INTRODUCTION

In fishes, both external (e.g., shape, size and position of mouth, shape of caudal fin) and internal morphology (e.g., stomach shape and size, gut length: GL) provide important information on a species’ feeding ecology (e.g., Keast and Webb 1966, Schmitt and Holbrook 1984, Kaiser and Hughes 1993, Juanes 1994, Juanes and Conover 1994, Hart 1997, Wootton 1998). Exploration of the relations between various feeding-related morphological characteristics with body length** is of increasing scientific interest. In the present study, information on intestine (gut) morphometrics that appear in the relevant literature has been compiled, analysed, and discussed.

Materials and Methods. Search of gut-related bibliography was conducted, using online literature databases on fish feeding and ecomorphology. The resulted data was tabulated. Relationships between mean, minimum, and maximum relative gut length (RGL) and intestine length weight index (ILW, Zihler’s index), as provided by the original author, with species’ fractional trophic levels (TROPHs; extracted from FishBase) were explored. Finally, using the relations between gut length (GL) and body length (L) provided by the original authors, regressions were reconstructed and compared based on species’ feeding habits and taxonomy.

Results. The amount of information related to gut morphometrics referred to 498 species. The relations between GL and L referred to 71 species, but four species were omitted from the analyses. Mean, minimum, and maximum RLG and ILW values were negatively related (for all cases: \( P < 0.01 \)) with TROPH. The GL–L regressions performed for 67 species revealed the presence of two major groups as herbivorous fishes and carnivorous fishes. Grouping according to species’ taxonomic order did not form any significant groupings.

Conclusion. Existing information on intestine morphometrics is generally accumulated in a few scientific papers. All the analyses performed on the compiled data reinforced the pattern generally accepted that herbivores have longer intestines than carnivores. In addition, the influence of species’ evolutionary history on comparisons of gut length between species with different feeding habits was not verified. Finally, equations relating RGL and ILW to TROPH can be used for TROPH value estimates from morphological data that are easy to obtain, especially in the lack of species’ feeding habits data.

Keywords: fish gut, relative gut, intestinal indices, bibliographic references
MATERIALS AND METHODS

An extended bibliographic search was conducted, in order to extract information related to gut of fishes. This search was based on online literature databases (e.g., Google Scholar, Scopus, Web of Science), covering a wide range of feeding-related papers (peer-reviewed and “grey” literature articles). The search was done using keywords, such as “gut”, “intestine”, “length”, “morphology”, “relative gut length”, “Zihler’s index”, in various combinations, excluding all papers in relation to “nutrition and aquaculture”, using analogous keywords. This was done consecutively several times, until no new results were found.

All available information provided in the original studies was tabulated by species, study area and year, and the following information was compiled: (a) length type and range of specimens studied, and number of individuals; (b) mean GL, relative GL (RGL), gut mass and relative gut mass, Zihler’s index (ILW; Zihler 1982) and mean intestinal valve content; and (c) equations relating GL to either body length (L) and/or weight (W). Valid species name and taxonomy, fractional trophic level values (TROPHs) and habitat type (i.e., marine or freshwater species) were extracted from FishBase (Froese and Pauly 2008).

Mean RGL and ILW values (RGLm and ILWm, respectively), as provided by the original author, were checked for normality (both were not normally distributed, since the values of skewness and kurtosis were outside the –2 to +2 range; Zar 1999) and grouped using the functional trophic groups, identified for the Mediterranean based on 332 stocks of 146 species by Stergiou and Karpouzi (2002). Those are: (a) pure herbivores (2.0 < TROPH < 2.1); (b) omnivores with preference for plants (2.1 < TROPH < 2.9); (c) omnivores with preference for animals (2.9 < TROPH < 3.7); (d) carnivores with preference for decapods/fish (3.7 < TROPH < 4.0); and (e) carnivores with preference for fish/cephalopods (4.0 < TROPH < 4.5). The median RGLm and ILWm values of the functional groups were compared using the Kruskal–Wallis test (Zar 1999). Mean, minimum and maximum RGL and ILW, originally reported in the bibliography, were related to TROPH values.

Finally, based on the GL–body length (L) relations, as given by the original authors, the regression lines were reconstructed. All regressions were plotted together and patterns of GL changes with L, according to species’ feeding habits and taxonomy at the order level (only when n > 5 families per order), were explored.

RESULTS

Overall, 766 data sets were collected from the literature, having information on fish gut (Table 1; Table A, electronic supplement, available at http://www.fishbase.org/Download/index.htm), which corresponded to 498 fish species belonging to 129 families and 29 orders. The most species rich family was Cichlidae (73 species; 14.7%), followed by Cyprinidae (34 species; 6.8%) and Gobiidae (25 species; 5%), with the majority of the species (238 species; 47.8%) belonging to the order Perciformes. Out of 498 species presented here, main habitat of 220 were freshwater, 233 marine and 37 both marine and freshwater (Table A).

Table 1

| Information                                                                 | General | GL    | RGL   | GM    | RGM   | ILW   | mGVC |
|----------------------------------------------------------------------------|---------|-------|-------|-------|-------|-------|------|
| Number of cases                                                            | 766     | 287   | 454   | 1     | 13    | 170   | 3    |
| Number of species                                                          | 498     | 118   | 293   | 1     | 5     | 123   | 3    |
| Number of GL–L relations                                                   | 79      | 9     | 10    | 23    | 37    | 56    | 23   |
| Linear (Y = a + bX)                                                        |         |       |       |       |       |       |      |
| Exponential (Y = ae^bX)                                                    |         |       |       |       |       |       |      |
| Power (Y = aX^b)                                                           |         |       |       |       |       |       |      |
| Power (logY = a + b logX)                                                  |         |       |       |       |       |       |      |
| Freshwater species                                                         |         |       |       |       |       |       |      |
| Marine species                                                             |         |       |       |       |       |       |      |
| Number of GL–weight relations                                              | 22      | 21    | 21    | 1     | 1     | 1     |      |
| Power (logY = a + b logX)                                                  |         |       |       |       |       |       |      |
| Logarithmic (Y = a + b lnX)                                                |         |       |       |       |       |       |      |
| Freshwater species                                                         |         |       |       |       |       |       |      |
| Marine species                                                             |         |       |       |       |       |       |      |
| Total number of sources                                                    | 59      | 17    | 38    | 1     | 2     | 7     | 1    |
| Peer-reviewed papers                                                       | 57      | 15    | 37    | 1     | 2     | 7     | 1    |
| Symposium proceedings                                                      | 1       | 1     | 1     | –     | –     | –     | –    |
| PhD theses                                                                 | 1       | 1     | –     | –     | –     | –     | –    |

GL = gut length; L = body length; RGL = relative GL; GM = gut mass; RGM = relative GM; ILW = Zihler’s index (Zihler 1982); mGVC = mean intestinal valve content.
The majority of the datasets referred to the Rio Charges system, Panama (120 datasets; Kramer and Bryant 1995a, b) and to a lesser extent to North Sea (83 datasets), the Mediterranean (58 datasets) and Red Sea (Ghardaqa; 56 datasets; Al-Hussaini 1947) (Table A). Sample size was reported in 642 data sets and ranged from 1 (58 cases) to 1461 (in the case of Heterotis niloticus), and for most data sets it was restricted to a small number of individuals (in 534 (83.2%) cases: n < 50).

Information on length structure of the specimens studied was provided in 512 datasets (66.8%), whereas the length range was provided in 364 datasets (Table A).

The type of length used in the majority of cases (448) was standard length, followed by total (178 cases) and fork length (66 cases) (Table A). The maximum reported body size of the 498 species ranged from 1.2 cm, for Acanthopagrus berda and Ancistrus spinosus, to 73.0 cm, for Chirocentrus dorab.

RGL values were reported in 454 cases (range = 0.21–28.71; mean ± SE = 2.05 ± 0.12; median = 1.22), and ILW values in 170 cases (range = 0.505–94.41; mean ± SE = 5.96 ± 0.65; median = 3.85) (Table A). For the mean values of both indices, there was an important overlap between the different functional trophic groups (Table 2, Fig. 1). Yet, Kruskal–Wallis test showed that the median RGLm and ILWm values differed significantly between groups (H: 70.01 and 18.71 respectively; P < 0.01 in both cases; Fig. 1). Finally, mean, minimum and maximum RLG were negatively related with TROPH (Fig. 2).

Significant regressions were also found between ILW and TROPH, but the R2 values (0.14 < R2 < 0.19, P < 0.01) were lower than those of the RGL–TROPH regressions.

Out of 498 species, GL–L relations were provided by the original author only for 79 cases (71 species, 48 freshwater and 23 marine species) (Table 1, Table A). All those equations were significant (P < 0.05). In 60 cases, the type of the relation was power (37 cases: log Y = a + b log X; 23 cases: Y = axb), in 10 cases exponential (Y = ae^bx) and in 9 cases linear (Y = a + bx) (Table 1, Table A). GL–W relations were provided only for 22 freshwater species. They were of the power type (log Y = a + b log X) in 21 cases and logarithmic (Y = a + b ln X) in only one case (Table 1, Table A).

Reconstruction of the GL–L relation was possible for 67 out of the 71 species. Since the equations for the remaining four species (all significant; P < 0.05) when solved have resulted to negative GL values, they were excluded from the analyses. When all those regressions were plotted together, there was a clear formation of two major groups based on the functional trophic groups (Fig. 3). The first one included all herbivores and omnivores with preference to plant material, along with two omnivores with preference to animal material (namely: Pomacanthus zoniceps, and Trichomycterus striatus (“Trichomycterus striatum”), and Ancistrus spinosus, for which no data on feeding habits is available. The second group included all the remaining omnivores with preference to animal material, and carnivores with preference to decapods, cephalopods and fish, as well as the remaining 20 species that were not classified into a functional trophic group (no TROPH value is provided in FishBase).

Finally, there was no group formation when the regressions were plotted all together and based on taxonomy at the order level (Fig. 4).

DISCUSSION

Bibliographic research revealed that the information related to the morphometrics of fish intestine is restricted to only a small number of species. Yet, this number could not be considered as low, taken into account that relations between length and weight, the most well studied parameters of the biology of fish (e.g., Anderson and Gutreuter 1983), are given for approximately over 2000 species (Binoohan and Pauly 2000). All the information presented here was either given in a few gut-related papers (such as those of e.g., Al-Hussaini 1947, Zähler 1982, Kramer and Bryant 1995a, b) and publications on fish morphology (e.g., Montgomery and Sanders 1985, Kassam et al. 2002) or usually provided as a by-product of research on feeding habits (e.g., Beumer 1978, Rosecchi 1983, Pölzer and Patzner 2000).

It is generally accepted that RGL < 1 indicates carnivorous diet, 1 < RGL < 3 indicates omnivory, whereas values of RGL > 3 indicate diet based on plant material or detritus (e.g., Ward-Campbell et al. 2005). Al-Hussaini (1947) identified four different trophic categories based on RGL for Red Sea fish species. Likewise, Kramer and Bryant (1995b) presented corresponding classifications, according to fish size (i.e., small, medium and large sized fishes). In the present study, the ranges of different RGLm and ILWm values per functional trophic group did not coincide with previously reported ones and there was no clear distinction of those ranges amongst the different trophic groups.

Cleveland and Montgomery (2003) suggested that values of these indices, for species of specific feeding habits, that fall outside a predefined range, should be attributed to “unusual biological phenomena” (e.g., a herbivore preying on diatoms, which are easier to digest and provide larger amounts of energy due to storage of lipids rather than starch; Cleveland and Montgomery 2003). Therefore, such indices can provide a rough estimate on a species’ feeding habits. However, they should be used with caution when comparisons among species with different or particular diets are being made (e.g., Cleveland and Montgomery 2003, German and Horn 2006).

When comparisons of such indices between species with different diets are attempted, evolutionary history (i.e., the influence of phylogeny) should be taken into consideration (e.g., Elliott and Bellwood 2003, German and Horn 2006). However this was not feasible in the present study.

The reconstructed regressions of the GL–L relations when plotted in the same graph (Fig. 3), revealed that, for the same body length, species that include plant material in their diet, either exclusively (pure herbivores) or in significant proportions (omnivores with preference to plant material) have larger GL than fishes that prey on other
animals (i.e., omnivores with preference to animal material, and carnivores). Only two species of the latter category were placed in the same group with plant-eating fish. For both of these species, TROPH values reported in FishBase are based on qualitative data and there are no quantitative descriptions on their feeding habits. The first one, *Pomacanthus zonipectus*, is a reef-associated species that preys mainly on algae, sponges and cnidarians (Pérez-España and Abitia-Cárdenas 1995, Froese and Pauly 2008: Ref. No. 28023). Despite this species feeds with food of low TROPH (i.e., algae: TROPH = 1 ± 0.00; sponges: TROPH = 2 ± 0.00; Pauly et al. 2000b), the fact that cnidarians are also consumed (TROPH = 2.50 ± 0.52; Pauly et al. 2000b) increases its TROPH. Hence, it is classified as an omnivore with preference to animal material (TROPH = 3.1 ± 0.32; Froese and Pauly 2008). Taken into consideration the fact that fishes that prey upon items difficult to digest (e.g., plant material, crustacean exoskeletons,

Fig. 1. Box-plots of mean relative gut length (RGL<sub>m</sub>) and Zihler’s index (ILW<sub>m</sub>; Zihler 1982) values provided by the original authors for the different functional trophic groups (FTGs) as identified by Stergiou and Karpouzi (2002); H = herbivores; OA = omnivores with preference to animal material; CD = carnivores with preference to decapods and fish; CC = carnivores with preference to fish and cephalopods; The central box indicates the range of values representing the 50% of cases around the median (vertical lines), the whiskers (horizontal lines) show the range of the values, and cross (+) indicates the mean value
Table 2

Range and mean values of mean relative gut length (RGL \textsubscript{m}) and Zihler’s index (ILW \textsubscript{m}; Zihler 1982) values, provided by the original authors, and their corresponding standard error (SE), per functional trophic group (FTG; Stergiou and Karpouzi 2002).

| FTG | RGL \textsubscript{m} | ILW \textsubscript{m} |
|-----|----------------|----------------|
|     | \(n\) | range | mean ± SE | \(n\) | range | mean ± SE |
| H   | 30   | 1.6–17.75 | 4.84 ± 0.60 | 5   | 4.49–53.6 | 20.31 ± 9.23 |
| OV  | 78   | 0.47–18.2 | 2.39 ± 0.28 | 42  | 1.7–66.22 | 8.13 ± 1.72  |
| OA  | 217  | 0.21–4.3  | 1.28 ± 0.06 | 26  | 1.5–12.7  | 3.75 ± 0.50  |
| CD  | 9    | 0.24–1.64 | 0.87 ± 0.14 | 1   | 5.3       |               |
| CC  | 13   | 0.6–1.6   | 0.98 ± 0.07 | 1   | 4.3       |               |

H = herbivores; OA = omnivores with preference to animal material; CD = carnivores with preference to decapods and fish; CC = carnivores with preference to fish and cephalopods; \(n\) = number of cases.

\[
\log\text{TROPH} = 0.485 – 0.1444 \log\text{RGL}
\]
\(n = 229, R^2 = 0.29\)
\(SE_b = 0.015, P < 0.01\)

\[
\log\text{TROPH} = 0.425 – 0.18\log\text{RGL}
\]
\(n = 28, R^2 = 0.52\)
\(SE_b = 0.034, P < 0.01\)

\[
\log\text{TROPH} = 0.486 – 0.184\log\text{RGL}
\]
\(n = 28, R^2 = 0.58\)
\(SE_b = 0.031, P < 0.01\)

Fig. 2. Relationship between fractional trophic level (TROPH) and relative gut length (RGL) mean values (a), minimum values (b) and maximum values (c), as provided by the original author. \(n\) = number of cases; \(R^2\) = coefficient of determination; \(SE_b\) = standard error of slope.
Fig. 3. Regressions between body length ($L$, in cm) and gut length ($GL$, in cm) for 67 fish species; Equations are given in Table A, electronic supplement (available at http://www.fishbase.org/Download/index.htm); Different line colours correspond to different functional trophic groups (by Stergiou and Karpouzi 2002); green: herbivores; turquoise: omnivores with preference to vegetable material (OV); blue: omnivores with preference to animal material (OA); pink: carnivores with preference to decapods and fish (CD); red: carnivores with preference to fish and cephalopods (CC); black: species that could not be classified to a functional trophic group because no trophic level values were reported in FishBase (www.fishbase.org; Froese and Pauly 2008); Ac = Aequidens coeruleopunctatus; Asp = Ancistrus spinosus; Ar = Anguilla rostrata; An = Anamia normani; As = Aphredoderus sayanus; Ap = Aplodactylus punctatus; Aa = Pennahia argentea (‘Argyrosomus argentatus’); Am = Conger myriaster (‘Astroconger myriaster’); Bn = Barbus neumayeri; Bc = Brachyraphis cascajalensis (‘Brachyraphis cascajalensis’); Bch = Brycon chagrensis; Bp = Brycon petrosus; Be = Bryconamericus emperor; Cf = Chaeotostoma fischeri; Cl = (‘Channa limbata’); Cp = Cryptoheros panamensis (‘Cichlasoma panamense’); Cc = Coelorinchus caelorhincus (‘Coelorhynchus coelorhynchus’); Eo = Erismyzo oblongus; Es = Erimyzon suetca; Ea = Esox americanus; Gc = Geophagus crassilabris; Ga = Gephyrocharax atricaudatus (‘Gephyrocharax atricaudatus’); Gd = Gobiomorus dormitor; Hn = Heterotis niloticus; Ho = Hexagrammos otakii; Hp = Holacanthus passer; Hm = Hoplias malabaricus; Hmi = Hoplias microlepis; Hpg = Hymenopterus italicus; Hng = Hypentelium nigricans; Hpn = Hyphessobrycon panamensis; Hpl = Hypostomus plecostomus; In = Ameiurus natalis (‘Ictalurus natalis’); La = Lepomis auritus; Lp = Lepomis punctatus; Lh = Lepomis herzensteini (‘Limanda herzensteini’); Ly = Pseudopleuronectes yokohamae (‘Limanda yokohamae’); Lt = Liparis tanakai; Mb = Macrourus berglax; Ms = Micropterus salmoides; Mc = Mugil cephalus; Na = Nezumia aequalis; Ns = Nezumia sclerorhynchus; Nm = Nibea mitsukurii; Ol = Osteochilus lini; Pe = Pagellus erythrinus; Pn = Percina nigrofasciata; Ps = Piaubacina panamensis; Pf = Pimelodella chagresi; Ps = Poecilia sphenops; Pz = Pomacanthus zonipectus; Pso = Poropuntius normani; Pr = Puntius rhombeus; Rp = Rastoria paviana (‘Rastoria paviei’); Rw = Rhamdia quelen (‘Rhamdia wagneri’); Rsp = Rhinogobius sp.; Ru = Rineloricaria uracantha; Rg = Roeboides guatemalenensis; Ss = Sarpa salpa; Sn = Schistura namboensis; Tt = Trachyrinchus scabrus (‘Trachyrhynchus trachyrhynchus’); Ts = Trichomycterus straiatus (‘Trichomycterus straiatum’); Vo = Malacocephalus occidentalis (‘Ventrifossa occidentalis’); and Xc = Xenentodon cancila

Fig. 4. Regressions between body length ($L$, in cm) and gut length ($GL$, in cm) for 53 fish species; Equations are given in Table A, electronic supplement; different colours correspond to classification, based on species’ order (by www.fishbase.org; Froese and Pauly 2008); black: Characiformes; blue: Cypriniformes; green: Gadiformes; red: Perciformes; and brown: Siluriformes (for species’ abbreviations, see Fig. 3)
sponge sclerites) tend to have longer intestines compared to their body length (e.g., Wootton 1998), it is not a surprise that this species groups with plant-eaters.

The second one, *Trichomycterus striatus* ("*Trichomycterus striaturn*"), is a freshwater benthopelagic omnivore (TROPH = 3.2 ± 0.40; Froese and Pauly 2008), that feeds on insects (Froese and Pauly 2008: Ref. No. 6868) and other benthic invertebrates (Kramer and Bryant 1995a, b). The fact that this species grouped along with the plant-feeders, could be attributed to its body form, which, in general, seems to define the general form and structure of gut (e.g., Montgomery 1977, Verigina 1991, Cleveland and Montgomery 2003, Karachle 2008). Its elongated body, therefore, might allow the species to have a gut longer than its body, assuming that it possesses folds and loops.

Finally, the results of the regressions of mean, minimum and maximum RGL and ILW with TROPH (Fig. 2), and the reconstructed GL–L relations (Fig. 3) reinforce the pattern that is believed to apply in all vertebrate classes, that is, herbivores tend to possess longer intestines than omnivores, and omnivores longer than carnivores.

Fish dissection is a prerequisite for the accumulation on raw data on fish intestine morphometrics, as well as stomach content analysis. Conversely, study of fish feeding habits can be performed without killing the specimens examined, using methods such as gastroscopy, stomach flushing, emetics (e.g., Kamler and Pope 2001). Yet, stomach content analysis for the estimation of a species’ TROPH is a rather time-consuming and difficult procedure, compared to measuring gut length. For example, uncoiling and measuring gut length could be done in less than a minute. Conversely, stomach content analysis requires stomach dissection, extraction of the content, identification and sorting of the different food items, and finally counting and/or weighing of each food item separately. It is obvious that stomach analysis procedures demand from a few minutes (e.g., when food items are few and only weighed) up to more than an hour (e.g., if counting is required in cases such as in zoo- or phytoplanktivorous species).

Therefore, the indices presented here (RGL and ILW), which are relatively easy to calculate, can be used for a rough estimation of TROPH (i.e., using equations such as those given in Fig. 2). This is of great importance, especially for less studied species lacking feeding data and TROPH values, or in cases where only a few museum specimens are available, or in fossil fishes. Such estimations can be very useful for ecosystem management, as in the case of the Marine Trophic Index (Pauly and Watson 2005), which demands species- and location-specific TROPH estimates that are not always available (e.g., Karachle and Stergiou 2008), and for developing ecosystem models (e.g., Ecopath with Ecosim; Pauly et al. 2000a).

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