas where it is not known whether capelin is a permanent or periodic inhabitant (from Stergiou 1989).



1917, 1919; Bigelow and Walsh 1924; Bigelow and Schroeder 1953; Bigelow 1963). There is no written record of capelin in the area during 1919-1965 (Bigelow and Schroeder 1953; Taylor *et al.* 1957; Bigelow 1963; Tibbo and Humphreys 1966). Capelin were found again in 1965-1968 in the waters of Yarmouth and Digby counties (Nova Scotia), Campobello (New Brunswick), and along the coast of Maine as far south as Boothbay Harbor (Tibbo 1965, 1968; Tibbo and Humphreys 1966; Tibbo and Messieh 1967; Tyler 1971). Furthermore, there are indications that capelin probably spawned in the Bay of Fundy during that period (Tibbo 1968). Capelin landings of 37 and 124 t were recorded in the ICNAF/NAFO Subarea 4X (southeastern Nova Scotia and Bay of Fundy) during 1965 and 1967 respectively and not for the remaining years of the 1964-1982 period.

Cape Cod seems to be the southern distributional limit of capelin in Northwest Atlantic; two specimens, caught at Wood's Hole, Massachusetts, are listed in the collections of the Smithsonian Institution (Bean 1880) and Academy of Natural Sciences of Philadelphia (Fowler 1911), respectively. Jordan and Evermann (1896), in their exhaustive monograph "*The Fishes of the North and Middle America*", mention that capelin occur as far south as Cape Cod, but they do not report the exact dates of such occurrences. In any case, there is no evidence that during the 20th century capelin have appeared as far south as Cape Cod.

## Greenland

In Greenland, capelin are common from Umanak fiord, on the west coast, to Angmagssalik on the east coast; however, a change in their distribution took place in the 1920s and 1930s (Jensen 1925, 1939, 1948; Hansen 1943; Taning 1948; Hansen and Herman 1953). During the first two decades of the 20th century capelin were absent north of Disko Bay and the middle of Vaigat, with the exception of sporadic occurrences at Upernavik (Jensen 1925, 1939, 1948). A profound change took place in the 1920s when capelin entered Northeast Bay. Capelin arrived at Ubekendt Island for the first time in 1927, at Ikerasak in 1933, becoming plentiful during 1934-1936, and at Svartenhuk peninsula (where they were not present before) in 1935. Capelin were reported for the first time from Kraul's Havn and Igdlulik in 1935. Two specimens were caught at Thule, in 1935 and 1936 respectively (Jensen 1925, 1939, 1948). Furthermore, there are indications that capelin spawned in Northeast Bay (Jensen 1925, 1939, 1948). At the same time capelin did not visit the southwestern part of the coast where they were common before the 1920s. The capelin fishery failed in 1925 in Julianehaab fiord and in 1926 and 1928 in all the southern districts of West Greenland (Jensen 1939, 1948). By the early 1970s, however, capelin were not found north of 68°N along the western coast of Greenland (Jakupsstovu and Rottingen 1975). Capelin in East Greenland, previously distributed as far north as Angmagssalik, also extended their distribution north to Scoresby Sound in 1927 (Jensen 1939, 1948; Taning 1948) where capelin were not present during 1891-1892 (Jensen 1939, 1948).

## Iceland, Jan Mayen, Faroes

Capelin are found around Iceland and Jan Mayen (Jespersen 1920; Saemundsson 1934; Jensen 1948; Taning 1948; Backus 1957; Vilhjálmsson 1968, 2002). During the 1930s capelin were rare, and in some years even absent, from the southern coast of Iceland and appeared in higher abundances of the northern and northeastern coasts (Jespersen 1920; Saemundsson 1934; Taning 1948; Jensen 1948). Capelin are also found sporadically in the Faroes Islands (Jensen 1948; Joensen and Taning 1970). Capelin were plentiful in the waters around the Faroes in 1867 and in May-August 1938 (Joensen and Taning 1970). They were also found in great numbers north of the Faroes (62°37'N, 06°19'W) at a depth of 80 fathoms in 1965 (Blacker 1965). Capelin larvae were caught in the area 62°40'-64°05'N, 6°20'-9°38'W north of the islands during the summer months of 1904 and 1905. Three capelin post-larvae were also caught at 62°26'N, 07°36'W in 1939 and at 60°36'N, 03°38'W to the south of the islands in 1927 (Joensen and Taning 1970). The distribution of capelin expressed as t of landings per square nautical mile for each year of the 1992-2001 period in the wider area of Iceland-Jan Mayen are presented in Vilhjálmsson (2002).

## Norwegian and Barents Seas

In the Norwegian and Barents Seas capelin are widely distributed from Bear Island and Spitsbergen in the west to Novaya Zemlya, Indiga Bay and White Sea in the east, and from Frans Josef Land in the north to the northern Norwegian coast and fjords in the south (Sars 1879; Fries *et al.* 1895; Rachmanova 1928; Rass 1933; Awerinzew 1934; Andriyashev 1964; Prokhorov 1965, 1968; Corlett 1968; Olsen 1968; Pashkova 1975; Altukhov 1977). They have been recorded periodically as far south as Oslo fiord in 1842 (Sars 1879; Fries *et al.* 1895) and Trondheim fiord in 1895-1899 (Hjort and Dahl 1900). The easternmost and southernmost occurrence of capelin along the Norwegian coast during 1950-1980 was recorded in 1951 at 13°E longitude (Stergiou 1984).

Official reports show that capelin migrated to the coast of Norway on an annual basis from 1840 throughout 1938 (Moller and Olsen 1962; Olsen 1968; Historical Statistics 1978). The abundance of capelin fluctuated strongly during that period. Capelin did not visit the Norwegian spawning grounds in 1938-42 (Moller and Olsen 1962; Olsen 1968; Nitter-Egenaes 1967a,b). Although the catch of capelin was also zero in 1945, this must be considered with caution inasmuch as in 1944 the Norwegian communities were burnt by the German army and the area was evacuated (Nitter-Egenaes 1967a,b). In 1962 capelin did not appear in the Norwegian territorial waters and the catch of 363 t registered in that year (Historical Statistics 1978) was fished in Soviet waters (Prokhorov 1965). Capelin visited the Norwegian coastal waters during 1962-1982 (Stergiou 1984).

## **NORTH PACIFIC OCEAN**

### **Northwest Pacific**

In the northwestern Pacific capelin abound along the Asiatic coast of the Bering Strait, Gulf of Anadyr, eastern coasts of Kamchatka, Okhotsk Sea (western coast of Kamtchatka, Gulf of Sakhalin, Shantar Islands, Baikal Bay), eastern and southern coasts of Sakhalin and Sea of Japan (Tatar Strait, Hokkaido, and Peter the Great Bay at the coasts of the Vladivostok district) (Gilbert and Burke 1910; Popov 1933; Rumyantsev 1946; Shmidt 1965; Andriyashev 1964; Lindberg and Legeza 1969; Savicheva 1982; Naumenko 1984; Velikanov 1984). Kobayashi (1962) did not find any capelin during 1957-1962 in Oshoro Bay, Hokkaido (Japan Sea). Similarly, Hikita (1951) did not find any capelin in Volcano Bay (on the south-western coast in Hokkaido and one of the most important fishing grounds), where, however, it was reported later by Amaoka *et al.* (1989).

Capelin has also been reported from Tumen River (part of the boundary between China, North Korea and Russia, flowing into the Sea of Japan), sometime before the 1920s (Mori 1930) but disappeared in the 1930s since the attempts of Schultz (1937) to locate any capelin in the 1930s in the same area was unsuccessful. Capelin has never been reported in the remaining part of the Sea of Japan and Yellow Sea.

### **Northeast Pacific**

In the northeastern Pacific capelin are distributed along the western coast of Alaska, at St. Lawrence Isles, St. Matthew Isles, Nunivak Isle, Pribilof Isles, Bristol Bay, North and south coasts of Alaskan Peninsula, Aleutian Isles, southeast and southwest of Chirikof Isles, Kodiak Isles, Kennedy entrance, Gulf of Alaska and southeastern coast of Alaska, Baranov Isles, Admiralty Isles, Kuiu Isles and Chichagof Isles (McAllister 1963; University of British Columbia, an out-of-date printout). Capelin also extend along the coast of British Columbia as far south as Georgia and Juan de Fuca Straits where they are found in the wintertime (Hart and McHugh 1944; McAllister 1963; Hart 1973; University of British Columbia, an out-of-date printout).

## **ARCTIC**

There is little information on the distribution of capelin in the Russian Arctic waters. Capelin have been found in the Kara and East Siberian Seas (Schultz 1937; Shmidt 1965; Andriyashev 1964; Mecklenburg and Steinke 2015), whereas a mature male, the third to be caught in the area, was recorded in the southeastern Laptev Sea in 1973 (Lutsik *et al.* 1981). The other two were reported by Pirozhnikov (1947) and Kirillov (1972) (cited by Lutsik *et al.* (1981)). Yet, Lutsik *et al.* (1981) maintain that it is not known whether the occurrences of capelin in the Soviet Arctic waters are of a permanent or intermittent nature.

In the Canadian Arctic, capelin are common in the waters off the Alaskan coast, Beaufort Sea (from Cape Lisburne to Cape Bathurst and Herschel Isles), Coronation Gulf (Coppermine, Bathurst Inlet), Chantrey Inlet, Foxe basin (Melville peninsula), Hudson Bay (off the estuary of Churchill river, to the west of Southampton Isle, Coats and Belcher Isles) and James Bay (Vladykov 1933; Walters 1955; McAllister 1962, 1963, 1964; Dunbar 1966, 1970; Leim and Scott 1966; Ochman and Dodson 1982; National Museum of Natural History, Records, Canada, 8 April 1987). They have been found in Hudson Strait, Baffin Island (southern tip of Hall peninsula, Salmon River) and at Resolution Isle (National Museum of Natural History, Records, Canada, 8 April 1987). Capelin visit Ungava Bay occasionally (Dunbar 1954, 1966, 1976, 1983). They were found in massed schools at the mouth of Koksoak River in 1884 and the natives never saw capelin before (Dunbar 1983). There is no information concerning the existence of capelin in Ungava Bay during 1884-1947 (Dunbar 1983). Three young individuals were caught in 1947-1950 at different areas in Ungava Bay, whereas no capelin were found in 750 cod

stomachs examined at Port Burwell (Dunbar and Hildebrand 1952). In 1959 capelin were again abundantly present in the eastern Ungava Bay (Lejeune 1959).

More recently, Davoren *et al.* (2014) write that “[i]n the last decade, capelin have been reported to persistently occur in coastal areas in the Canadian Arctic and local residents have reported spawning-like behavior, similar to sub-Arctic regions (e.g. Newfoundland).” Davoren *et al.* (2014) in their investigations in the southern Darnley Bay (near Paulatuk, Beaufort Sea) and in July 16-17 in Pangnirtung Fjord (near Pangnirtung, Cumberland Sound, Baffin Island), in July 7-10 caught many capelin that were all either in spawning condition (i.e., with ripe gonads) or spent.

## DISCUSSION

Figure 1 shows the geographic distribution of capelin over the world ocean based on the accounts presented herein (which also formed the basis for the same figure in Stergiou 1989). The matching of the distribution of capelin with that of the marine subarctic waters, *sensu* Dunbar (1968, 1972), that is, the zone “...in which Arctic water from the Arctic Ocean is found mixed, or in close association with, water from the Atlantic and Pacific Oceans. [...]. It extends vertically, in the present definition, to the 250 or 300 metre level.” (Dunbar 1972), is apparent in the North Atlantic. The marine subarctic is characterized by certain properties (temperature, ice extent, vertical stability of the water column, diversity of biota, production, seasonality, and sensitivity to climatic change) that clearly define an ecosystem different than the temperate and arctic ecosystems (see Dunbar 1968, 1972).

The situation is different in the Pacific Ocean, where the marine subarctic, *sensu* Dunbar, is the restricted area of mixed waters in the Bering Strait and along the coast of North Alaska (Figure 1). Dunbar (1979) points out that this area of mixed Arctic and non-Arctic water must not be confused with the Pacific Subarctic Water (the zone of cool upper water in the Northern north Pacific) as defined by Svedrup *et al.* (1946). In the Pacific Ocean capelin are found mainly within the cool temperate zone, the southern limit of which is bounded by the 15°C isotherm (the so called Ortmann line; Ortmann 1896). The major exception is that capelin do not appear in the Yellow Sea, to the west, and south of Vancouver Island to the east.

From Figure 1 it seems that the distribution of capelin is probably discontinuous in the Arctic rather than circumpolar as maintained, inasmuch as there are gaps in Arctic distribution of capelin. It seems probable that capelin in the Arctic are relicts from previous warm periods, existing there mainly because of high summer temperatures. For instance, the southeastern part of the Laptev Sea (where capelin exist locally) is the warmest part of the sea a fact attributed to the effect of the Lena River waters; summer sea surface temperatures range between 5-8°C (Zenkevitch 1963), which is within the range of spawning temperatures of capelin (Stergiou 1989). Dunbar (1976, 1983) also proposes that capelin in Hudson Bay are climatic relicts from the warm period of the 1880s (or other) and persist locally due to high summer sea temperatures. Indeed, studies (Davenport *et al.* 1979; Davenport and Stene 1986) show that capelin eggs, larvae, and adults can resist cold temperatures by supercooling in the absence of ice nuclei, whereas temperatures of -1.4°C are lethal in the presence of ice. Hence in the Arctic regions capelin presumably survive in winter by remaining in deeper waters where ice is not present. This has been observed in some fiords in Labrador (Templeman 1948) and Norway (Sars 1879).

The distribution (and abundance) of capelin changes greatly with time and this has been related to large-scale climate changes (Barents Sea: Sars 1879; Konstantinov 1965; Prokhorov 1965, 1968; Olsen 1968; Konstantinov and Svetlov 1974; Stergiou 1984; Iceland: Saemundsson 1934; Jensen 1939, 1948; Taning 1948; Malmberg 1983; Greenland: Jensen 1939, 1948; Hansen and Hermann 1953; Vibe 1967; Stergiou 1984; Newfoundland: Templeman and Fleming 1953; Bay of Fundy: Kendall 1917; Bigelow and Welsch 1924; Ungava Bay: Dunbar 1954, 1966, 1976, 1983; Korea: Stergiou 1984). In fact, Rose (2005) examines 12 documented shifts in the distribution of larval and adult capelin on the world ocean and finds that the displacement distance depends on temperature change:  $[\log_{10}(\text{distance, in km}) = 0.28 \times \text{temperature change} + 2.16 \text{ (} p < 0.05, r^2 = 0.91, n = 12 \text{)}]$  with the response being quick and consistent. He further suggests that capelin can be considered “... as a sea ‘canary’ for northern boreal marine ecosystem responses to climate variability and change.”

Thus it is evident that the distribution of capelin shifts, as a unit, from south to north and back from north to south as a response to cooling (from north to south) and warming (from south to north) trends, i.e., phenomena also studied by M.J. Dunbar (undated).

The occurrence of capelin larvae and adults in the southern Gulf of St. Lawrence, eastern coast of Nova Scotia, Bay of Fundy, Gulf of Maine, Northwestern part of the Greenland coast, southwest Iceland, and at Faroes is most probably passive and mediated by the direction of the existing currents; population may be then established there when oceanographic conditions are favorable for the development of the early life stages (e.g. the occurrence of capelin in the Bay of Fundy in 1965-1968). The occurrence of capelin in southwestern Norway (Vesteralen, Trondheim, and Oslo), northern part of East Greenland and Ungava Bay, however, cannot be attributed to a passive dispersal of larvae or juveniles because the existing currents in these areas are in the opposite direction (see e.g. Vilhjálmsson 2002). Capelin populate these areas by a direct migration, involving time lags, reacting to changing environmental signals (increasing or decreasing temperature, salinity, ice-cover, food etc). A population is then established when conditions for spawning and development of the early life stages are suitable (e.g. occurrence of capelin in Trondheim in 1890s).

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I dedicate this essay to the memory of my supervisor, Maxwell Dunbar, who greatly shaped my ecological thinking.

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## TENTATIVE VON BERTALANFFY GROWTH PARAMETERS OF LITTLE-STUDIED FISHES<sup>\*</sup>

Lincoln Hood and Daniel Pauly

Sea Around Us, Institute for the Oceans and Fisheries,  
University of British Columbia, Vancouver, Canada  
[l.hood@oceans.ubc.ca](mailto:l.hood@oceans.ubc.ca); [d.pauly@oceans.ubc.ca](mailto:d.pauly@oceans.ubc.ca)

### ABSTRACT

The parameters of the von Bertalanffy growth function were estimated from limited age-at-growth data published for various species of fish (marbled rock cod, *Notothenia rossii* at two locations; black rock cod, *N. coriiceps*; the two sexes of humphead wrasse, *Cheilinus undulatus*; brilliant pomfret *Eumegistus illustris*, and snubnosed spiny eel, *Notacanthus chemnitzii*). These parameters are tentative because the (non-validated) age-length data pairs used for curve fitting (as performed with the Solver routine of Microsoft Excel) were relatively scarce and covered only a small range of sizes. Still, these estimates are now available at FishBase ([www.fishbase.org](http://www.fishbase.org)), where they will serve as placeholders until better estimates become available.

### INTRODUCTION

Although it does not exactly fulfill the requirements of a physiological growth model (Pauly 1981, 2010), the von Bertalanffy growth function (VBGF) can be used to describe the growth of most fishes, and to summarize it in the form of its three parameter estimates. The conventional form of the VBGF for length is:  $L_t = L_{\infty} (1 - e^{-K(t-t_0)})$  where  $L_t$  is the length at age  $t$  predicted from  $L_{\infty}$ ,  $K$  and  $t_0$  (Beverton and Holt 1957). Herein,  $L_{\infty}$  is the asymptotic length, i.e., the mean length the fish would reach, under the local conditions, if they were to grow ‘indefinitely’, or a very long time. As such,  $L_{\infty}$  should roughly correspond to the mean length (slightly above that) of a very old and large fish, i.e.,  $L_{\max}$  that this is the case for most species (see Froese and Binohlan 2000). This rule does not apply to very large, fast-growing fishes such as bluefin tuna (*Thunnus thynnus*) because the assumptions built into the VBGF do not apply to such fishes (Pauly 1981, 2010).

The fact that  $L_{\max} \approx L_{\infty}$  in medium-size and small fishes allows using  $L_{\max}$  or other estimates of asymptotic size, which reduces the number of parameters to be estimated from a set of age-at-length data, e.g., from a small number of otoliths whose ‘rings’, presumably annual, have been counted. Also, based on first principle, it can be shown that  $t_0$  should take negative values in the overwhelming majority of cases, due to the fact that larvae and early juveniles grow faster than predicted from the VBGF from small sizes (Pauly 1981, 2010). This implies that a negative  $t_0$  can be given as a constraint to the choice of  $L_{\infty}$ , leaving only the curvature parameters of the VBGF ( $K$ ) to be freely estimated from age-length data pairs.

These considerations were here applied to a few fish species lacking growth parameters in FishBase ([www.fishbase.org](http://www.fishbase.org)), or to species whose growth parameter estimates were even more doubtful than those obtained here.

### MATERIALS AND METHODS

Length-at-age data were read off figures in Choat *et al.* (2006) and Vedishcheva *et al.* (2016) for *Cheilinus undulatus* and *Notacanthus chemnitzii* respectively, from Tables 4-6 in Cali *et al.* (2017) for *Notothenia* spp., and kindly supplied in a spreadsheet by Kélig Mahé for *Eumegistus illustris*.

The VBGF was fitted to each set of age-length data with or without a fixed, external estimate of  $L_{\infty}$  using the Solver routine of Microsoft Excel, and the results tabulated and plotted as growth curves with superposed age-at-length data.

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<sup>\*</sup> Cite as Hood L. and Pauly D. (2017) Tentative von Bertalanffy growth parameters of little studied fishes. Pp. 58-60. In Pauly D., Hood L., and Stergiou K.I. (eds.) Belated contributions on the biology of fish, fisheries and features of their ecosystems. Fisheries Centre Research Reports 25(1). Institute for the Oceans and Fisheries, University of British Columbia.

## RESULTS AND DISCUSSION

Table 1 summarizes our results, which cover eight sets of growth parameter estimates pertaining to five species. As might be seen, it was necessary, due to insufficiency of the age-at-length data, to impose external values of  $L_{\infty}$  in 7 (87.5%) of the 8 cases evaluated, mainly to generate negative values of  $t_0$ .

**Table 1.** Summary of the von Bertalanffy growth parameters for *Cheilinus undulatus*, *Eumegistus illustris*, *Notocanthus chemnitzii*, *Notothenia rossii*, and *Notothenia coriiceps*

Common name	Scientific name	$L_{\infty}$ (cm)	$t_0$ (cm)	K (year <sup>-1</sup> )	n	Remarks/Location
Humphead wrasse	<i>Cheilinus undulatus</i>	200	-2.61	0.04	17	Male
Humphead wrasse	<i>Cheilinus undulatus</i>	80	-4.29	0.09	70	Female
Brilliant pomfret	<i>Eumegistus illustris</i>	80	-0.34	0.13	11	Male and Female
Snubnosed spiny eel	<i>Notocanthus chemnitzii</i>	90	-1.52	0.08	6	Male
Snubnosed spiny eel	<i>Notocanthus chemnitzii</i>	120	-1.85	0.04	6	Female
Marbled rockcod	<i>Notothenia rossii</i>	75	-0.05	0.15	65	South Shetland Islands; Male and Female
Marbled rockcod	<i>Notothenia rossii</i>	77*	-7.40	0.08	65	South Georgia Islands; Male and Female
Black rockcod	<i>Notothenia coriiceps</i>	62	-0.13	0.11	39	South Shetland Islands; Male and Female

\* indicates an  $L_{\infty}$  that was estimated using Microsoft Excel Solver

The 8 panels of Figure 1 (next page) illustrate the growth curves thus obtained. Note that it was necessary in one case (female *Notocanthus chemnitzii*) to omit an obvious outlier from the growth parameter estimation (Figure 1D).

These growth curves appear reasonable and thus can be used for descriptions of the life history of the species in question, or, more tentatively, for assessing their likely response to exploitation by a fishery.

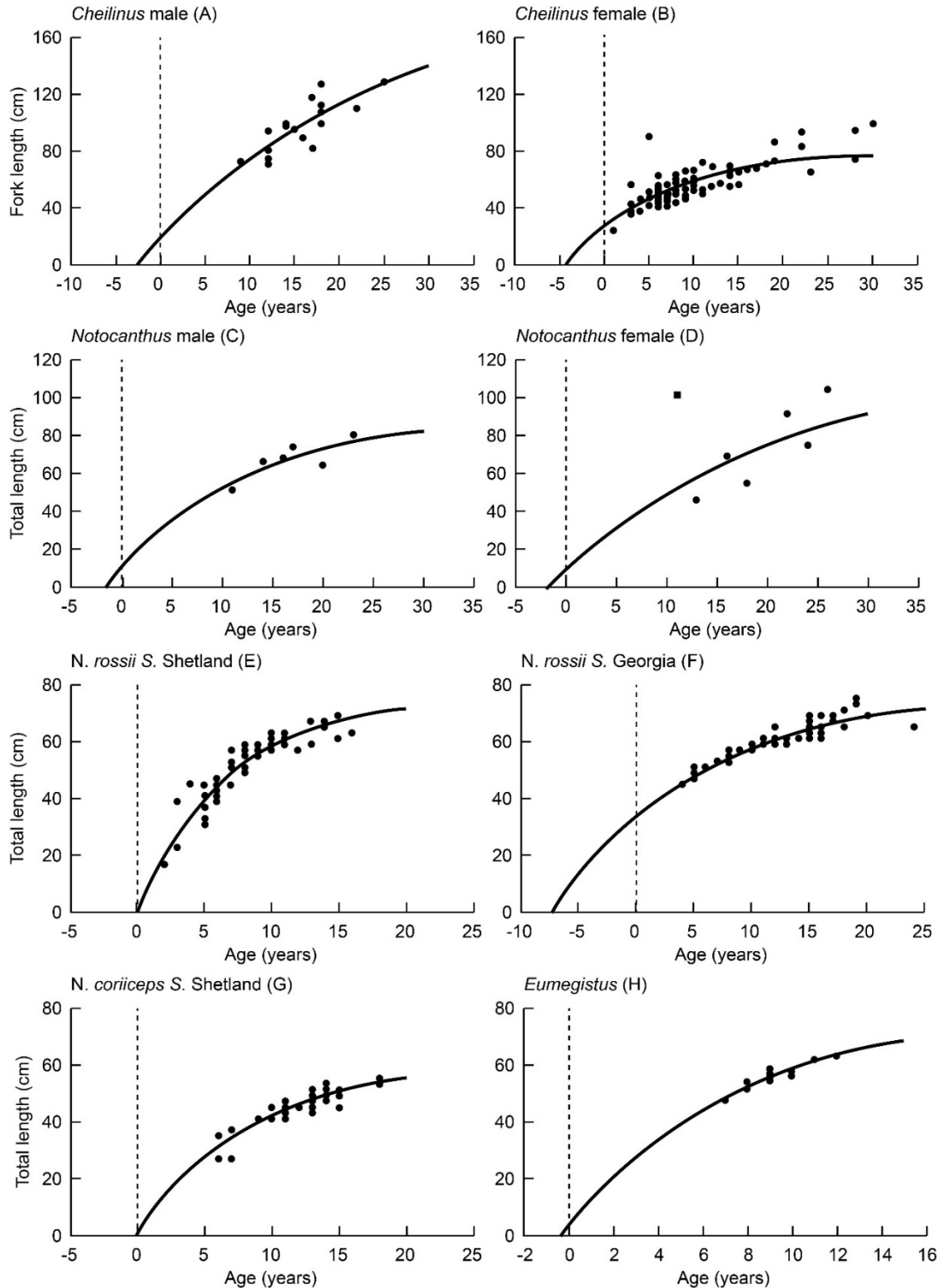
## ACKNOWLEDGEMENTS

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**Figure 1.** Von Bertalanffy growth parameter curves fit using limited age-length data pairs for A) *Cheilinus undulatus* male, B) *Cheilinus undulatus* female, C) *Notacanthus chemnitzii* male, D) *Notacanthus chemnitzii* female; the outlier (•) was not included in growth parameter estimation, E) *Notothenia rossii* at South Shetland Island, F) *Notothenia rossii* at South Georgia Island, G) *Notothenia coriiceps* at South Shetland Island, and H) *Eumegistus illustris*.

## ASPECTS ON AGE AND GROWTH OF *HELICOLENUS DACTYLOPTERUS* FROM THE DEEP WATERS OF THE EASTERN IONIAN SEA\*

Aikaterini Anastasopoulou<sup>1</sup>, Chryssi Mytilineou<sup>1</sup>, Gerasimos Dimitriadis<sup>2</sup> and Christopher J. Smith<sup>1</sup>.

<sup>1</sup> Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Aghios Kosmas, Athens, and Heraklio, Crete, Greece

<sup>2</sup> Department of Aquaculture and Fisheries Management, TEI Mesolonghi, Mesolonghi, Greece  
[kanast@hcmr.gr](mailto:kanast@hcmr.gr)

### ABSTRACT

Length-weight relationships and age and growth of *Helicolenus dactylopterus* in the Eastern Ionian Sea deep-waters were studied from longline experimental surveys. A total of 579 individuals were measured, weighted and sexed. Total length ranged from 119 to 341 mm with males presenting larger mean sizes. Length-weight relationships were estimated for females ( $W_F = 0.015 \cdot TL^{3.03}$ ), males ( $W_M = 0.016 \cdot TL^{3.00}$ ) and sexes combined ( $W = 0.015 \cdot TL^{3.03}$ ). Weight increased isometrically with size for both sexes. Age was determined by reading whole sagittal otoliths of 364 individuals and corresponded to fish from 1 to 23 years old. Growth parameters were estimated using the von Bertalanffy growth model ( $L_\infty = 36.0$  cm,  $K = 0.099$  year<sup>-1</sup>,  $t_0 = -2.16$  years for females;  $L_\infty = 38.7$  cm,  $K = 0.082$  year<sup>-1</sup>,  $t_0 = -3.11$  years for males; and  $L_\infty = 37.5$  cm,  $K = 0.09$  year<sup>-1</sup>,  $t_0 = -2.56$  years for combined sexes), and the growth parameters were significant different between sexes, which the females showing a higher growth performance, as reflected in the values  $\phi' = 2.11$ , against 2.09 for the males.

**Key words:** *Helicolenus dactylopterus*, length distribution, length-weight relationship, age, growth

### INTRODUCTION

The bluemouth rockfish, *Helicolenus dactylopterus* (Delaroche 1809), is a benthic species widely distributed in the Atlantic and Mediterranean Sea but not in the Black Sea (Hureau and Litvinenko 1986). In 1991, it was also reported in the North Sea for first time (Heessen *et al.* 1996). Depth distribution ranges from 50 to 1100 m (Fischer *et al.* 1987).

Bluemouth rockfish is commercial species with an important economic value for some areas (e.g. Atlantic: Allain 2001; Sequeira *et al.* 2009) or of no economic importance in others (e.g. North Sea: Mamie *et al.* 2007). It is caught by long-lines and bottom trawls (Abecasis *et al.* 2006; Sequeira *et al.* 2009) but mostly appears in the by-catch of bottom trawls and pots targeting other deep-water commercial species (Consoli *et al.* 2010 and references therein).

Bluemouth rockfish has been characterized as a slow growing and long-lived species that can live more than 30 years (Abecasis *et al.* 2006; Sequeira *et al.* 2009). Though several studies have been published on age and growth of bluemouth rockfish there are still many gaps regarding its biology and mainly its maximum age (Abecasis *et al.* 2006).

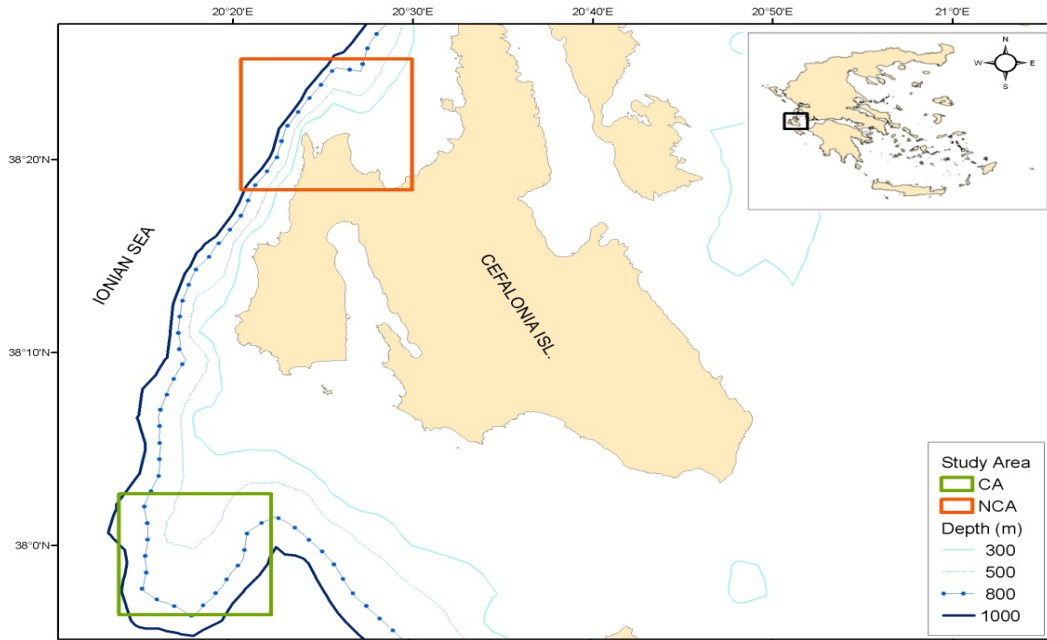
In Greek waters, there are not data available on its age and growth. The aim of this work is to provide information on its age and growth caught in the Eastern Ionian Sea and to compare the results with previously published information.

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## MATERIALS AND METHODS

A total of 652 individuals were captured with experimental bottom long line fishing in the Eastern Ionian Sea off Cefalonia Island (Fig.1) during 2010. Sampling was carried out with a commercial fishing boat in waters ranging between 300 and 857 m in depth during summer and autumn.



**Figure 1.** Map of the study area in the Eastern Ionian Sea showing the two sampling quadrates off Cefalonia Island.

Samples were frozen immediately after capture and examined in the laboratory where total length (TL), total weight (TW) and sex of 579 individuals were recorded. Age of 364 specimens was estimated using otolith readings. From each specimen, sagittal otoliths were extracted, cleaned and photographed through a stereoscope equipped with camera. Otolith radius and the radius of each ring were measured using the Image analysis Pro Plus system. Broken or unclear otoliths were excluded from the analysis. The 1<sup>st</sup> of January was considered as birthday date for the calculations of growth parameters.

ANOVA was used to compare the mean length between sexes. Length-weight relationship was based on the equation  $TW = a TL^b$ . This equation was transformed to a linear form:  $\ln TW = \ln a + b \ln TL$  and the parameters  $a$  and  $b$  were estimated. The parameters  $a$  and  $b$  for the female and male equations were compared statistically using t-test (Zar 1984). The isometry of  $b$ -values was also examined using t-test (Sokal and Rohlf 1981). Von Bertalanffy parameters were based on otolith readings and calculated with non-linear regression for females and males separately. Statistical comparisons between growth parameters were made using t-test. Finally, the growth performance index  $\phi' = \log_{10} K + 2 \cdot \log_{10} L_{\infty}$  (Pauly and Munro 1984) was estimated.

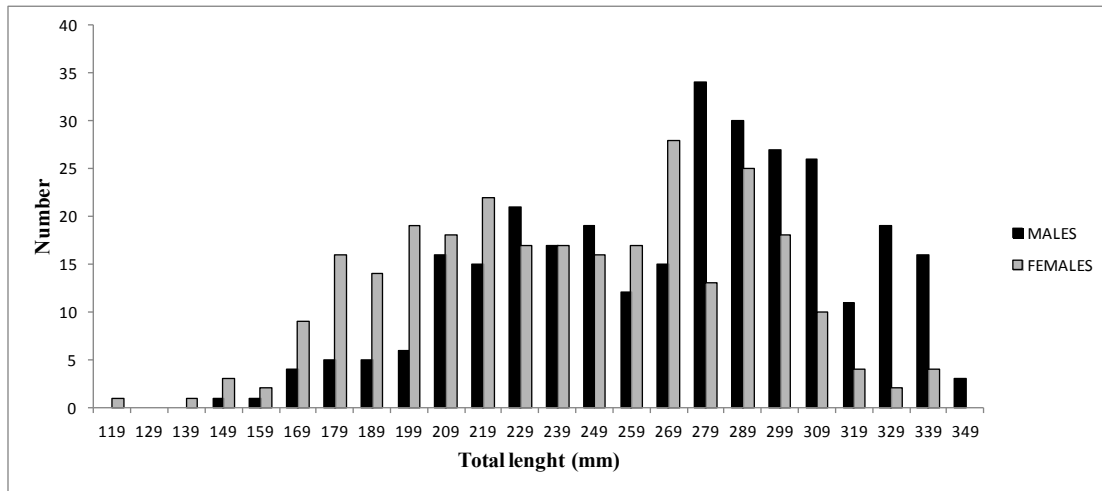
## RESULTS

The size of bluemouth rockfish caught in the Eastern Ionian Sea ranged between 119 and 341 mm (Fig.2). ANOVA showed a significant difference in the mean length (ANOVA,  $p < 0.005$ ;  $N = 578$ ) between sexes with males reaching higher mean length (mean  $\pm$  s.e:  $TL_M = 265 \text{ mm} \pm 2.6$  and  $TL_F = 238 \text{ mm} \pm 2.7$ ).

Length-weight relationships were calculated as follows:

$$\begin{aligned} W_F &= 0.015 \cdot TL^{3.03} \quad (N=275; R^2=0.98) \text{ for females;} \\ W_M &= 0.016 \cdot TL^{3.00} \quad (N=302; R^2=0.98) \text{ for males; and} \\ W &= 0.015 \cdot TL^{3.03} \quad (N=577; R^2=0.98) \text{ for sexes combined.} \end{aligned}$$

Weight increased isometrically with size for both sexes ( $b$  did not differ significantly from 3.0) (Student's  $t$ -test: females:  $t = 1.73$ ;  $p = 0.09$ ,  $n=275$ ; males:  $t = 0.01$ ,  $p = 0.99$ ,  $n = 302$ ).



**Figure 2.** Length frequency distribution by sex of bluemouth rockfish *Helicolenus dactylopterus* in the Eastern Ionian Sea, 2010.

The slope ( $b$ ) of the length-weight relationship did not differ with sex ( $t$ -test,  $t = 1.13$ ,  $p = 0.26$ ). The same was also true for the intercept ( $a$ );  $t$ -test,  $t = -1.49$ ,  $p = 0.62$ .

The analysis of 364 otoliths showed a maximum age of 23 years, but specimens aged more than 15 years and less than 3 years were uncommon in the study area. The von Bertalanffy growth curves are presented in Figure 3.

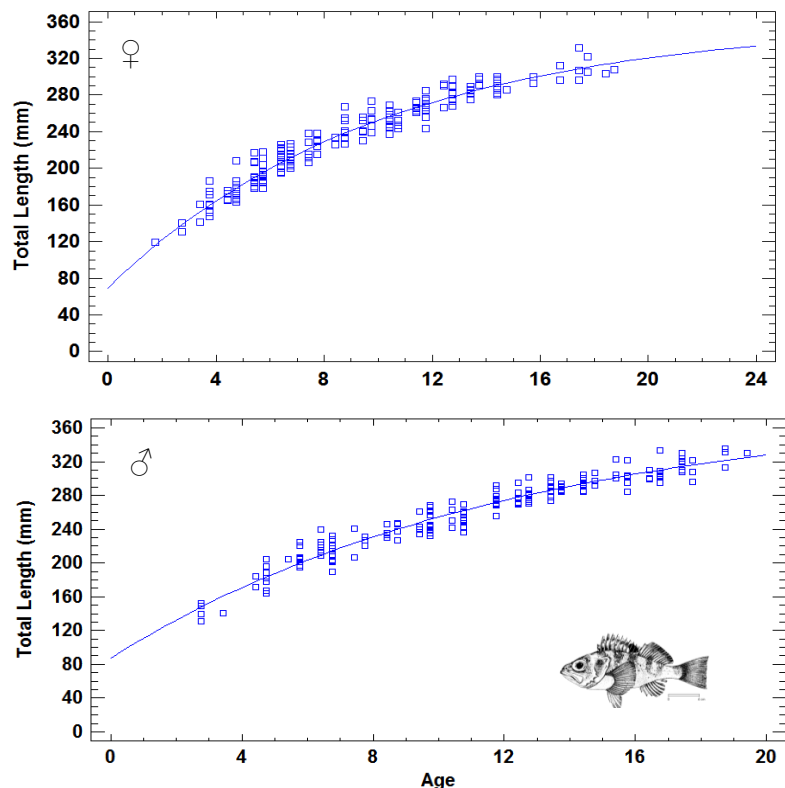
The von Bertalanffy growth parameters ( $\pm$ standard error (SE)) were:

females:  $L_{\infty}=36.0 (\pm 11.0)$  cm,  
 $K= 0.099 (\pm 0.009)$ ,  $t_0= -2.16$  years;  
 males:  $L_{\infty}=38.7 (\pm 14.1)$  cm,  $K= 0.082$   
 $(\pm 0.06)$ ,  $t_0= -3.11$  years; and  
 combined:  $L_{\infty}=37.5 (\pm 8.8)$  cm,  
 $K= 0.09 (\pm 0.006)$ ,  $t_0= -2.56$  years.

The asymptotic length of males was higher than that of females ( $t$ -test,  $p < 0.005$ ). Similarly, significant difference was detected between sexes for  $K$  parameter ( $t$ -test,  $p < 0.005$ ). The values of growth performance index ( $\phi'$ ) for females and males were 2.11 and 2.09, respectively.

## DISCUSSION

The present study provides information on the age and growth of bluemouth rockfish *Helicolenus dactylopterus* from the Eastern Ionian Sea. Results showed that the maximum total length of the species in the study area was 336 mm, corresponding to an estimated age by otolith readings of 23 years, even if only a



**Figure 3.** Von Bertalanffy growth curves by sex determined from otolith readings of bluemouth rockfish *Helicolenus dactylopterus* in the Eastern Ionian Sea, 2010 (fish picture from FishBase (Froese and Pauly 2016)).

few samples were over 15 years old. The maximum size recorded was in most cases, similar to other reported for other Mediterranean areas (e.g. Romanelli *et al.* 1997; Massutí *et al.* 2000). However, the minimum total length of 119 mm recorded in this study was higher than those reported in other studies (e.g. Sequeira *et al.* 2009; Pirrera *et al.* 2009). This could be attributed to the use of longlines in the present study, which is considered a selective gear (Bjorndal and Løkkeborg 1996). Furthermore, Massutí *et al.* (2001) stated that smaller sized individuals are concentrated in shallow waters.

The length-weight relationship describes an isometric growth for bluemouth rockfish in the study area, confirming the results reported from Mediterranean studies (Table 1).

**Table 1.** Length-weight relationship and age growth parameters for *Helicolenus dactylopterus*, reported by several authors in different areas (a: intercept; b: coefficient of allometry;  $L_{\infty}$ : asymptotic length (TL, cm); K: growth coefficient (year<sup>-1</sup>);  $\Phi'$ : growth performance index. C = combined sexes, M = male and F = female.

Study area	Sex	A	b	Growth parameters			Author
				L <sub>∞</sub>	K	Φ'	
Mediterranean Sea							
Ligurian Sea	C			70.7*	0.05	2.35	Peirano and Tunesi (1986)
Sicilian Channel	C			39.2	0.13	2.29	Ragonese and Reale, (1986)
Ionian Sea	C	0.012	3.06	30.7	0.16	2.17	D'Onghia <i>et al.</i> (1994)
	F	0.025	2.92				
	M	0.010	3.07				
Alborán Sea	C	0.013	3.02	30	0.1	1.95	Massutí <i>et al.</i> (2000)
	F	0.019	2.96	27.1	0.1		
	M	0.015	3.00	32.3	0.09		
Balearic Sea	C	0.020	2.98	29.9	0.13	2.06	Massutí <i>et al.</i> (2000)
	F	0.010	3.08	27.0	0.16		
	M	0.009	3.09	32.5	0.10		
North Aegean Sea	C	0.0079	3.28				Filiz and Bilge, (2004)
South Tyrrhenian	C			30	0.16	2.16	Pirrera <i>et al.</i> (2009)
Tyrrhenian Sea	C	0.016	2.99	26.1	0.14	1.98	Consoli <i>et al.</i> (2010)
Turkey waters	C	0.0145	3.06	35.4	0.06		Demihran and Akbulut (2015)
	F	0.0135	3.08	35.7	0.05		
	M	0.0141	3.09	37.6	0.06		
Northern waters of Tunisia	C	0.0221	2.87	37.2	0.14	2.30	Mili <i>et al.</i> (2016)
	F			36.5	0.14	2.28	
	M			39.3	0.12	2.29	
Atlantic Ocean							
Azores	C	0.0104	3.14	47.0	0.08		Monteiro <i>et al.</i> (1991)
Azores	F			54.7	0.10	2.48	Esteves <i>et al.</i> (1997)
	M			50.2	0.16	2.61	
Azores	C			50.5	0.14	2.55	Krug <i>et al.</i> (1998)
NE	C	0.022	2.92				Kelly <i>et al.</i> (1999)
	F			31.0	0.09	1.94	
	M			37.2	0.06	1.92	
Azores	F			56.5	0.07	2.28	Abecasis <i>et al.</i> (2006)
	M			59.1	0.07	2.39	
North Sea	C			28.2	0.12	1.98	Mamie <i>et al.</i> (2007)
Portuguese waters	C			46.5	0.05		Sequeira <i>et al.</i> (2009)
	F			45.3	0.05		
	M			43.3	0.05		

\*Asymptotic length too high, due to some source of bias.

Maximum age recorded in the present study is in accordance to other studies from the Mediterranean (Consoli *et al.* 2010, Massutí *et al.* 2000). Bluemouth rockfish is a slow growing fish with  $K = 0.09$  year<sup>-1</sup>, as also confirmed by other studies (Table 1). Statistically significant difference between female and male growth curves have been also reported by Massutí *et al.* (2000) from Spanish waters, but not from Portuguese waters (Sequeira *et al.*



2009). The values of growth performance index ( $\Phi'$ ) from this study were similar to those reported for some Mediterranean areas and lower than those reported for Sicilian Channel, Ligurian Sea, Tunisian waters, and Azorean waters (Table 1). Spatial differences in growth parameters can be attributed to a variety of reasons notably differences in environmental temperature, fishing pressure, sampling gears, sampling period (e.g. Consoli *et al.* 2010; Mili *et al.* 2016), and ageing methods (e.g. Sequeira *et al.* 2009). As the bluemouth rockfish is a slow growing long-lived species that can attain late first maturity (320mm, Kelly *et al.* 1999) it is particularly vulnerable to overfishing. Thus, the exploitation of this fish should proceed with caution, if at all.

## ACKNOWLEDGMENTS

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## THE GROWTH AND MORTALITY OF SINARAPAN (*MISTICTHYS LUZONENSIS*) IN LAKE MANAPAO, BUHI, CAMARINES SUR PROVINCE, PHILIPPINES\*

Victor S. Soliman<sup>1</sup> and Daniel Pauly<sup>2</sup>

<sup>1)</sup> Bicol University College of Fisheries, Tayhi, Tabaco, Albay 4511, Philippines

<sup>2)</sup> Sea Around Us, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, Canada

[d.pauly@oceans.ubc.ca](mailto:d.pauly@oceans.ubc.ca)

### ABSTRACT

The parameters of the von Bertalanffy growth function were estimated from length-frequency data of ‘sinarapan’ (*Mistichthys luzonensis* Smith 1902; Family Gobiidae) collected in 1988-1989 in Lake Manapao, Philippines, one of the few natural habitats of this tiny fish, which reaches at most 2.5 cm and may be the “world's smallest commercial fish.” Various aspects of the biology of *sinarapan*, which is on the IUCN Red List of Threatened Species (as “conservation-dependent”), are discussed, relative to their conservation in the face of exploitation by an uncontrolled fishery and the presence of invasive predatory species. This gains greater significance in view of the near total collapse of *sinarapan* stocks in Lakes Buhi and Bato where the species was once exceedingly abundant.

### INTRODUCTION

Knowledge of the vital population parameters of fish is essential both for understanding their basic biology and for designing rational exploitation policies. The case of ‘sinarapan’ (*Mistichthys luzonensis* Smith 1902), the world’s “smallest commercial fish”, in Lakes Buhi and Bato, in the Bicol Region of the Philippines, is a case in point. The minute fish was extremely abundant in both lakes from the 1930s to the 1960s, but had almost completely disappeared by 1980. Two hypotheses were offered by Gindelberger (1981b) for the near extinction of *sinarapan* in Lake Buhi: (i) overfishing by motorized ‘sakag’, i.e., collapsible Y-shaped push net, and (ii) predation by the introduced tilapia *Oreochromis mossambicus*. Reliable data (e.g., catch and effort data from well-planned surveys) to test these hypotheses are not available.

The dearth of field data is coupled with the general lack of published information on the species. During the heyday of the *sinarapan* fishery, no one has ever thought of the ruinous turns of events its fishery would be in a decade later. The motorization of *sakag*, employees of the then Bureau of Fisheries and Aquatic Resources (BFAR) and artisanal fishers agree, led to the overfishing of both lakes, besides destroying much of the bottom structures that provided habitat and refuges for this goby. Lake Manapao, where this study was performed, was thus, at that time, one of the few remaining natural freshwater bodies where the goby occurred in any abundance.

Lake Manapao (3.75 ha area and 7.6 m mean water depth) is a tarn or mountain lakelet in San Ramon, in Camarines Sur Province. It is 102 m above sea level and lies approximately 13°26' N, 132°29' E. It was probably formed, together with Lake Katugday, after the last eruption of Mount Iriga in 1641. Despite being declared a “sanctuary” for *sinarapan* by virtue of a municipal ordinance in 1982, Lake Manapao is still being fished by fishers residing along the nearby mountain slopes. Tilapia, common carp, mudfish, and catfish (all introduced species) constitute the bulk of the catch. Sergistid shrimps, which aside from tilapia and mudfish, are suspected to prey on *sinarapan*, also occur in the lake.

*Sinarapan* is viewed as a delicacy and is of great economic value to people residing along the lakeshore areas of Lakes Buhi and Bato, who, according to Gindelberger (1981b), eat this minute fish for breakfast, lunch, and dinner. The collapse of the commercial *sinarapan* fishery of Lake Buhi in early 1979 removed the major source of livelihood of 200 fishers (Gindelberger 1982).

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There are very few published studies on *sinarapan*. Smith (1902) presented a description of its external morphology and its habitat, while Te Winkel (1935) discussed aspects of its anatomy with emphasis on the effect of its small size, respiration, and a general discussion of its habitat. Pauly (1982) demonstrated, based on data in Te Winkel (1935), a limiting role of gill size on the growth of *sinarapan*. The elongated body of *sinarapan* is covered by deciduous ctenoid scales extending from the first dorsal to the posterior margin of the gill cover (Herre 1927). *Sinarapan* can be distinguished from similar freshwater gobies by its three-spined first dorsal fin.

Based on its teeth on the jaws and the pharynx and its exceptionally short digestive tract (Te Winkel 1935), Gindlberger (1981a) suggested that *sinarapan* is zooplankton feeder. In a 10-month study by Traichaiyaporn (1985) in Lake Katugday, she identified 53 phytoplankton species that constituted 30-50% of the stomach content of *sinarapan*. However, she suggested that the “ingestion of the phytoplankton was incidental to the swallowing of the zooplankton which they selectively feed.”

## MATERIALS AND METHODS

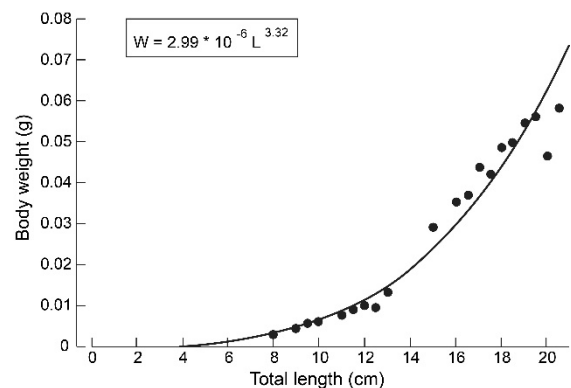
The data used here, extracted from the Master’s thesis of the first author (Soliman 1989), consisted of 10-month length-frequencies (L/F) collected from May 1988 to April 1989 and paired length-weight measurements of 151 individuals of *sinarapan* collected in parallel with the L/F data.

A push net, locally called a *sakag* was used to collect *sinarapan* samples from Manapao. The small catchment area of the lake let (c. 3 ha) allowed the reliable execution of stratified random sampling procedure. Two strata (A and B) were designated based on preliminary sampling in March 1988, with more hauls in the high-density stratum. The selectivity of *sakag* can be assumed to be low, given its meshes of 1 mm<sup>2</sup>. The sampling gear was operated by thrusting 2/3 of the total length of its 2 pole supports into the water; the push net, positioned in the boat’s bow, was pushed forward while the boat was paddled (a motorboat was not available, due to the remoteness of the lake). Organisms other than *sinarapan* (e.g., tilapia, shrimps, other gobies) were sorted out of the catch.

There were 9 to 10 hauls per month, all taken during one sampling date at 08:00-11:00 hours. The absence of length-frequency samples in August and September 1988 was due to the heavy rains that flooded the road to the site.

Length measurements ( $\pm 0.5$  mm) were done under a magnifier, using an improvised fish measuring sheet calibrated using a Vernier caliper. During the analyses, however, the length-frequency data were grouped into twenty 1.0 mm class intervals. A log regression model was fitted to the Total lengths (L) and their corresponding weights (W), estimated using an electronic balance (gravid females were not included in this model).

The length frequency data for 10 sampling months were entered in a format accessible to the ELEFAN software (Gayanilo and Pauly 1989)<sup>5</sup>, which was used to estimate the parameters of the von Bertalanffy growth function (von Bertalanffy 1938) and total mortality (Z) of *sinarapan*. The latter, which was estimated from a length-converted catch curve, was decomposed into fishing mortality (F) using  $Z=F+M$ , with M estimated from the empirical equation of Pauly (1980; 1984).



**Figure 1:** Length-weight relationship of *sinarapan* (*Mistichthys luzonensis*) in Lake Manapao, Philippines.

## RESULTS AND DISCUSSION

The relations of total length to live weight in *sinarapan* is given in Figure 1. Its estimated exponent ( $b=3.45$ ) significantly differed from 3, indicating positive allometric growth.

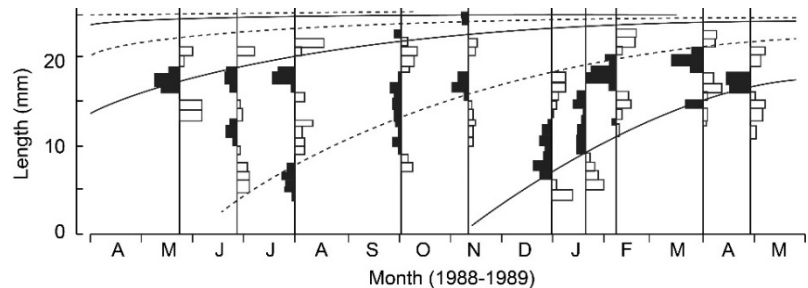
<sup>5</sup> Now available in R, see Pauly, D. and A. Greenberg (Editors). 2013. ELEFAN in R: A new tool for length-frequency analysis. Fisheries Centre Research Reports 21(3) Fisheries Centre, University of British Columbia, Canada, 52 pp.

Figure 2 presents the growth curve for 2 seasonal cohorts of *sinarapan* ( $L_{\infty} = 24.6$  mm and  $K = 2.25$  year<sup>-1</sup>) superposed on the available length-frequency (L/F) data, as restructured by the ELEFAN software to emphasize peaks and troughs in the original L/F data (solid line: main cohort; dotted line: secondary cohort). The relatively high K value obtained is typical of most short-lived tropical fish (see FishBase; [www.fishbase.org](http://www.fishbase.org)).

The total mortality estimated through a catch curve (not shown) was 9.23 year<sup>-1</sup>, and the M and F estimates were 6.201 and 3.033 year<sup>-1</sup>, respectively. It must be emphasized that these estimates are very tentative, notably because Pauly's empirical equation did not include, for its derivation, fishes as small as *sinarapan*.

The high estimate of M may be compatible with high predation experienced by a fish such as *sinarapan*, which does not guard its eggs and young (Gindelberger 1981a). After the females extrude ripe eggs into the water (with some becoming attached to plant roots), the male fertilizes them; then the eggs are abandoned. This makes the eggs and young vulnerable to predators and adverse environmental factors (e.g., sulphur upwelling).

Lake Manapao is a *sinarapan* sanctuary in the sense that it is still abundant here, while it has virtually disappeared from Lakes Buhi, Bato, and Katugday. The estimate of exploitation rate ( $E = F/Z = 0.33$ ) is relatively low and is consistent with Lake Manapao functioning as a 'sanctuary' of sorts.



**Figure 2:** Growth curves (solid: main cohort; dotted: secondary cohort) of *sinarapan* *Mistichthys luzonensis* in Lake Manapao, Philippines, superposed on length-frequency data 'restructured' by the ELEFAN software. The estimated parameters are for both cohorts.  $L_{\infty} = 24.6$  mm and  $K = 2.25$  year<sup>-1</sup>.

With the almost complete disappearance of the Lakes Bato, Buhi, and Katugday populations, Lake Manapao is the only remaining source of *sinarapan* for study, which we recall, is (as of the writing; January 2017) on the IUCN Red List of Threatened Species (as "conservation-dependent"). Hence, studies will have to be carefully planned, and not unduly impact on its populations. This should be considered in the future, notably by the Fisheries and Aquaculture Divisions of the Department of Agriculture.

## ACKNOWLEDGMENTS

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## QUALITATIVE OBSERVATIONS ON *PLECTROPOMUS LEOPARDUS* BEHAVIOR: TESTABLE EXPRESSIONS OF THE OXYGEN-LIMITATION THEORY?

Dirk Zeller

Sea Around Us, Institute for the Ocean and Fisheries, University of British Columbia, Vancouver,  
Canada

[d.zeller@oceans.ubc.ca](mailto:d.zeller@oceans.ubc.ca)

### ABSTRACT

I present a number of qualitative observations made over 10 years of extensive field research on the behavior of the coral trout or leopard coral grouper (*Plectropomus leopardus*) and other large reef fishes. I then suggest that these, and similar observations of the behavior and ecology of reef fishes could be explained by the oxygen-limitation theory proposed by Pauly (2010, *Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals*. International Ecology Institute, Excellence in Ecology, Vol. 22). I suggest that, given the apparent lack of an overarching explanatory biological theory of fish behavior and ecology in coral reef science, these and similar observations can be turned into testable hypotheses, which can be used to quantitatively test the explanatory oxygen-limitation theory.

### INTRODUCTION

During the 1990s, I spent a large amount of time investigating the movement behavior of the coral trout *Plectropomus leopardus* (Serranidae), mainly on Lizard Island on the northern Great Barrier Reef (GBR). While much of this work utilized remote tracking via the first successful application of ultrasonic telemetry on the GBR (Zeller 1997,1998; Zeller and Russ 1998; Zeller 1999,2002), it also involved hundreds of hours spent underwater for visual specimen confirmation, manual underwater tracking, transmitter recovery, underwater visual census, and mark-release-recapture studies (e.g., Zeller and Russ 2000). Numerous qualitative observations I made at that time, and which I internalized as part of my research on movement and behavior patterns of *P. leopardus*, were never documented and summarized until now. Importantly, I never attempted to place these qualitative observations into the context of a deeper explanatory theory of what could be ultimately influencing some of these behaviors.

Here, I summarize these qualitative observations, and attempt to place them in the context of the well-documented oxygen-limitation theory of Pauly (2010) and Bakun (2011), the foundation of which was first developed much earlier (e.g., Pauly 1980,1981). I suggest that these and similar observations lend themselves to quantification as testable hypotheses.

### OBSERVATIONS

#### Predator behavior

I had the opportunity to make many observations of coral trout predation attempts during the extensive aquarium trials I held as part of the telemetry development phase of my studies (Zeller 1999). During these aquarium experiments, I kept a large number of coral trout captive for periods exceeding many weeks to conduct transmitter attachment experiments, and later for recovery of specimen after surgical implantation of ultrasonic transmitters (Zeller 1999). While I generally utilized frozen pilchards (*Sardinops sagax*, at the time the typical bait used for commercial hook-and-line fishing on the GBR) as food for captive specimens, I also experimented repeatedly with feeding live fish to captive coral trout. This consisted of opportunistically netting an array of different species of damselfish (Pomacentridae), small fusiliers (Caesionidae) and cardinalfishes (Apogonidae) on nearby reefs, and carefully introducing these on a one-by-one basis as individual live fish into the aquarium tanks containing acclimatized coral trout.

The surprising observation I made repeatedly was that any individual coral trout made never more than a few attempts (at best 2-3) to strike at and capture the introduced 'food' fish before ignoring these specific individuals

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completely. If such a 'food' fish survived the first few strike attempts from each coral trout in a given tank, it seemed to be immune from any further predation attempts. Thus, these 'food' parcels were subsequently perfectly safe from predation by the coral trout, as long as they remained in that tank. In many cases this situation lasted for weeks, even when I provided no food for the coral trout, i.e., initiated a starvation period. Interestingly, in all cases where I removed the successful 'survivor' damselfish in question and then re-introduced the same individual damselfish back into the same tank 24 hours later, the cycle started over again, i.e., it was again targeted with numerous strike attempts leading either to successful predation or to ignoring the surviving individual damselfish.

After noting this behavior in the aquarium setting, I made it a point to also try and observe the hunting behavior in the field. I repeatedly noted that individual coral trout, when stalking a group of damselfish or other small reef fish species on the reef crest or reef flat, gave up after making a small number of attempts on that group. In case of a successful strike, it seemed that the predator stopped immediately or almost immediately targeting that group. This observation may also be supported by noting that most coral trout examined during a dietary study around One Tree Island (Kingsford 1992) had only one or two prey items in their stomachs. However, of greater interest here seems to be the observation that after unsuccessfully attempting a *small* number of strikes on members of a given group, the individual coral trout seemed to ignore the group of fish for the remainder of my observational time.

Could these and similar observations be explained by physiological constraints on activity patterns, and if so, what is the constraint that drives this pattern?

### **Size differences in vertical distribution behavior over time**

As part of searching for, and also regularly observing, transmitter-equipped specimen of coral trout, I casually noted at the time that larger individuals seemed to spend less time on reef flats during the summer period, but could be found there more readily in the winter period. After some time, I intuitively start looking for smaller individuals in shallower waters in summer months and for larger individuals in deeper waters. Unfortunately, I did not quantify any such potential seasonal vertical space-use patterns at the time, as my focus was mainly on horizontal use patterns as obtainable by the, at that time novel use of ultrasonic telemetry, such as home ranges and activity patterns (Zeller 1997) or spawning aggregation movements (Zeller 1998).

I also regularly observed 'stationarity' of individual coral trout, with the specimen typically holding station under plate-coral (e.g., *Acropora* spp.) or similar cover, and often on up-current sides of reef structures. This behavior was noted more typically in larger individuals, and often seemed accompanied by intense opercula action, used to pump water across its gills. I did not test for observational bias as related to species size and visibility, other than to note here that after explicitly focusing on coral trout for many years, I had developed a very good 'eye' for spotting *P. leopardus* and other grouper species under virtually any circumstances. The current-related behavior has also been described in Zeller (2002), and the long-term stationarity at a single location by large individuals had been noted previously by Samoilys (1987).

Occasional chance observations of several other species of large coral reef fishes, such as two resident individuals of mature and large Queensland or giant grouper (*Epinephelus lanceolatus*), and numerous individuals of humphead wrasse (*Cheilinus undulatus*) also resulted in me making a potentially key observation. Although excursions to shallow waters, e.g., reef flat and reef crest areas, occurred, regular returns to deeper waters (i.e., lower slope) seemed to be a normal part of the activity patterns of these species.

For example, in numerous cases I observed at least one of the two resident Queensland grouper 'patrolling' or moving along in deeper water, i.e., on the lower reef slope around Lizard Island, with only a small number of occasions of these individuals coming to upper slope and reef crest depths. All these 'excursions' into shallower waters seemed to be driven by 'curiosity' (for lack of a better term) about a disturbance, such as, e.g., my colleague, Prof. Garry Russ head-first examining a small cavern near the reef crest, resulting in a large amount of air-bubble formation through the local reef structure with concomitant increased small-fish disturbance associated with the bubble-affected area around the reef cave. These shallow water excursions seemed always short in duration, before the individuals returned to deeper waters. Unfortunately, I did not quantify any of these observations at the time.

Other observations on size patterns do exist. For example, Kingsford (1992) documented that generally, larger individuals of coral trout were observed at reef locations near channels with stronger currents during flooding

tides (providing cooler, oxygen-rich waters, Zeller, pers. obs.), and significant size differences were found between individuals inside lagoons (with generally warmer, oxygen-poorer waters with less mixing, D. Zeller, pers. obs.), and fish on reef slopes, with no fish larger than 440 mm (SL) being observed inside the lagoon at One Tree Island.

I again ask myself what ultimately drives such patterns, once we move beyond the immediate consideration of localized predator-prey interactions and availability of prey in space and time (which are often the focus of scientific investigations in tropical marine ecology). Is there a 'deeper' biological reason for these patterns?

### Spawning aggregations

Spawning aggregations of *P. leopardus* occur in deeper waters, e.g., on deep slope areas around Lizard Island at depths of 15-25 m (Zeller 1998). Similarly, other large reef fishes seem to have spawning aggregations in deeper waters. For example, the Nassau grouper (*Epinephelus striatus*) in the Bahamas, has major spawning sites at waters depths of 20-38 m (Smith 1972; Colin 1992), while the tiger grouper (*Mycteroperca tigris*) in Puerto Rico has been documented at spawning sites on 'deep reef' extending to over 30 m depth (Sadovy *et al.* 1994). In contrast, smaller coral reef fish species seem to utilize more shallow waters, e.g., several species of surgeonfish (Acanthuridae) being observed to spawn along 'reef edges' (Robertson 1983), the bluehead wrasse (*Thalassoma bifasciatum*) in the U.S Virgin Islands had a major spawning location in 7 m depth (Warner 1995), and Sancho *et al.* (2000) observed a large number of species of small reef fishes (Chaetodontidae, Mullidae, Labridae, Scaridae etc.) utilizing a shallow water spawning site (average depth 4.5 m) at Johnston Atoll in the Pacific. I am sure numerous more recent observations on spawning depth by average size of fish species exist, but were not investigated here.

While water currents, and hence egg dispersal and/or egg-predation avoidance patterns are one potential explanatory variable for the evolution of spawning location choices, any potential depth-by-size pattern in species choice of the depth of spawning sites may be influenced by the generally cooler water temperatures and hence higher oxygen availability at greater depth (Pauly 2010; Bakun 2011) during the metabolically challenging courtship and spawning periods.

### CONCLUSIONS

Over 35 years ago, Pauly (1980) documented the relationship between average environmental temperature and fish growth, followed by the demonstration of a relationship between gill surface area and growth in fishes (Pauly 1981). This led directly to the suggestion that fish growth and other aspects of the ecology of fishes (and all 'water-breathing' animals) is ultimately limited by oxygen availability, driven by the limitations of the surface-area-to-volume relationship between gill surface area and volume of the animal. This led to the synthesis of the oxygen-limitation theory now clearly laid out and supported in great detail in Pauly (2010). Bakun (2011) neatly summarized the impact this oxygen-limitation theory has on tuna behavior, as demonstrated using telemetry by Block *et al.* (2001): "...fish finding themselves in the throes of oxygen deficit might be impelled to move temporarily to a depth zone of higher oxygen concentration if that option is available, or to a cooler depth where oxygen usage is less, in order to achieve more rapid relief. Rapid switching between food-rich, but warm surface waters, and less productive, but cooler waters is known to occur".

Thus, based on my limited qualitative observations laid out above, and the (very) limited addition of other published examples of such depth-to-size relationships, I would like to propose here the testable hypothesis that the behavior and ecology of coral trout (and other reef fishes), including predator behavior, vertical spatial residence patterns as well as the evolution of spawning site depth may be explained by the oxygen-limitation theory of Pauly (2010). Coral reef fishes lend themselves exceptionally well to quantitatively testing hypotheses associated with this theory, due to relative ease of observation, high average surface water temperatures close to species temperature maxima, and the increasing impact of climate change. Thus, I would encourage researchers in tropical marine science to engage in such hypothesis testing of this theory. After all, to my knowledge, tropical marine science is full of hypotheses and 'regional', 'topical' or species-specific explanations, but seem to have no unifying, underlying biological theory that can explain many (possibly all?) of the ecological patterns and behaviors in space and time that we observe in reef fishes. The oxygen-limitation theory seems to provide such a deep explanatory theory. Go forth and test!

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## TRENDS IN NORTHEASTERN MEDITERRANEAN ARTISANAL FISHERIES

Konstantinos I. Stergiou<sup>1,2</sup>, Athanasios Machias<sup>1</sup>, Stylianos Somarakis<sup>1</sup> and Argyris Kapantagakis<sup>1</sup>

<sup>1)</sup> *Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Aghios Kosmas, Athens, and Heraklio, Crete, Greece*

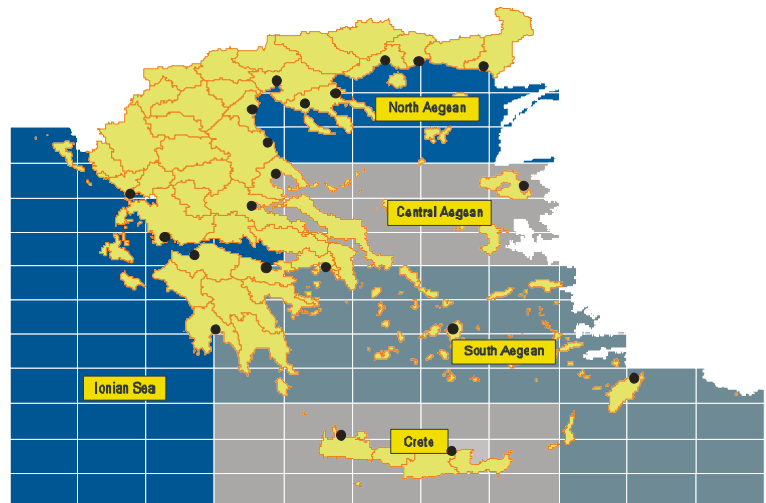
<sup>2)</sup> *Laboratory of Ichthyology, Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece*  
[kstergio@bio.auth.gr](mailto:kstergio@bio.auth.gr), [kstergio@hcmr.gr](mailto:kstergio@hcmr.gr)

### ABSTRACT

Data on fishing effort (i.e., gross tonnage GRT, fishing days at sea) and total catch/day by main fishing gear (trawlers, purse seiners, longliners, netters, beach seiners, and other small-scale boats) started to be collected in the second half of 1995 (and up to 2000) by the Institute of Marine Biology of Crete (which in 2003 was merged with the National Centre for Marine Research to form the Hellenic Center for Marine Research). Data were collected over 21 stations distributed in the Greek Seas. In the present study, we analyzed the historical monthly fishing effort and total catch/day for longliners and netters. Two vessel size groups were considered, smaller and larger than 10 m, and the data collected were aggregated for five subareas (North Aegean, Central Aegean, South Aegean, Cretan waters and Ionian Sea). Our results indicated that the numbers of days at sea were lower in the wintertime than in other seasons, a fact that must be attributed to the adverse weather conditions prevailing during this period. Spatially, the number of days at sea was generally lower in Cretan waters and higher in the North Aegean Sea than in the remaining subareas. This is also attributed to the worst sea conditions prevailing in southern than northern areas because of the higher fetch. The dynamic regression models built for the total catch/day time series allowed us to draw certain general conclusions with respect to the dynamics of the fisheries in concern. Firstly, effort, expressed either as boat GRT or days at sea, seemed to affect catch/day, and thus could be used as a predictor of catch/day. Secondly, the models built predicted persistence of catches (i.e., lags 1-3 months) and seasonality.

### INTRODUCTION

The Institute of Marine Biology of Crete (IMBC), which in 2003 was merged with the National Centre for Marine Research to form the Hellenic Center for Marine Research, started in the second half of 1995 (and up to 2000) to collect, within the framework of various projects funded by National and EU sources, data on fishing effort (gross tonnage and days at sea) by main fishing gear (trawlers, purse seiners, longliners, netters, beach seiners, and other small-scale boats) as well as the corresponding catch/day for a large number of species. These data, which were collected on a monthly basis over a net of 21 stations, distributed throughout the Greek Seas (Figure 1), by local Fisheries Inspectors. After 2003 such data were collected within the Data Collection Framework (DCF) of the European Union.



**Figure 1.** The main subareas and sampling stations (black circles) in Greek waters.

In this paper, we analyzed the monthly data of fishing effort and total catch per day for longliners and netters during 1996-2000 in order to identify trends as well as the underlying dynamics of these fisheries at the spatial and temporal scale. This is important especially for the small-scale fisheries because of the large number of operating artisanal vessels (e.g. more than 19,000 in Greek waters) and the large number of landing sites, extending all along

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the coastline. In addition, these historical data cover the full fishing fleet as opposed to other sources (e.g. National Statistical Service), which in that period covered only vessels with more than 19 horsepower (HP).

## MATERIALS AND METHODS

Data on fishing effort (i.e., fishing days at sea) and the corresponding total catch/day for longliners and netters, have been collected since the second half of 1995 under the framework of various projects funded by several national and EU sources.

Data have been collected on a monthly basis from vessels that display full activity, over a net of 21 stations located at the main fishing ports throughout the Greek Seas (Figure 1). Collected data were grouped into two vessel size categories: smaller than 10 m and larger than 10 m. The former generally operate off the coast, while the latter operate in deep waters as well. Collected data were also aggregated into five major fishing subareas: North Aegean, Central Aegean, South Aegean, Cretan waters, and Ionian Sea (Figure 1). These subareas generally differ in terms of NSSG catch species composition and biological productivity (see review by Stergiou *et al.* 1997a). The mean percentage of vessels sampled for effort when compared to the mean number of registered vessels (Table 1) ranged from 2.4 to 13.2% for longliners and from 1.5 to 6.0% for netters. The mean percentage of registered vessels sampled for catch/day ranged from 2.2 to 11.8% for longliners and from 1.3 to 5.1% for netters (Table 1).

Mean monthly fishing effort, expressed either as fishing days at sea as well as total catch/day for each gear type, size, and subarea were plotted against time and trends with slopes significantly ( $p < 0.05$ ) different from 0 were identified. In general, the same vessels operate either longlines or nets. However, the effort expressed as days/sea as well as the catch/day were treated separately for vessels operating as netters or longliners.

For each subarea and gear size, simple or multiple regression models, subsequently improved by dynamic regression techniques (see Stergiou and Christou 1996; Stergiou *et al.* 1997a,b; Christou and Stergiou 1997), were fitted to the logged catch/day time series using both effort indices (number of fishing days/vessel and GRT) and time as independent variables.

The multiple regression models developed were subsequently examined for inclusion of Cochrane-Orcutt autoregressive error terms (Cochrane and Orcutt 1949), autoregressive terms of the dependent variable and lagged terms of the independent variable(s). The general form of a dynamic regression model including  $k$  autoregressive terms of the dependent variable of interest,  $X_t$ ,  $m$  lags of an independent variable,  $Y_t$ , and  $n$  Cochrane-Orcutt autoregressive error terms,  $e_t$ , is:

$$X_t = c + a_1X_{t-1} + \dots + a_kX_{t-k} + b_0Y_t + b_1Y_{t-1} + \dots + b_mY_{t-m} + c_0e_t + c_1e_{t-1} + \dots + c_ne_{t-n}$$

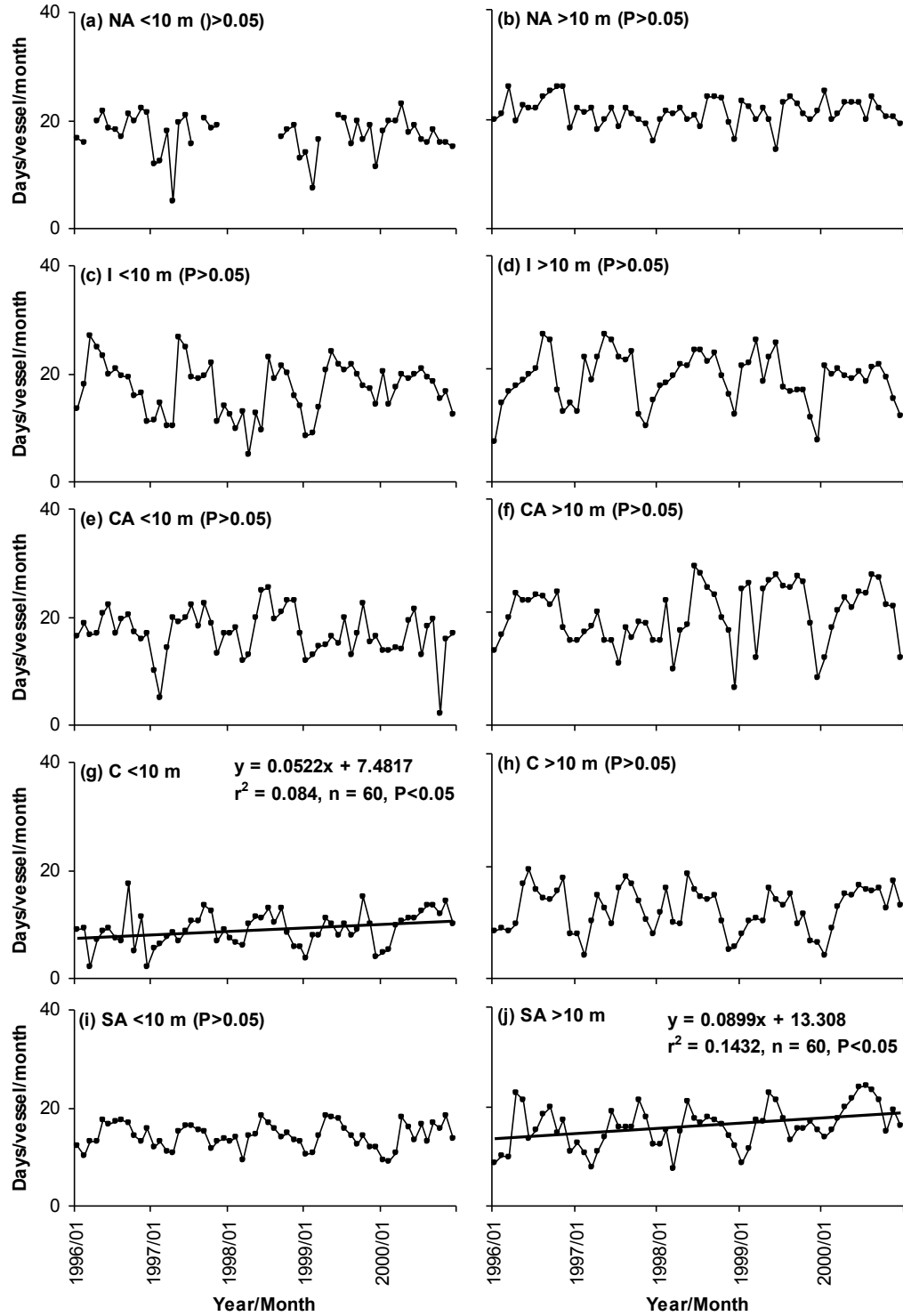
For all multiple regression models built, a Lagrange multiplier test (Engle 1984) was performed for the first twelve lags of the Cochrane-Orcutt errors, dependent and independent variable(s). New terms were included in the models when the Lagrange multiplier test was significant at the level 0.01 (Stellwagen and Goodrich 1993). All multiple and dynamic regression models were developed using Forecast/Pro for Windows (Stellwagen and Goodrich 1993). All models were checked for residual autocorrelation using the Ljung-Box statistic (Ljung and Box 1978) for the first 18 lags of the residuals (Stellwagen and Goodrich 1993).

Finally, comparisons of mean effort and mean catch/day between gears, gear sizes, and subareas were done using one-way analysis of variance (ANOVA) and Fisher's Least Significance Difference (LSD) tests (Zar 1984).

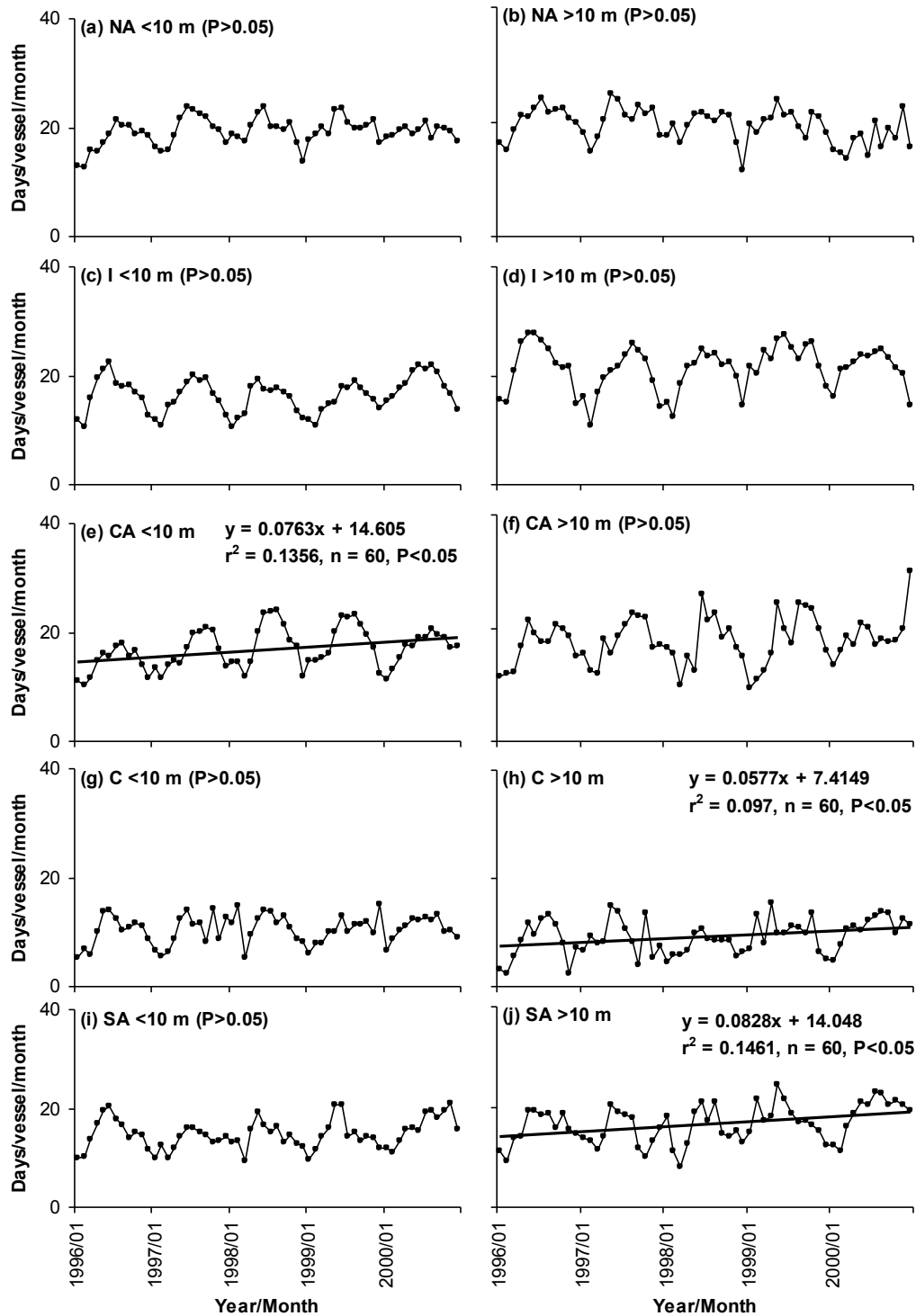
## RESULTS

Time series of monthly number of days/vessel for small and large longliners and netters in the five subareas during 1996-2000 are shown in Figures 2 and 3. With the exception of small longliners operating in Cretan waters and the large ones operating in South Aegean, for which the mean number of days/vessel increased significantly ( $p < 0.05$ ) with time, mean number of days/vessel did not change with time in the remaining cases (Figure 2). The mean number of days/vessel increased significantly ( $p < 0.05$ ) with time for small netters operating in the Central Aegean Sea and large ones operating in South Aegean and Cretan waters whereas it did not change significantly ( $p < 0.05$ ) with time for all remaining cases (Figure 3).





**Figure 2.** Mean monthly number of fishing days/vessel for longliners. Greek waters, 1996-2000. a) North Aegean, NA, vessels <10 m; b) North Aegean, vessels >10 m; c) Ionian, I, vessels <10 m; d) Ionian, vessels >10 m; e) Central Aegean, CA, vessels <10 m; f) Central Aegean, vessels >10 m; g) Cretan waters, C, vessels 10 m; h) Cretan waters, vessels >10 m; i) South Aegean, SA, vessels <10 m; and j) South Aegean, vessels >10 m. Trend lines with slopes significantly ( $p < 0.05$ ) different from zero are also shown.



**Figure 3.** Mean monthly number of fishing days/vessel for netters. Greek waters, 1996-2000. a) North Aegean, NA, vessels <10 m; b) North Aegean, vessels >10 m; c) Ionian, I, vessels <10 m; d) Ionian, vessels >10 m; e) Central Aegean, CA, vessels <10 m; f) Central Aegean, vessels >10 m; g) Cretan waters, C, vessels <10 m; h) Cretan waters, vessels >10 m; i) South Aegean, SA, vessels <10 m; and j) South Aegean, vessels >10 m. Trend lines with slopes significantly ( $p < 0.05$ ) different from zero are also shown.



For longliners, the mean number of days/vessel ranged from 9.07, for small vessels operating in Cretan waters, to 21.34 for large ones operating in North Aegean (Table 1). For netters, the mean number of days/vessel ranged from 9.17 days, for large vessels operating in Cretan waters, to 21.42 days for large vessels operating in the Ionian Sea (Table 1). For both gears, the mean number of days/vessel differed significantly (ANOVA, for all  $F > 48.9$ ,  $p < 0.05$ ) among gear-size/subarea categories (Table 1). The mean monthly number of days/vessel for longliners and netters exhibited a seasonal cycle, being generally higher in the summertime (not shown).

The mean monthly catch/day for small and large longliners and netters in the five subareas are shown in figures 4 and 5. For longliners, the monthly catch/day increased significantly ( $p < 0.05$ ) with time in three cases (large vessels in the Ionian Sea; small vessels in the Ionian and Central Aegean Seas) and declined significantly with time in two cases (small vessels in South Aegean and Cretan waters). It ranged from 7.47 kg/day, for small longliners operating in the Central Aegean Sea, to 156.22 kg/day for large ones operating in Cretan waters (Table 1) and differed significantly among gear-size/subarea categories (ANOVA,  $F = 53$ ,  $p < 0.05$ ). For netters, the monthly catch/day decreased significantly ( $p < 0.05$ ) with time only for two cases (large vessels in North and South Aegean). It ranged from 16.8 kg/day, for small netters operating in the Central Aegean, to 60.2 kg/day for the large ones in Cretan waters (Table 1) and differed significantly among gear-size/subarea categories (ANOVA,  $F = 18.2$ ,  $p < 0.05$ ). Finally, the monthly catch/day was, in many cases, higher during the summertime for longliners (Figure 6) whereas it exhibited maxima in different months depending on subarea for netters (Figure 6).

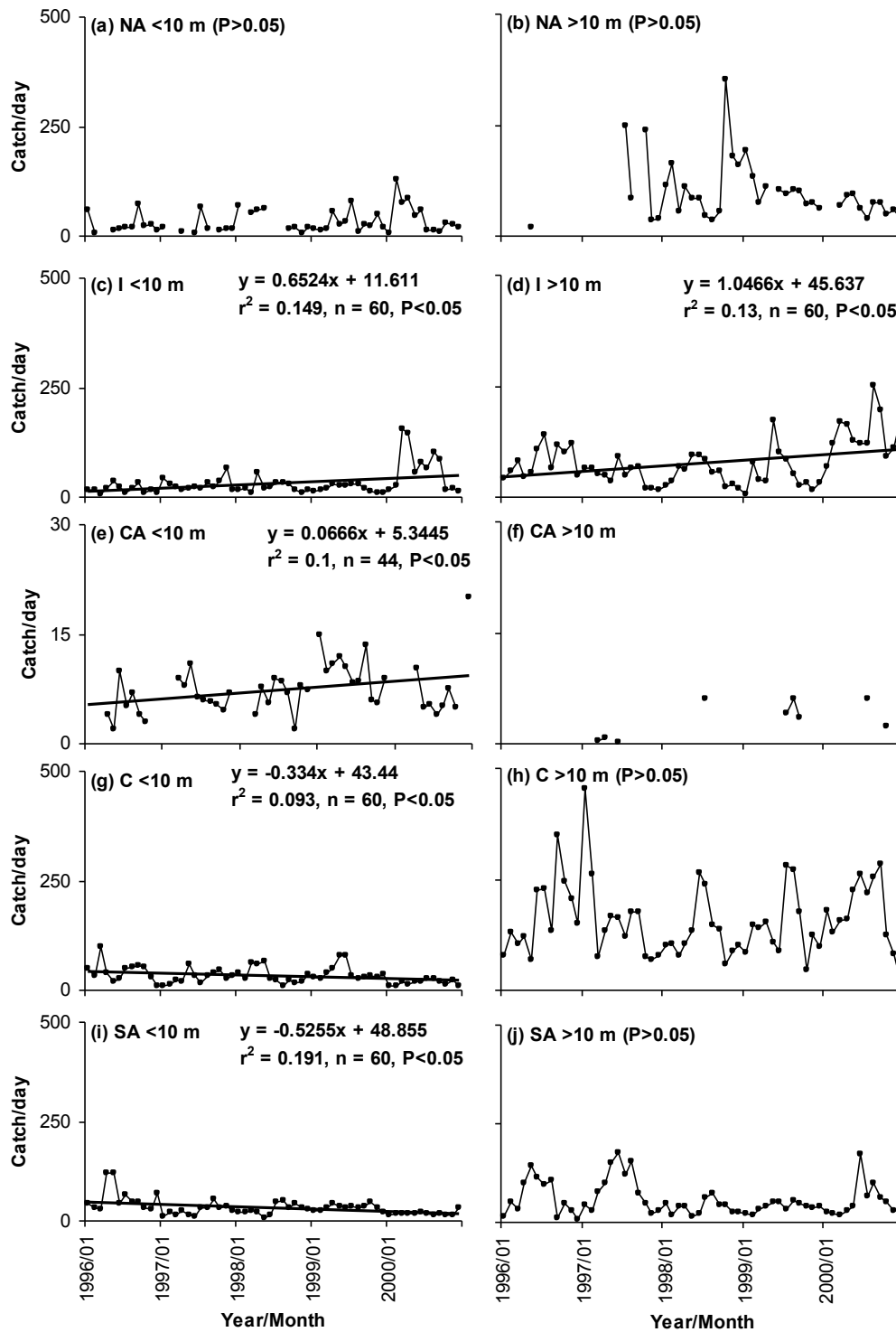
For longliners, all 6 full catch/day time series were modeled and the number of data points used in the final models ranged from 57 to 59, depending on the number of lags used (Table 2).  $R^2$  values ranged from 0.18 to 0.49, and the use of the Ljung-Box statistic indicated that residuals were not autocorrelated (Table 2). Effort, expressed either as number of days or GRT, entered into 4 out of the 6 models built. The trend term entered into 2 models, effort in number of days into 3 models, boat GRT into 2 models and lagged (i.e., 1 and 3 months) catch/day into all models (Table 2). Similarly, all 10 full time series of catch/day for netters were modeled and the number of data points used in the final models ranged from 52 to 59, depending on the number of lags used (Table 2).  $R^2$  values ranged from 0.19 to 0.43, and the use of the Ljung-Box statistic indicated that residuals were not autocorrelated. Effort, expressed either as number of days or GRT, entered into 8 out of the 10 models. The trend term entered into 6 models, effort in number of days into 4 models, boat GRT into 4 models and lagged (i.e., 1, 7 and 8 months) catch/day into 9 models (Table 2).

## DISCUSSION

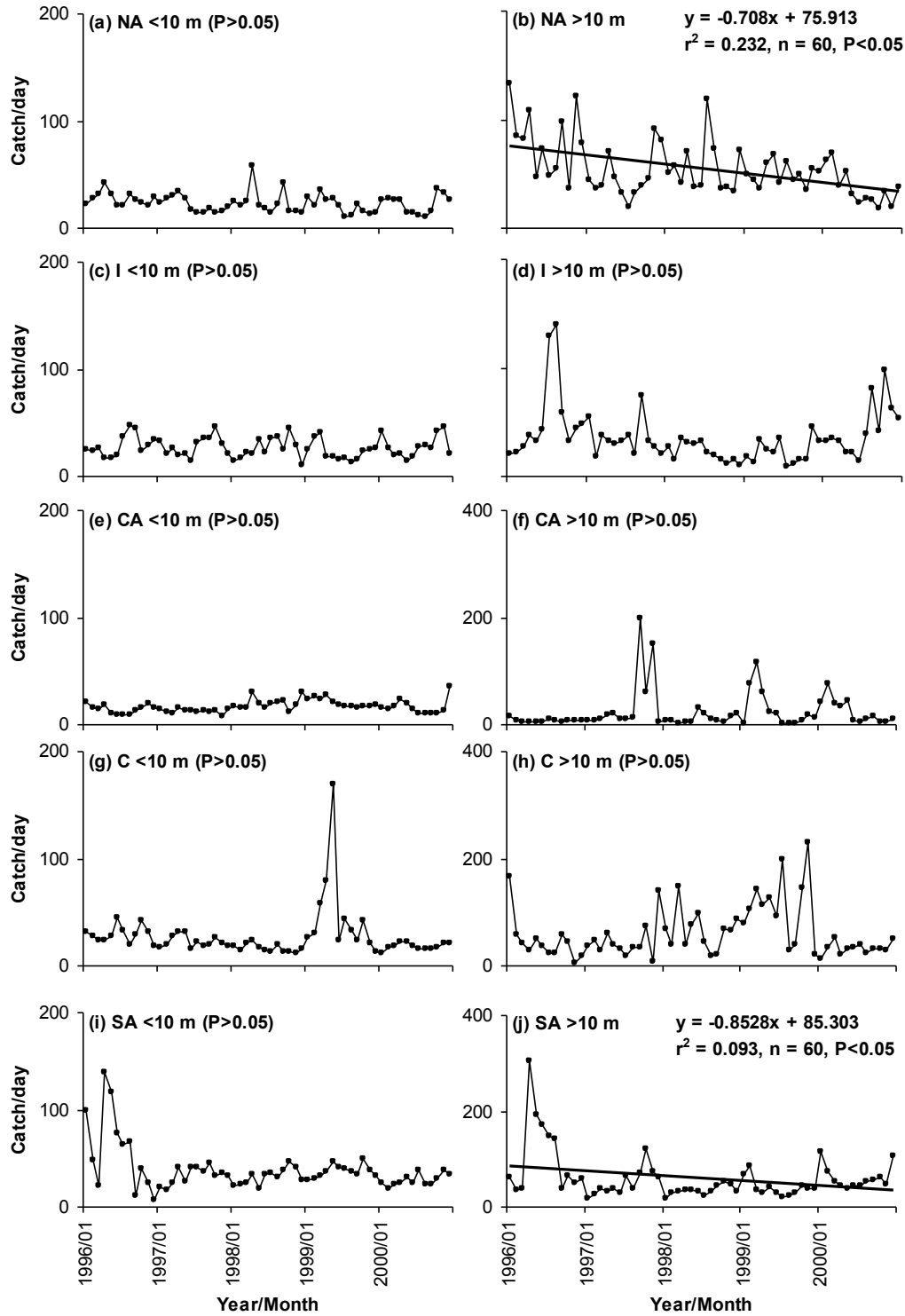
In the present study we analysed monthly data of fishing effort and catch/day for netters and longliners operating in Greek waters during 1996-2000. Our results indicated that the numbers of days at sea were lower in the wintertime than in other seasons, a fact that must be attributed to the adverse weather conditions prevailing during this period. Spatially, for both longliners and netters the number of days at sea was generally lower in Cretan waters and higher in the North Aegean and Ionian Seas when compared to the remaining subareas. This is also attributed to the worst sea conditions prevailing in southern than northern areas because of the higher fetch (Stergiou *et al.* 1997a). Days at sea were generally lower for small boats, which are most severely affected by bad sea conditions.

The large netters and longliners attained the highest mean catch/day in Cretan waters and South Aegean, a fact attributed to their engagement into the fishery of *Xiphias gladius* and the deep-water fisheries (e.g. *Pagellus bogaraveo*, *Polyprion americanus*) (Anon. 2001) as well as in the North Aegean Sea, one of the most productive Greek area (Stergiou *et al.* 1997a).

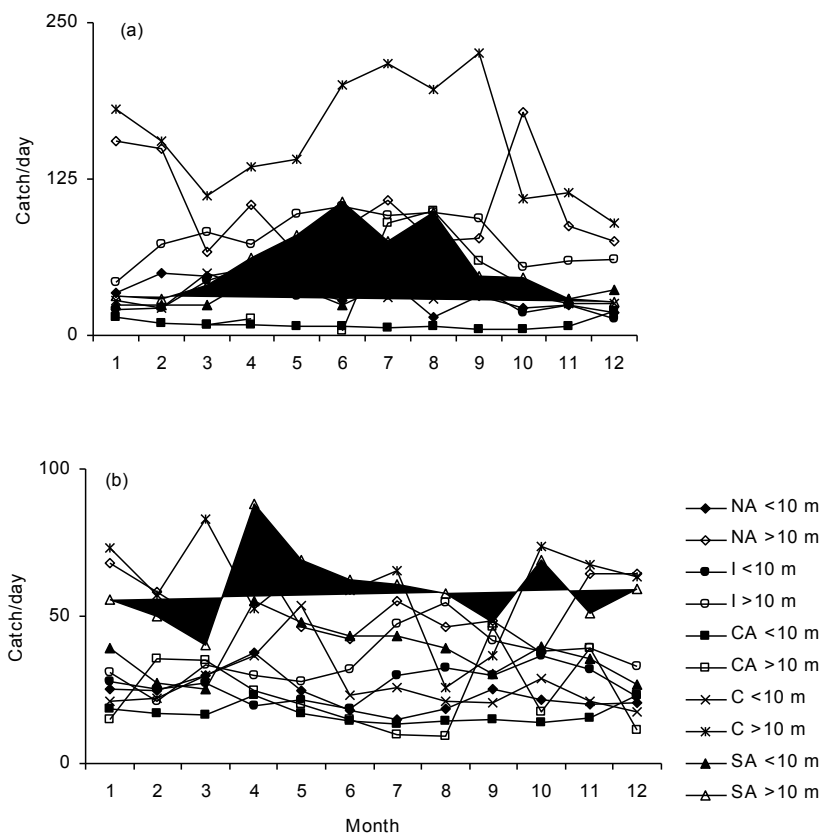
The dynamic regression models built for the full time series of the total catch/day for longliners and netters (Table 2) allowed us to draw certain general conclusions with respect to the dynamics of the fisheries in concern. First, effort, expressed either as GRT or days at sea, seemed to affect catch/day, and thus could be used as a predictor of catch/day. Second, catch/day could generally be partially predicted from the value of the catch/day itself 1 to 3 months earlier. Thus, the models built predicted persistence of catches, i.e., once catches are high they tend to remain high for 1 to 3 successive months. Persistence may imply that environmental conditions favouring the formation of "hot spots" and/or other factors (e.g. microeconomics) affecting the fisheries in concern also tend to persist (Stergiou and Christou 1996). Longer lags ( $> 7$  months) might indicate seasonality (Stergiou *et al.* 1997b). It must be pointed out, however, that the results of the dynamic regression analysis must be considered with caution because of the shortness of the existing time series.



**Figure 4.** Mean monthly catch/day (in kg/day) for longliners. Greek waters, 1996-2000. a) North Aegean, NA, vessels <10 m; b) North Aegean, vessels >10 m; c) Ionian, I, vessels <10 m; d) Ionian, vessels >10 m; e) Central Aegean, CA, vessels <10 m; f) Central Aegean, vessels >10 m; g) Cretan waters, C, vessels <10 m; h) Cretan waters, vessels >10 m; i) South Aegean, SA, vessels <10 m; and j) South Aegean, vessels >10 m. Trend lines with slopes significantly ( $p<0.05$ ) different from zero are also shown.



**Figure 5.** Mean monthly catch/day (in kg/day) for netters. Greek waters, 1996-2000. a) North Aegean, NA, vessels <10 m; b) North Aegean, vessels >10 m; c) Ionian, I, vessels <10 m; d) Ionian, vessels >10 m; e) Central Aegean, CA, vessels <10 m; f) Central Aegean, vessels >10 m; g) Cretan waters, C, vessels <10 m; h) Cretan waters, vessels >10 m; i) South Aegean, SA, vessels <10 m; and j) South Aegean, vessels >10 m. Trend lines with slopes significantly ( $p < 0.05$ ) different from zero are also shown.



**Figure 6.** Monthly averages of catch/day (in kg/day) for longliners. Greek waters, 1996-2000. NA: North Aegean; I: Ionian; CA: Central Aegean; C: Cretan waters; SA: South Aegean; the symbols < and > imply vessels smaller and larger than 10 m.

To sum up, despite the shortness of the available time series (i.e., 5 years), various patterns and propensities were identified. Such historical data are especially useful because small-scale fisheries are largely underrepresented in the national (i.e., NSSG: vessels smaller than 19 HP are not monitored) and international (i.e., Food and Agricultural Organization, FAO) statistics. Because the data presented here are also compatible with the DCF data for the years 2003-2008, they can be used to extend the latter back to 1996.

## ACKNOWLEDGEMENTS

This essay is dedicated to the late John Laurensen who was the soul of the database on which this paper was based.

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**Table 1.** The mean monthly (1996-2000) percentage of vessels sampled for fishing effort and catch/day, and the mean number of vessels registered, for each subarea and gear by vessel size. The results of the Least Significant Difference test for differences in the mean number of fishing days/vessel by gear and the mean catch/day (in kg/day) by gear are shown. N = number of data points. CA = Central Aegean; C = Cretan waters; I = Ionian; NA = North Aegean; SA = South Aegean. '**H. Group**' refers to homogeneous groups.

Gear	Sub-area	Vessel size	Effort (%)	Catch/day (%)	Mean # N of vessels	Days/vessel			Catch/day (kg/day)		
						N	Mean	H. Group	N	Mean	H. Group
Longliners	CA	>10m	2.7	3.0	207.3	60	19.48	F	9	55.00	BCD
	CA	<10m	4.5	2.7	4294.7	60	17.09	DE	44	7.47	A
	C	>10m	13.2	11.8	101.5	60	12.33	B	60	156.22	F
	C	<10m	2.6	2.5	838.0	60	9.07	A	60	33.25	B
	I	>10m	8.0	7.1	161.0	60	18.31	EF	60	77.56	D
	I	<10m	2.4	2.2	4388.7	60	17.23	DE	60	31.51	B
	NA	>10m	5.0	4.6	228.8	60	21.34	G	39	100.21	E
	NA	<10m	4.0	3.8	2828.8	47	17.43	DE	50	32.59	B
	SA	>10m	3.1	2.9	562.0	60	16.05	D	60	55.91	C
	SA	<10m	2.7	2.5	5145.7	60	14.24	C	60	32.83	B
Netters	CA	>10m	1.5	2.6	207.3	60	17.83	E	60	23.21	A
	CA	<10m	2.8	2.3	4294.7	60	16.93	DE	60	16.81	A
	C	>10m	3.8	2.7	101.5	60	9.17	A	60	60.21	D
	C	<10m	1.4	1.9	838.0	60	10.49	B	60	26.83	AB
	I	>10m	6.0	5.1	161.0	60	21.42	G	60	35.79	BC
	I	<10m	2.9	2.6	4388.7	60	16.45	D	60	26.89	AB
	NA	>10m	4.2	3.9	228.8	60	19.38	F	60	54.32	D
	NA	<10m	1.7	1.3	2828.8	60	19.29	F	60	23.49	A
	SA	>10m	1.7	1.4	562.0	60	16.57	D	60	59.29	D
	SA	<10m	2.2	2.1	5145.7	60	14.78	C	60	37.72	C

**Table 2.** Final dynamic regression models of monthly (1996-2000, 60 data points) catch/day (logged) for vessels smaller and larger than 10 m (<10 and >10 respectively) in the five subareas using time and monthly effort (days at sea). NA=North Aegean Sea; I=Ionian Sea; CA=Central Aegean Sea; C=Cretan waters; SA=South Aegean Sea. R<sup>2</sup>=coefficient of determination; N=number of data points; LB(18)=Ljung-Box statistic, 18 degrees of freedom; all values indicate that residuals are not autocorrelated at  $\alpha=0.01$ . Lags in months.

Gear	Parameters	Vessel size category per subarea									
		NA <10	NA >10	I <10	I >10	CA <10	CA >10	C <10	C >10	SA <10	SA >10
Longliners	R <sup>2</sup> (adj.)			0.26	0.49			0.39	0.18	0.31	0.37
	N			59	59			57	59	57	59
	LB(18)			12.26	21.83			10.83	19.46	18.02	26.99
	Constant							1.924	2.641		1.465
	Time			0.001	0.002						
	<i>Catch/day</i>										
	Lag 1			0.525	0.384			1.924	0.461	0.525	0.547
	Lag 3									0.220	
	<i>Effort in days</i>										
	Lag 0				0.056					0.058	
	Lag 3							-0.053			
	<i>Effort in GRT</i>										
	Lag 0										0.099
	Lag 1				0.088						0.120
Netters	R <sup>2</sup> (adj.)	0.39	0.43	0.24	0.33	0.41	0.19	0.42	0.27	0.38	0.38
	N	59	59	58	52	59	58	57	59	52	59
	LB (18)	20.31	17.82	22.50	20.73	18.26	12.63	15.44	15.74	23.60	9.96
	Constant		197.738								
	Time	0.002	-0.098	0.001				0.001	0.001	0.003	
	<i>Catch/day</i>										
	Lag 1	0.359	0.258	0.378	0.449	0.555	0.619	0.547			0.582
	Lag 7									-0.279	
	Lag 8				0.373					-0.244	
	<i>Effort in days</i>										
	Lag 0							-0.049			
	Lag 1	-0.068									
	Lag 2			0.033	0.027						
	Lag 3							-0.046			
	<i>Effort in GRT</i>										
	Lag 0										0.113
	Lag 1					0.366		0.050			
	Lag 2						0.064				



## SIZE SELECTIVITY OF DIAMOND AND SQUARE MESH COD-ENDS IN FOUR MEDITERRANEAN FISH SPECIES<sup>1</sup>

Konstantinos I. Stergiou<sup>1, 2</sup> and George Petrakis<sup>1</sup>

<sup>1)</sup> Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Aghios Kosmas, Athens, Greece

<sup>2)</sup> Laboratory of Ichthyology, Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece  
[kstergio@bio.auth.gr](mailto:kstergio@bio.auth.gr), [kstergio@hcmr.gr](mailto:kstergio@hcmr.gr)

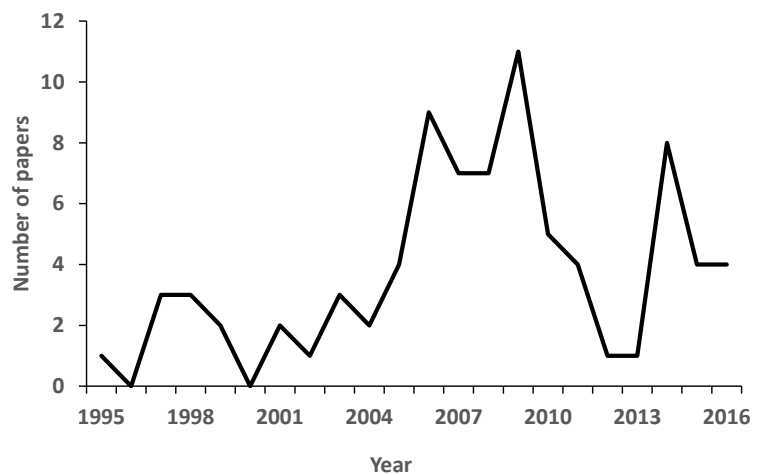
### ABSTRACT

We present trawl cod-end selectivity estimates (based on the covered cod-end method) for red bandfish *Cepola macrophthalma*, silvery pout *Gadiculus argenteus*, elongate tonguesole *Symphurus ligulatus*, and red mullet *Mullus barbatus* for three cod-end mesh sizes: 14 mm (knot-to-knot) diamond-shaped, which was used in the Greek commercial trawl fishery before the end of June 2008, and the 20 mm square-shaped and 20 mm diamond-shaped ones, the former being the cod-end mesh size used nowadays (EU regulation 1967/2006). The present study was based on experiments conducted in the western Aegean Sea in October 1993 and March 1994. Our results, which suggested that 14D was not selective for any of the target species studied, although 'outdated' have an inherent historical value and can be used for setting a 'time series' of selectivity data and as a baseline for recent selectivity experiments.

### INTRODUCTION

We present trawl cod-end selectivity estimates for red bandfish *Cepola macrophthalma*, silvery pout *Gadiculus argenteus*, elongate tonguesole *Symphurus ligulatus*, and red mullet *Mullus barbatus* for three cod-end mesh sizes: 14 mm (knot-to-knot) diamond-shaped, which was used in the Greek commercial trawl fishery before the end of June 2008, and the 20 mm square-shaped and 20 mm diamond-shaped ones, the former being the cod-end mesh size used nowadays (EU regulation 1967/2006). The present study was based on cod-end selection experiments conducted in the western Aegean Sea in October 1993 and March 1994. Although the results presented here are 'outdated' they have an inherent historical value. The experiments described here were among the first ones to be conducted in the

Mediterranean and part of the results of these experiments, which were published 20 years ago (i.e., Petrakis and Stergiou 1997, Stergiou *et al.* 1997a), were also among the first ones to appear in the primary literature for the Mediterranean (Figure 1). Thus, they potentially influenced the change in EU policy on this issue. The results presented here can also be used for setting a 'time series' of selectivity data and as a baseline for recent selectivity experiments (e.g., Mytilineou *et al.* 2015; Brčić *et al.* 2016; Deval *et al.* 2016).



**Figure 1.** Number of papers published in the literature with 'trawl' and 'selectivity' and 'Mediterranean' in the title abstract and keywords (Scopus database, 27-2-2017).

. Cite as Stergiou K.I. and Petrakis G. (2017) Size selectivity of diamond and square mesh cod-ends in four Mediterranean fish species. Pp 85– 90. In Pauly D., Hood L., and Stergiou K.I. (eds.) Belated contributions on the biology of fish, fisheries and features of their ecosystems. Fisheries Centre Research Reports 25(1). Institute for the Oceans and Fisheries, University of British Columbia

## MATERIAL AND METHODS

Sampling took place at five stations in the Trikeri Channel (Figure 2) in October 1993 and at seven stations in the North Euboikos Gulf (Figure 2) in March 1994. Sampling was conducted with a chartered commercial trawler during daylight at depths ranging between 73 and 170 m in the Trikeri Channel, and between 73 and 210 m in the North Euboikos Gulf. The duration of the hauls ranged between 45 and 60 min, in October 1993, and between 60 and 105 min, in March 1994, being longer at deeper stations but constant for all trials at each station. In all cases, the towing speed was 3 knots, same as in the commercial trawl fishery.

In the experiments we compared the size selectivity of the 14 mm (knot-to-knot) diamond-shaped cod-end (14D) with those of 20 mm square-shaped (20S) and 20 mm diamond-shaped cod-end (20D). All mesh sizes refer to nominal sizes. We used the covered cod-end method (Pope *et al.* 1975). The three cod-ends were made by the same material and covered by a multi-monofilament diamond-shaped net of 10 mm (knot-to-knot) mesh size that was used in order to retain the specimens escaping from the test cod-ends. The cover was attached directly to the funnel end of the net. In order to maintain a good flow of water and to avoid masking of the cod-end meshes, the stretched cover net was 2 m wider in radius and 2 m longer than the test cod-ends. During the experiments, the 14D, 20D and 20S cod-ends were used on the same net and exchanged randomly at convenient intervals. Each cod-end fished for twelve hauls. After each haul, the catches of the cod-end and cover were removed and sorted completely into species separately. Catches were analyzed only for the hauls for which the cod-end was undamaged. The total number and weight per species caught and the individual length (for *Mullus barbatus* fork length FL; for all remaining species total length, TL; to the nearest mm) of a large subsample of the target species (i.e., number of individuals > 150) were measured. The size distributions of the measured subsamples of each species were then raised to the totals for the whole catches in the cod-end and cover. Length measurements were used for the estimation of: a)  $L_{50}$ ,  $L_{25}$  and  $L_{75}$ , the lengths at which 50%, 25% and 75% of the fish entering into the gear are retained; b) selection factor, SF; and c) selection range, SR.

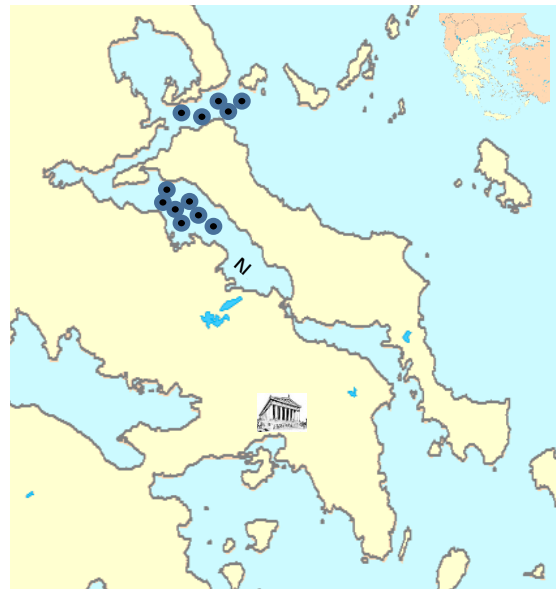
The size selectivity of the cod-end was determined from the relationship between the probability  $p$  of an individual entering the cod-end and body length  $l$  (Holden 1971). This relationship is described by the logistic function (Fryer 1991):  $p = (e^{(v_1 + v_2 l)}) / (1 + e^{(v_1 + v_2 l)})$ , where  $v_1$  represents the intercept and  $v_2$  the slope of the curve after applying a logit transformation. The values of  $L_{50}$ ,  $L_{25}$  and  $L_{75}$  can then be estimated from  $L_{50} = -v_1 / v_2$ ;  $L_{25} = (-\ln(3) - v_1) / v_2$ ;  $L_{75} = (\ln(3) - v_1) / v_2$ ; and Selection range (SR) =  $L_{75} - L_{25}$  and Selection factor (SF) =  $L_{50} / (\text{mesh size})$ .

The parameters  $v_1$  and  $v_2$  were estimated using the log-likelihood method of Fryer (1991). Selectivity estimates were derived from pooling the data over all hauls and seasons. Selectivity parameters were estimated using the algorithm of Petrakis and Stergiou (1997).

Cod-end selectivity was estimated for three non-commercial species (red bandfish *Cepola macrophthalmia* and silvery pout *Gadiculus argenteus*, which were caught in abundance in both trials, and elongate tongue sole *Symphurus ligulatus*, which was caught in relatively large numbers only in October 1993) and for one commercial species, red mullet *Mullus barbatus* (caught in some numbers only in March 1994).

## RESULTS

Our results are summarized in Table 1. The following text provides details by species.



**Figure 2.** Stations in the Trikeri Channel and the Euboikos Gulf, Greece, where trawl selectivity experiments were conducted.

### Red bandfish *Cepola macrophthalma*

The number of specimens that entered into 14D and 20S were approximately the same whereas that for 20D was 1.2 times higher than that for 14D. The 14D cod-end retained about three times more specimens than the other two cod-ends. The proportion of population retained ratio was 0.97 for 14D, 0.23 for 20D and 0.40 for 20S (Table 1). The number of specimens that escaped from 14D was very low (23 fish).

The length-frequency distributions of the entered and retained individuals (not shown here) showed two general modes, one at lengths ranging between 10-43 cm and another one between 50-60 cm. The cod-ends used were selective for the specimens belonging to the first length group since the lengths of the escaped specimens ranged between 10 and 45 cm.

**Table 1.** Estimated selectivity parameters for *Cepola macrophthalma*, *Gadiculus argenteus*, *Mullus barbatus*, and *Symphurus ligulatus*. RR = (retained/entered) ratio, SE = standard error,  $\Delta$  = deviance statistic (over-dispersion), dof = degrees of freedom. All length units are in cm. The RR for *Mullus barbatus* 14D is 0.98. The RR for *Symphurus ligulatus* 20D and 20S are 0.26 and 0.32, respectively.

	<i>Cepola macrophthalma</i>			<i>Gadiculus argenteus</i>			<i>Mullus barbatus</i>		<i>Symphurus ligulatus</i>
Estimates	14D	20D	20S	14D	20D	20S	20S	20D	14D
RR	0.97	0.23	0.40	0.96	0.20	0.31	0.86	0.89	0.40
$v_1$	-3.37	-5.00	-2.71	-2.18	-5.28	-6.28	-15.16	-8.60	-3.10
$v_2$	0.42	0.13	0.08	0.74	0.51	0.67	1.41	0.80	0.33
SE $v_1$	1.00	0.46	0.29	0.85	0.24	0.35	2.65	3.55	0.91
SE $v_2$	0.08	0.02	0.01	0.13	0.03	0.04	0.23	0.28	0.11
$L_{25}$	5.45	29.02	20.72	1.46	8.11	7.77	9.99	9.38	6.07
$L_{50}$	8.08	37.20	34.88	2.95	10.25	9.42	10.78	10.76	9.39
$L_{75}$	10.72	45.38	49.04	5.43	12.38	11.06	11.56	12.13	12.72
SF	5.77	18.60	17.44	2.11	5.13	4.71	5.39	5.38	6.71
SR	5.27	16.36	28.32	3.97	4.27	3.29	1.56	2.75	6.66
CI $L_{50}$	5.30- 9.55	34.77- 40.44	2.1- 38.24	0.84- 3.95	9.91- 10.66	9.17- 9.70	10.31- 11.11	6.35- 11.89	8.58 - 12.74
$\Delta$	14.39	133.63	102.84	76.99	75.76	226.66	8.09	15.93	26.63
Dof	55	56	54	18	21	21	24	19	13
p-value	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

The estimated selectivity parameters are shown in Table 1. Estimates for 14D were based on 23 escapes and, hence, must be considered with caution. Although the number of small specimens caught in 14D was high, very few specimens escaped. The 14D cod-end was not selective even for such an elongated, laterally compressed species. The data for 20D was overdispersed at significance level  $\alpha=0.05$  ( $\Delta=133.63 > X^2_{(56,0.05)}=74.468$ ). The 95% confidence interval of the 20S  $L_{50}$  overlapped with that of 20D whereas both did not overlap with that of 14D. The data for 20S was also overdispersed at significance level  $\alpha=0.05$  ( $\Delta=102.84 > X^2_{(54,0.05)}=72.15$ ). The retention probability of fish with lengths  $> 40$  cm was higher whereas that of the fish with lengths  $< 40$  cm was lower for 20D than for 20S, a fact indicating that 20D is more selective.

### Silvery pout *Gadiculus argenteus*

The number of specimens that entered into 20D and 20S was 1.85 times more than that for 14D and 3.10 times more than that of 14D, respectively. The proportion of population retained was 0.96, 0.20 and 0.31 for 14D, 20D and 20S, respectively (Table 1). Only 192 specimens escaped from 14D whereas 6562 specimens escaped from 20D and 9525 from 20S.

The length-frequency distributions of the entered and retained individuals (not shown here) showed two general modes, one at lengths ranging between 5 and 9 cm and another one at lengths between 10 and 12 cm. The 14D cod-end was not selective (i.e., the majority of the individuals that entered into that cod-end were retained). The 20D and 20S cod-ends were selective for the specimens belonging to the first length group since the lengths of the escaped specimens also ranged between 5 and 9 cm.

The estimated selectivity parameters are shown in Table 1. The 95% confidence interval of 20S  $L_{50}$  marginally overlapped with that of 20D. The estimated retention probability of the individuals with lengths >7 cm is lower for 20D than for 20S.

### Red mullet *Mullus barbatus*

The proportion of population retained was 0.98 for 14D, 0.89 for 20D and 0.86 for 20S (Table 1). The length-frequency distributions of the individuals (not shown here) showed two modes for 14D, a major one at lengths 13-15 cm and a minor one at 11-12 cm. Only 7 specimens escaped from that net. For 20S, the length-frequency distributions of the individuals also showed two modes, a major one at lengths 11-14 cm and a minor one at 17-19 cm whereas those of the escaped ones exhibited a mode at lengths 10-12 cm. Finally, for 20D, the lengths of the individuals ranged between 11-22 cm whereas those of the escaped ones between 10-15 cm.

For 14D the data was very poor (few individuals entered and only 7 individuals escaped) and the resulting standard errors of the parameters  $v_1$  and  $v_2$  were larger than the values of the parameters themselves. The estimated selectivity parameters for 20S and 20D are shown in Table 1. Although the numbers retained and escaped were also low for 20D, there was a relatively good fit of the model. A rough estimate of the  $L_{50}$  value for 14D, from the SF value of 20D, is 7.55 cm.

### Elongate tonguesole *Symphurus ligulatus*

For *Symphurus ligulatus*, the proportion of population retained was 0.53 for 14D, 0.09 for 20D and 0.19 for 20S (Table 1). The length-frequency distributions of the individuals (not shown here) showed one general mode at lengths 8-10 cm for all three cod-ends. The selectivity parameters were not estimated for 20S and 20D because the numbers of specimens per length class that escaped from these cod-ends were, for all length classes, generally much higher than the numbers of those retained. In addition, the length ranges of the individuals in the cover cod-ends were generally wider than those retained by 20S and 20D. These facts rendered the estimation of selectivity parameters impossible because the resulted arithmetic values of the parameter  $v_2$  were negative.

For 14D, the estimated values of  $L_{25}$ ,  $L_{50}$  and  $L_{75}$  were 6.07, 9.39 and 12.72 cm, respectively (Table 1). The data for this net was overdispersed at a significance level of  $\alpha=0.05$  ( $\Delta = 26.63 > X^2_{(13,0.05)} = 22.36$ ) (Table 1). A rough estimate of the  $L_{50}$  value for 20D, from the SF value of 14D, is 13.4 cm.

## DISCUSSION

In the present study we compared the size selectivity of the 14D cod-end, which was used in Greek waters before 2008, with those of the 20S (which is nowadays used) and 20D ones for four demersal fish species, which make up a substantial part of the trawl catches in Greek waters. We point out that we did not examine the seasonal effect and between-haul variability, both of which affect selectivity estimates (e.g. Fryer 1991). Our results, which have historical value, clearly showed that 14D was not selective for the four species studied (Table 1). Because the majority of the individuals of the commercial fish species escaping through the 14D meshes are undersized (i.e., their body size is smaller than the minimum legal landing size (Stergiou *et al.* 1997b; Petrakis and Stergiou 1997) and, hence, are not marketed, the shift from 14D to 20S was not accompanied by any commercial loss. At the same time, the weight of discards, which amounts to about 38-45% of the total Greek trawl catch (Tsangarakis *et al.* 2014), is considerably reduced because 20S is characterized by much higher commercial/non-commercial ratios in terms of both weight and number (e.g. Stergiou *et al.* 1997b, Guijarro and Massuti 2006). Thus, the banning of 14D and the use of 20S since 2008 was essential for the management and conservation of the Greek demersal resources and the Mediterranean ones in general (e.g. WWF 2008).

In general, it is well known that square-shaped meshes can increase selectivity because in contrast to diamond-shaped ones they remain open during towing (e.g., Robertson and Stewart 1988). Yet, the effect of the shape of the mesh on selectivity depends on the body shape of the target species [square-shaped meshes are generally more selective than diamond-shaped ones of similar mesh size for roundfish: e.g. haddock, whiting (Robertson and Stewart 1988), hake, horse mackerel (*Trachurus trachurus*), axillary seabream (*Pagellus acarne*) (Petrakis and Stergiou 1997; Campos and Fonseca 2003) as well as Norway lobster *Nephrops norvegicus* (Robertson *et al.* 1986; Stergiou *et al.* 1997a); the opposite is true for flatfish (Millar and Walsh 1992; Harris and DeAlteris 1992; Walsh *et al.* 1992; Petrakis and Stergiou 1997; Guijarro and Massuti 2006)].

The estimated 20S  $L_{50}$  value for *Mullus barbatus* (Table 1) was higher than its minimum landing size (MLS; 11 cm), notwithstanding the fact that  $L_{50}$  may probably be slightly underestimated because of the masking of the cod-end meshes. Yet, both  $L_{50}$  and MLS are not generally larger than its length at 50% maturity in Greek waters (=10.3-12.5 cm; Stergiou *et al.* 2011), a fact indicating that even the use of 20S provides small opportunities for reproduction. The same is also true of other large-sized fish species such as *Lophius budegassa*, *Zeus faber*, *Uranoscopus scaber*, *Torpedo marmorata*, and *Trigla lucerna* (in the study area all test cod-ends retained all individuals: Stergiou *et al.* 1997b). In contrast, this was not true of *T. m. capellanus* and *M. poutassou*, (Petrakis and Stergiou 1997). This is a well-known problem for multispecies fisheries (e.g., Sainsbury 1984; Liu *et al.* 1985), such as the Mediterranean trawl fisheries, where the catch is composed of many species differing in their body morphology and sizes (e.g., from small 5-6 cm Gobiidae to very large rays), the use of a single mesh size is always a compromise in which some species will have a smaller chance to escape through the cod-end whereas others will have a smaller chance to be retained.

## ACKNOWLEDGEMENTS

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## PRIMARY PRODUCTION ENHANCEMENT BY OCEANIC SEAMOUNTS<sup>1</sup>

Daniel Pauly

*Sea Around Us, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, Canada*

[d.pauly@oceans.ubc.ca](mailto:d.pauly@oceans.ubc.ca)

### ABSTRACT

Oceanic seamounts are known to have a rich endemic fauna and high biomasses of fish and invertebrates, sustained by a primary production that they locally enhance and by secondary production, which the seamount animals capture from passing currents. There has been much debate about the relative contribution of these two sources of food for seamount animals. Here, a method is presented for detecting the primary production signature of seamounts from remote sensing data. The results suggest the occurrence of a strong enhancement of primary production for seamounts reaching close to the surface, which, however, quickly tapers with depth.

### INTRODUCTION

Various mechanisms have been advanced to explain how generally conical seamounts, located in the path of marine currents, would generate an upwelling-like transfer of deep, nutrient rich water toward the surface, and thus increase local primary production (Dower *et al.* 1992; Bakun 1996). While such local upwelling allows patches of high primary production to be detected, using field sampling over certain well-studied seamounts (Peláez and McGowan 1986; Dower *et al.* 1992; Comeau *et al.* 1995; Mouriño *et al.* 2001), a general procedure for remotely sensing the enhanced pigment signature of seamounts has been lacking so far. This is not surprising, as visual examination of large-scale satellite imagery does not display anything resembling the distribution patterns of known seamounts. Thus, it might be inferred that satellite imagery, perhaps because of random variations at various scales, cannot detect seamount signatures (Peláez and McGowan 1986). However, it is shown here that this is not the case, and that satellite imagery does contain the primary production signature of seamounts.

### MATERIAL AND METHODS

#### Definition and identification of seamounts

In the absence of a global registry of seamounts and of standards upon which such registry could be based, a mid-resolution bathymetric map (NOAA/NGDC 2001) was used to identify seamounts, using two techniques (Kitchingman and Lai 2004; Kitchingman *et al.* 2007):

The first technique was the identification of a subset of the seamounts of the world via the application to a map distributed by NOAA of the flow direction and sink algorithms that are part of ESRI's ArcGIS software, and the standard deviation of the depth estimates in a three by three block including and adjacent to the cell being examined. Seamounts differ from other areas of the sea floor in that there is a steep change in depth as they reach toward the surface, and they can thus be identified by the high standard deviation of depth estimates in their area of occurrence, compared to nearby areas of sea floor. About 30,314 'steep structures' (likely seamounts) were identified using this method and a threshold of a 300 m standard deviation in depth.

The other technique started from the tip of every identified steep structure identified by the first, but then scanned depths around each, along eight radii of 90 km each, at 45° intervals, and recording the lowest and

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<sup>1</sup> This contribution was originally submitted to a high impact journal, but rejected due to one of three reviewers suggesting that it suffered from a "crucial flaw", although we thought that it didn't (see the Appendix for details). The paper was not re-submitted, nor submitted elsewhere, and the co-authors lost interest. It is now included here, in shortened form, under the name of its original first author, who still thinks that it presented a good idea, as also stated in the other two reviews originally received.

highest depths over a distance of 90 km (10 pixels near the Equator, more at high latitude). A steep structure was considered a seamount if three conditions were met: (i) Each and all of the eight radii include depths differing by at least 300 m; (ii) If two radii include depths between 300 and 1000 m, the shallowest point is closer to the peak than to the deepest point, and the two radii form an angle of less than 135°; and (iii) At least five of the eight radii around a peak include depths with a difference of at least 1000 m, and the shallowest point is closer to the peak than to the deepest point. Jointly, these three conditions eliminated the ridges formed by lines of adjacent seamounts, and the 15,962 seamounts thus identified can be considered well isolated from each other. Of these, 14,287 overlapped with the 'steep structures' identified by the first approach, i.e., could be considered to be well defined, despite the low resolution of the bathymetric map used.

The bathymetric data were available with a 2 minute resolution, while primary production data were available with 6 minute resolution only. Merging these datasets led to 12,977 large, well-defined seamounts being available at the 6 minute resolution-level used for this study. Coordinates and depths of the seamounts identified, along with a global map showing their distribution, are available elsewhere (Kitchingman and Lai 2004; Kitchingman *et al.* 2007).

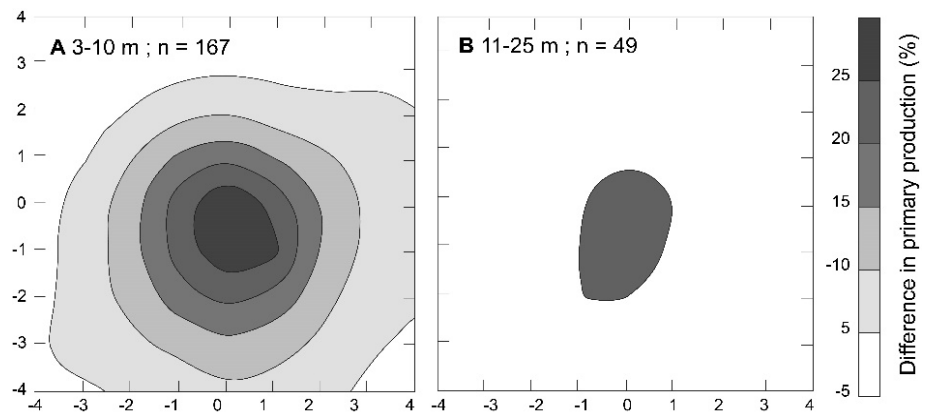
### Primary production

The primary production estimates used here were generated by the Inland and Marine Waters Unit, Institute for Environment and Sustainability, EU Joint Research Center, Ispra, Italy, and had a 6 minute resolution. They represented an annual average from November 1997 to December 1998, based on chlorophyll pigment concentration from SeaWiFS data and photosynthetically active radiation (see Appendix).

Seamounts for which no primary production value was available ( $n = 39$ ), owing to gaps in the satellite coverage, were not considered. Each pixel covers an area of 81 km<sup>2</sup> and 'seamount pixels' were defined as those whose center was closest to tip of a seamount. 'Control pixels' were sampled at random from a circular band of 50 km inner and 100 km outer diameter around each seamount pixel. Values were rejected (with replacement) if they fell into a gap in the primary production map.

## RESULTS AND DISCUSSION

Figure 1 shows that a consistent signal can be obtained by comparing the primary production estimated above known seamounts with that of control points selected at random from a radius of 50-100 km from each seamount. The two panels of Figure 1 thus illustrate the combined effects of depth and surface current velocity on primary production enhancement by seamounts. As might be seen, shallow seamounts exposed to currents of velocities above 5 m·s<sup>-1</sup> can locally increase primary production by more than 50%, with the effect fading within a radius of about 30-40 km around the tip of each seamount (Figure 1A). Conversely, shallow seamounts exposed to low current velocities generate less enrichment. Deep seamounts, whose tip reaches to less than 100 m, do not appear to enrich local productivity (Figure 1B).



**Figure 1.** Mean primary production enhancement over 10,226 seamounts (relative to control points at 50-100 km) as a function of depth to the surface of the seamount peak, by square panels with sides of about 118 km. A. Shallow seamounts. B. Intermediate depth seamounts. Seamounts peaking at depths of less than 100 m do not enhance pigment visible through satellite imagery (see Figure 2), and are therefore not considered here.

Figure 2 shows the relative difference in primary production between seamount pixel and their controls for 12,848 seamounts with distance from the sea surface ranging from 1 to 5,600 m. As might be seen, only shallow seamounts, reaching to about 100 m of the surface, generate surface pigmentation increases that are detected by the SeaWiFS satellite sensors. It cannot be excluded that deep primary production is enhanced by deeper seamounts, but this would imply a form of primary production not considered in the algorithm commonly used

to turn observed surface pigment concentrations into estimates of primary production<sup>2</sup>. The approach used here can be also be straightforwardly extended to atolls and islands small enough to function as net nutrient importer (Polis and Hurd 1996), i.e., those whose surrounding waters are enriched solely by the island mass effect. The results presented here also suggest, if indirectly, that the high biomasses of fish and other organisms reported from various seamounts rely largely on drifting zooplankton and marine snow (Koslow 1997), rather than on local primary production. This emphasizes the need to protect from destructive fishing methods the deep coral and other sessile organisms which, jointly with seamount fishes such as orange roughy (*Hoplostethus atlanticus*), capture the drifting organisms that fuel seamount ecosystems, and also provide the shelter required by juvenile seamount fishes.

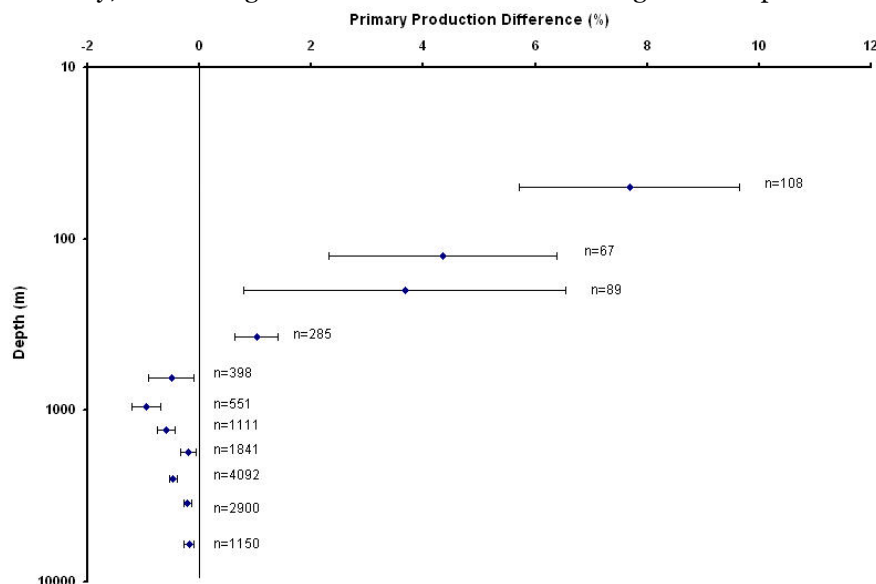
## ACKNOWLEDGEMENTS

This is a contribution of the *Sea Around Us*, mainly funded by the Pew Charitable Trusts at the time the work was undertaken. The work was based on a global map of (large) seamount developed by Adrian Kitchingman and

Sherman Lai of the *Sea Around Us*. The original submission also included, as co-authors, Reg Watson, Telmo Morato, and Villy Christensen, who had discussed the results with the (first) author, and Nicolas Hoepffner, EU JRC, who had supplied the SeaWiFS production estimates.

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**Figure 2.** Primary production difference (means  $\pm$  1 s.e.) above seamounts of various depths as evaluated by reference to control points at distances of 50-100 km. Overall, 12,848 large (>1000 m) conical oceanic seamounts for which primary production pixels were available are included here.

<sup>2</sup> The “crucial flaw” alleged by one of the 3 reviewers of the original version of this contribution thought that the primary production estimates over shallow seamounts were inflated due to the ‘shadows’ of (i.e., the reflection from) the seamounts themselves. Such ‘shadow’, however, would not generate the pattern documented in Figure 1. Moreover, the text stated that the algorithm used for inferring primary production for sea surface colors took care of reflection from the seafloor, and hence also from shallow seamounts. However, you can’t really argue with anonymous reviewers, even when they are clearly wrong.

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## APPENDIX

Remarks from Nicolas Hoepfner, Joint Research Center, Ispra, Italy, from an email sent to the author on April 22, 2005.

The situation with respect to shallow waters is as follows:

Within the NASA processing chain for SeaWiFS (i.e., SeaDAS), a routine can be activated to flag out waters shallower than 30 m (with reference to bathymetry database ETOPO 2). However, the standard level 3 chlorophyll products from NASA that we used to derive primary production maps do not include this flag because, in many cases, the first optical depth sensed by the satellite is still significantly shallower than the bottom depth (in other words, the bottom reflectance would have little effect on the surface chlorophyll). Exceptions occur in areas combining shallow and clear waters, e.g., around The Bahamas where the 'surface chlorophyll values' from NASA are indeed the reflection from the bottom. In that particular case, the chlorophyll data and, thus, the [primary production] data are likely to be not reliable.

In other cases, where chlorophyll can be assumed to be reasonable, the effect of shallow waters (seamounts or coastal waters) on the depth-integrated primary production should be studied on a case by case basis, because it depends on the biogeographical province that includes the seamount area and the dataset used for that province. Basically, the model estimates integrated primary production from surface down to the 0.1% light level. Let's now suppose that a seamount is included in a larger province where the representative chlorophyll profile has been established with a rather low chlorophyll values in the upper layer (indexed from satellite) and a deep chlorophyll maximum at 80 m. If the seamount is at 30 m and the satellite-derived surface chlorophyll signature over the seamount does not differ very much from that surrounding the seamount, the primary production estimate will use a similar chlorophyll profile but the integration will stop at 30 m. The resulting effect would be a tendency to obtain lower integrated production over the seamount when compared to primary production in the surrounding waters.

But again the magnitude of this artificial effect should really be studied case-by-case because, even with subsurface or deep chlorophyll maximum, the model is giving most of the primary production in the upper layer (e.g. 100% to 10% light level). This is confirmed by field measurements. Therefore, the bias on integrated primary production should not be too bad.

## THE POPULATION DENSITY OF MONSTERS IN OKANAGAN LAKE, BRITISH COLUMBIA<sup>1</sup>

Aran Kay<sup>1</sup> and Daniel Pauly<sup>2</sup>

<sup>1</sup> Department of Zoology, University of British Columbia, Vancouver, Canada

<sup>2</sup> Sea Around Us, Institute for the Ocean and Fisheries, University of British Columbia, Vancouver, Canada  
[d.pauly@oceans.ubc.ca](mailto:d.pauly@oceans.ubc.ca)

### ABSTRACT

A quantitative food web of Okanagan Lake, British Columbia, Canada, is presented which shows that the lake could support a small population of large reptilian monsters, lending credence to recurring sightings of a creature called 'Ogopogo.' Using arguments drawn from population genetics, we suggest two alternative population structures for Ogopogo, and a number of phenotypic attributes, notably dimorphism and a pale coloration, which explain certain aspects of the sightings reported so far. Whatever their actual population structure, Ogopogo appear endangered by the present fisheries in Lake Okanagan, which should be immediately closed.

### INTRODUCTION

It is well known that there are monsters in Okanagan Lake. Between 1874 and 1991, over 300 very credible people reported a total of 174 sightings (Mangiacopra 1992). The actual number of sightings is probably higher than this, as some may have kept silent for fear of ridicule. Most recent sightings occurred near the bridge between Kelowna and Westbank (Mangiacopra 1992), which runs over an underwater ridge that separates the lake into two basins (Ashley *et al.* 1999), forcing any large animal crossing from one basin to the other to come closer to the surface, and thus becoming visible.

As for monsters in many other areas (see Sheldon and Kerr 1972), the sightings elicit similar descriptions from viewers: the animal is 15-25 feet long (5 to 8 m) and is 2-5 feet in diameter (about 1/2 to 2 m) with a head sporting features reminiscent of horses, goats and snakes (Gaal 1986; [www.strangemag.com/ogopogo.html](http://www.strangemag.com/ogopogo.html)).

Some critics have suggested that the sporadic nature of Ogopogo sightings and the absence of hard evidence (carcasses, feces, bones, etc.) imply that there are no monsters in Okanagan Lake. But absence of evidence is not evidence of absence. Indeed, as Sheldon and Kerr (1972) have stated in dealing with similar criticisms regarding the existence of the Loch Ness monster, "this is both irresponsible and illogical." This is especially true as Okanagan Lake is quite large (113 km in length and 5.2 km across at its widest point; Clemens *et al.* 1939; Ashley *et al.* 1999), and deep (maximum depth 242 m), thus offering many hiding places.

To advance the overdue scientific and public debate on Ogopogo, this contribution examines the food web of Okanagan Lake in terms of its ability to supply the food resources required by a small population of monsters.

We used for this the widely used Ecopath modeling approach and software (Christensen and Pauly 1992; Pauly and Christensen 1996; Pauly *et al.* 2000; see [www.ecopath.org](http://www.ecopath.org)). Herein, the biotic resources within an ecosystem (here: Okanagan Lake) are represented as single species or as groups of functionally similar species, interlinked through their energy requirements. The key feature of the Ecopath approach is that it assumes mass-balance, i.e., the biomass flows out of groups within the system (through predation, feces, or respiration) must equal the flows into these same groups (i.e., their consumption).

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<sup>1</sup> Originally submitted (in 2001) to a journal called *Cryptozoology*, where it was kind of accepted just before the journal foundered, possibly because the *Crypto*- part overwhelmed the *-zoology* part.



The food web presented here represents Okanagan Lake during the year 2000. The carrying capacity of the lake has fallen dramatically since 1970, leading to the decline of its kokanee salmon population to 10% of 1970 abundance levels (Ashley *et al.* 1998). As this would have affected the Ogopogo population, it can be assumed that the lake could have supported their population in previous years if it can be shown that the lake now still has the resources necessary to support an Ogopogo population.

A total of 17 functional groups were included in the food web: Ogopogo; young kokanee (age 0+); adult kokanee (age 1-3); four groups of 'other fish' (juveniles and adults, inshore and deep water), two groups of *Mysis relicta* (juvenile and adults); midge larvae, other insect larvae, copepods, cladocerans, *Daphnia* spp., rotifers, phytoplankton, and detritus. The basic input parameters for all groups are given in Table 1, while their diet composition is given in Table 2. For all groups except Ogopogo, these values in these tables were adapted (in that order) from studies of Lake Okanagan, other lakes in British Columbia, or other aquatic systems (details in Kay 2002).

**Table 1.** Basic inputs for constructing of food web model of Okanagan lake.

Group	P/B (year <sup>-1</sup> )	Q/B (year <sup>-1</sup> )	P/Q
Ogopogo	0.080 <sup>a</sup>	1.110 <sup>g</sup>	-
Adult other Fish (deep water)	-	1.990 <sup>d</sup>	0.182 <sup>f</sup>
Juvenile other Fish (deep water)	-	4.570	0.300
Kokanee (age 1-3)	0.710 <sup>b</sup>	3.700 <sup>d</sup>	-
Kokanee (age 0+)	-	8.500 <sup>h</sup>	0.300 <sup>j</sup>
<i>Mysis relicta</i> (adult)	2.659 <sup>c</sup>	18.250 <sup>i</sup>	-
<i>Mysis relicta</i> (juvenile)	-	25.000	0.221 <sup>k</sup>
Adult other Fish (near shore)	0.646 <sup>d</sup>	3.304 <sup>d</sup>	
Juvenile other Fish (near shore)	-	7.590	0.300
Midge larvae	-	30.000	0.143
Aquatic insect larvae	-	30.000	0.143
Copepods	18.250 <sup>e</sup>	-	0.143
Cladocerans	47.500 <sup>e</sup>	-	0.143
Daphnia	47.500 <sup>e</sup>	-	0.143 <sup>f</sup>
Rotifers	50.000	-	0.099 <sup>f</sup>
Phytoplankton	150.000 <sup>f</sup>	-	-

a) Webb *et al.*, 1987; b) Sandercock (1969); c) Stockwell and Johannsson (1997); d) Froese and Pauly (2000); e) Langeland (1982); f) Thompson (1999), including EE estimate of 0.757 for rotifers; g) Auffenberg (1981); h) Foerster (1968); i) Langeland *et al.*, (1991); j) Johnston *et al.* (1988); k) Chess and Stanford (1999).

The parameters for Ogopogo were adapted from consumption/biomass ratio for Komodo dragon, *Varanus komodoensis* (Auffenberg 1981), and production/biomass ratio for large Australian sea-going crocodiles, *Crocodylus porosus* (Webb *et al.* 1987), scaled down to an average temperature of 10 degrees Celsius, and up to an mean body weight of 1,000 kg.

Sheldon and Kerr (1972) evaluated the requirements for a monster population to persist over time, and suggested a population consisting of no fewer than 10 animals, each with a minimum adult weight of 100 kg. The food web we constructed shows that Okanagan Lake could support a population of Ogopogo with a total biomass not exceeding 50 t, i.e., about 5 t per animal given a population of 10 animals. This is very close to the mean weight of 5160 kg that can be estimated from the average body length and diameter reported for Ogopogo by Mangiacopra (1992). Thus, we find an amazing match between the mean body weight predicted from the food web analysis and the estimate based on actual sightings.

However, a more recent underwater sighting of Ogopogo suggests another possibility. On August 24<sup>th</sup>, 2000, Mr. Darryl Ellis was swimming in Okanagan Lake when he noticed two Ogopogo swimming directly underneath him ([www.sunnyokanagan.com/ogopogo](http://www.sunnyokanagan.com/ogopogo)). He described one of the animals to be 20 feet long, with a long slender body, as reported by earlier observers, while the other, described as "fat" and of a "boxy shape," was thought to be only 100-200 kg. An obvious interpretation is that the smaller animal was a pup.

An alternative, and we believe, more likely, explanation is that most Ogopogo are relatively small, and hence usually overlooked. Large Ogopogo, then would be exceptional (i.e., rare), but over-represented in sightings, due to their size.

Small, isolated populations, whose members are forced to interbreed, are susceptible to a number of hereditary diseases. One such disease, Homocystinuria, is an autosomal recessive condition that results in abnormally tall and slender offspring (Brenton *et al.* 1972; Boers 1986; Gilbert 1996), an effect called 'gigantism.' Two giant

Ogopogo (of 5 t each) would allow the lake's food web to also sustain approximately 200 smaller (200 kg) Ogopogo.

Another effect of Homocystinuria is short-sightedness, perhaps the reason why large Ogopogo are only sporadically seen lifting their head above the water surface. Being short-sighted, they have no reason to lift their heads more than required for surface respiration. While many hereditary diseases result in some form of arrested mental development, Homocystinuria sufferers have normal mental capabilities (Gilbert 1996), and hence we can expect large Ogopogo to remain circumspect, as other wildlife do.

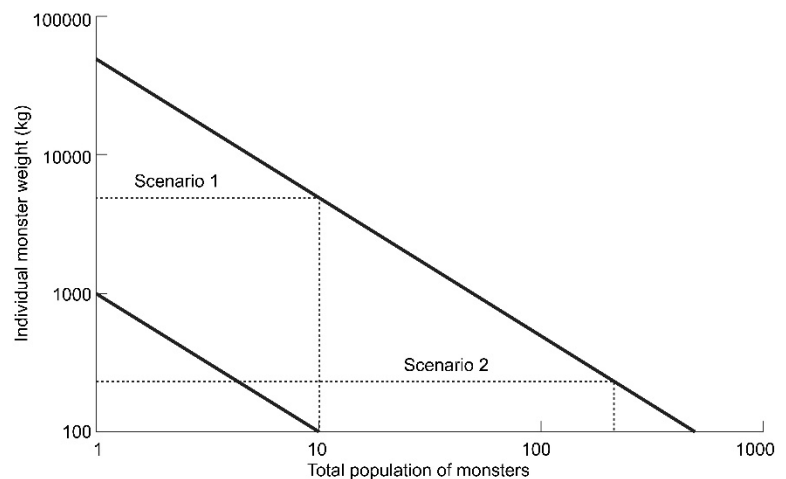
**Table 2.** Diet composition for food web model of Okanagan Lake in the year 2000 (all entries in ‰; based on sources documented in Kay (2002); d.w. = deep water; n.s. = near shore.

Predator\Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Ogopogo														
2 Ad. other fish (d. w.)	0.014													
3 Juv. other fish (d. w.)	0.001													
4 Kokanee (1-3)	0.685	0.422												
5 Kokanee (0+)	0.050	0.168						0.009						
6 <i>M. relict</i> a (adult)	0.250													
7 <i>M. relict</i> a (juv)														
8 Adult other fish (n.s.)		0.035												
9 Juv. other fish (n. s.)								0.025						
10 Midge larvae			0.460					0.323	0.387					
11 Aquatic insect larvae			0.357					0.290	0.357	0.200				
12 Copepods		0.020	0.005	0.125	0.211	0.100	0.071	0.108	0.075		0.050	0.050		
13 Cladocerans		0.057	0.011	0.031	0.026	0.025	0.018	0.168	0.100			0.025	0.025	
14 <i>Daphnia</i>		0.228	0.041	0.844	0.763	0.555	0.034					0.050	0.025	
15 Rotifers						0.095	0.068					0.050	0.025	
Phytoplankton		0.070	0.126				0.286	0.077	0.081	0.500	0.150	0.825	0.925	1.000
Detritus						0.225	0.254			0.300	0.800			

The greatest worry for Homocystinuria sufferers is their propensity for thromboses. However, diets that are high in vitamin B6 appear to limit this aspect of the disease (Gilbert 1996). Fish are known to contain high levels of vitamin B6 compared to other meats and salmon, in particular, contain very high levels of this vitamin (Ensminger *et al.* 1983; Leveille *et al.* 1983); hence Ogopogo would be protected, as they consume fish (Table 2).

Another condition frequent in small vertebrate populations is albinism, i.e., complete or extensive lack of pigmentation. The latter has been reported from the large sea-going crocodiles, *Crocodylus porosus* (Kar and Bustard 1982). A similar condition also affects the Great Spirit or Kermode Bear, inhabiting the coastal rainforests of British Columbia, which have pigment only in their iris and on their nose. Partial albinism, occurring both in reptilians related to Ogopogo, and in British Columbian predators, provides another explanation why Ogopogos are not seen as frequently as their number warrant: it is likely that they surface in the morning, when a fog covers both Okanagan Lake, and the white bodies of the monsters.

Figure 1 shows the two population scenarios described earlier. Scenario 1 is a lake that



**Figure 1:** Probable number of monsters in Okanagan Lake, British Columbia. Upper solid black line: maximum sustainable standing stock; lower solid black line: minimum viable population.



contains 10 large Ogopogos, each weighing approximately 5 t. Scenario 2 is a lake with about 200 smaller, 200 kg Ogopogo, with one or two larger Ogopogo (5 t each) appearing as genetic oddities. The upper and lower lines in Figure 1 thus represent the maximum possible population, as calculated from the food web analysis and the constraints of Sheldon and Kerr (1972) for Loch Ness monsters. Scenario 1 allows all Ogopogo to match the mean weight estimated from the sightings in Mangiacopra (1992). The problem is that 10 large Ogopogo would lead to more sightings than are recorded. Also, this scenario does not account for the recent sighting of a small Ogopogo, unless one assumes it was a pup. Scenario 2 offers the possibility of a few large Ogopogo that do not surface often and smaller Ogopogo that remain less conspicuous. Even if the smaller Ogopogo are sighted, they are more likely to be misidentified as logs or other objects, and remain unreported.

We cannot tell which of the two scenarios is most likely, given present knowledge on their population dynamics. The important point is that one can make a scientific case that Okanagan Lake can support the Ogopogo living therein. Therefore, measures to ensure their protection must be taken immediately. While the shooting of Ogopogo is currently considered illegal under section 26 of the Fisheries Act (Gaal 1986), it would not be illegal to cause the death of Ogopogo through other means. Effective immediately, Ogopogo should be listed under the Endangered Species Act, and all fishing on Okanagan Lake should be stopped. It is realized that the fishery for kokanee salmon is already closed, but this should be expanded to halt the budding *Mysis relicta* fishery and all other fisheries as well. In the absence of such strict measures, depletion of the remaining food sources for Ogopogo could cause a food web collapse that would lead to their extinction.

We hope that this contribution, will lead not only to the protection of Ogopogo, but also to the protection of monsters in other North American lakes. However, we are well aware that the sterile debates about their very existence will continue, and, in many cases, even preclude the implementation of effective measures for their protection.

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