Fish functional traits are affected by hydrodynamics at small spatial scale

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ABSTRACT

The Mediterranean damselfish *Chromis chromis* is a species with a broad distribution found both in the Mediterranean Sea and Eastern Atlantic as far south as the coast of Angola. We hypothesized that the species may have significant functional morphological plasticity to adapt along a gradient of environmental conditions. It is a non-migratory zooplanktivorous species and spends the daytime searching for food in the middle of the water column. Therefore, local hydrodynamics could be one of the environmental factors affecting traits of *C. chromis* with repercussions at the population level. We compared the body condition, individual growth and body shapes of damselfish collected under two different hydrodynamic conditions (low ~10 cm s^{-1} vs. high ~20 cm s^{-1}). Specimens showed higher body condition under high-hydrodynamics, where conditions offered greater amounts of food, which were able to support larger individuals. Individuals smaller than 60-mm were more abundant under low-hydrodynamics. Morphometric analysis revealed that high-hydrodynamics were favored by fish with a more fusiform body shape and body traits developed for propellant swimming.

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1. Introduction

Hydrodynamics affects many ecological aspects of aquatic habitats, such as seagrass landscapes (Robbins and Bell, 2000; Gaylord et al., 2002), larvae dispersal (Eckman, 1990; Crimaldi et al., 2002) and plankton distribution (George and Edwards, 1976). Hydrodynamics can make the availability of food unpredictably variable in abundance and patchily distributed challenging the ability of secondary consumers to get sufficient food to permit the overtime persistence of local populations (Frechette et al., 1989; Beaulieu, 2003; Sarà, 2006). However, high hydrodynamics can increase the prey encounter rate (Rothschild and Osborn, 1988; Gabel et al., 2008) and provide ephemeral patches of increased food availability although at some point, the conditions become too high-energy and make feeding functional traits such as food searching and manipulation more difficult. Thus, hydrodynamics can modify the fish activity costs due to swimming performance

requirements through the impairment of feeding behaviors (Stoll and Fisher, 2010). The search for food in particular is an important functional trait (Shoener, 1986; Sarà et al., 2014) whose effects have rebounds in terms of the energy budget of any fish. The amount of energy spent for searching is usually paid on food through a major quota of energy spent for food searching due to environmental changing conditions affecting *in ultimis* somatic maintenance and fish life history traits such as growth and reproduction (*sensu* Kooijman, 2010). To live under unpredictable changing environmental conditions, fish have to optimize the energetic ratio between income and costs; a phenotypic response to hydrodynamic variability may be a solution (Sfakiotakis et al., 1999; Lauder and Drucker, 2004) as when fish adapt their body shape to the hydrodynamics of sites in which they live (Cakic et al., 2002). Santos et al. (2011) found morphological divergences at the intra-specific level between individuals living in river channels and lagoons. Under quicker currents (i.e. river), individuals are more fusiform, reflecting a functional (behavioral and morphological) plasticity (Cunico and Agostinho, 2006; Pulcini et al., 2008; Borazjani and Sotiropoulos, 2010). Thus, it is reasonable to assume that broadly-distributed species living under changing environments can adapt some traits (i.e. have phenotypic plasticity;

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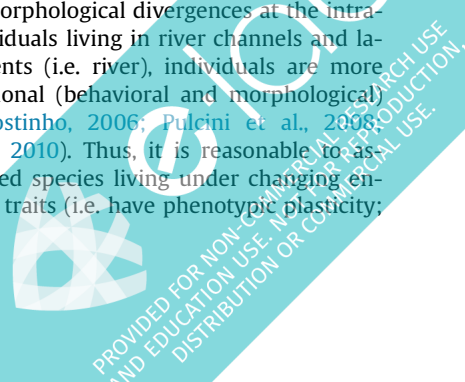
sensu Rosenweig and Lomolino, 1997; Lefebvre et al., 1997) by which they are able to live along a gradient of different environmental conditions (Losos et al., 2004). Here, we used a classical morphometric analysis (Cheverud et al., 1983) to test whether two different hydrodynamics conditions elicited different expressions in functional trait patterns in a zooplanktivorous model fish, *Chromis chromis*. (Actinopterygii: Perciformes: Pomacentridae; Fasola et al., 1997; Guidetti, 2000), at small spatial scale (few kms).

Damselfish is an useful model for this purpose as it is a strictly territorial non-migratory species (the home range is thought to be only few hundreds of meters from where they build their nests; Picciulin et al., 2004) that abundantly inhabits Mediterranean subtidal habitats from few meters to more than 35 m (Aguzzi et al., 2013). It reproduces in summer up early autumn in Southern Mediterranean, diurnally relies on zooplankton, spends most daytime for food searching at the middle column (Pinnegar et al., 2007; Braccali et al., 2012, 2014). As most zooplanktivorous fish, *C. chromis* has limited energetic reserves and need to feed continuously (Boddeke, 1963; Charnov et al., 1976) during both larval/juvenile (Macpherson and Raventos, 2005) and adult (Dulcic and Kraljevic, 1995) stages. Thus, local oceanographic conditions affecting food availability may emerge as primary factors indirectly influencing life history of this species (Macpherson and Raventos, 2005). Here, we hypothesized that hydrodynamics at small spatial scale (at the scale of km) plays a role of effector in determining both individual growth (via food encountering-energetic costs ratio) and body shape — by affecting swimming performance and water column position in our Mediterranean damselfish.

2. Materials and methods

2.1. Study area and a-priori oceanographic contextualization

The study was conducted in the Egadi Marine Protected Area, on the Island of Marettimo (Egadi Archipelago, western Sicily) in two areas with different hydrodynamic conditions located less than 5.0 km from one another (Fig. 1). Cammello Bay on the north coast

was a sheltered site exposed to the north-east and characterized by a gently sloping bottom and a maximum depth of 20 m. In contrast, Punta Basana was situated on the southern coast, where study site is exposed to the main current of the open sea Sicilian Strait, and characterized by a steeply sloped bottom and a maximum depth of 40 m. The hypothesis of different hydrodynamics was generated from the observation made at the beginning of 2007 that two sites had different water current velocities when a Valeport current meter was kept in situ in both sites for four days in three occasions (January, March and June 2007). This field dataset was later used to validate seasonal hydrodynamics patterns as downloaded from MyOcean daily database (http://marine.copernicus.eu). Field observed and satellite derived hydrodynamics data were highly confident and two sites resulted to have water current velocity on average 10.1 ± 4.9 cm s^{-1} and 17.2 ± 5.2 cm s^{-1}, respectively in Cammello Bay (hereafter LOW-HYDRO) and Punta Basana (hereafter HIGH-HYDRO) (Table 1). Contextually, to test the hypothesis that different hydrodynamics would have been able to generate different trophic conditions affecting functional and life history traits in damselfish, experimental trophic conditions were set by measuring some water column variables. Water samples were collected through a Niskin bottle at middle water column (~10 m) to measure suspended chlorophyll-a, total (TSM), inorganic (ISM) and organic matter (POM). Once brought back to the laboratory, water samples were filtered on Whatman GF-F 0.45 µm fiberglass filters and stored at −20 °C. POM was estimated by ignition loss and chlorophyll-a through the classical acetone extractive method, according to details reported in many companion studies (e.g. Sarà et al., 1999, 2003; 2011). Unfortunately, we did not collect zooplankton at the time of this study, and then the chosen water column variables indirectly described the amount of suspended food available for zooplanktivorous species as damselfish. Thus, we did some assumptions to support our experimental hypothesis, as follows (i) chlorophyll-*a* concentration, a proxy of the phytoplankton biomass, can be in turn used as a proxy of trophic substrates for zooplankton (e.g. ciliates; Stromberg et al., 2009) and (ii) some zooplankton species, such as cladocerans and copepods being the main feeding resource to *C. chromis*, have similar fatty acids
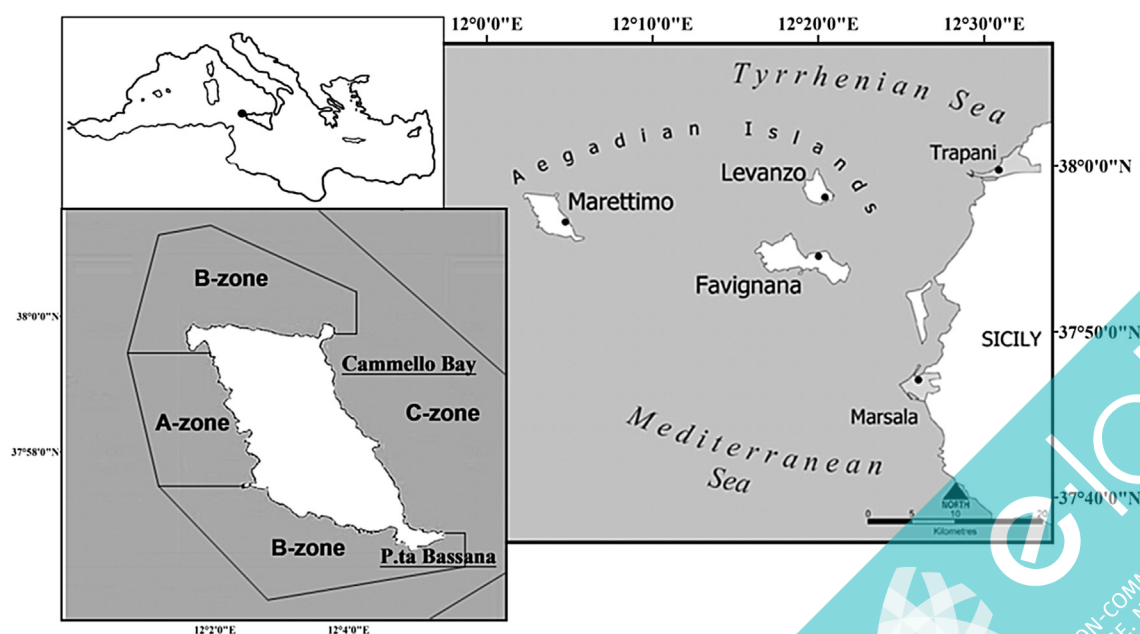

Fig. 1. Location of the Island of Marettimo. The map shows the position of the LOW-HYDRO site of Cammello Bay and the HIGH-HYDRO site of Punta Bassana.

Table 1
Features and range of values recorded from March to August in LOW-HYDRO site of sheltered and shallow Cammello Bay and deeper and opener HIGH-HYDRO site of Punta Bassana (CHL-a = chlorophyll-a, Pheo = pheopigment, TSM = total suspended matter, ISM = inorganic suspended matter, OSM = organic suspended matter).

Site characteristics	LOW HYDRO	HIGH HYDRO
LAT	37° 59′ 00″	37° 56′ 59″
LONG	12° 03′ 56″	12° 05′ 23″
Site description	http://www.parks.it/indice/iti_dettaglio.php?id_iti=2068	http://www.parks.it/indice/iti_dettaglio.php?id_iti=2061
Exposition	north-east	south-east
Depth (m)	20	40
Bottom slope	gradual	steep
Bottom cover	sand covered by *P. oceanica* mixed to rocky reef	sand covered by *P. oceanica* mixed to rocky reef
Temperature (°C)	13—25.5	12—24
CHL-a (µg l^{-1})	0.12—0.26	0.08—0.12
Phaeo (µg l^{-1})	0.05—0.23	0.02—0.10
TSM (mg l^{-1})	6.93—9.68	5.10—13.45
ISM (mg l^{-1})	5.37—7.22	3.43—10.20
OSM (mg l^{-1})	1.57—2.47	1.67—3.25
Hydrodynamics (source: http://marine.copernicus.eu)		
Winter	11.9 ± 4.4	15.2 ± 3.3
Spring	7.1 ± 2.5	19.9 ± 5.7
Summer	6.6 ± 3.6	20.6 ± 6.6
Autumn	14.9 ± 5.8	13.3 ± 2.2
Year	10.1 ± 4.9	17.2 ± 5.2

composition to phytoplankton on which they rely and show negative correlation with chlorophyll-*a* concentration due to their grazing (Calbet et al., 2001); (iii) higher current velocities should result in higher rates of food supply (amount per unit time − *sensu* Sarà and Mazzola, 2004). Thus, accordingly, damselfish of the HIGH-HYDRO sites should be exposed to higher amount of food per time unit than LOW-HYDRO co-specifics (Table 1) at only few kms one each other.

2.2. Fish sampling and processing

Damselfish were later collected, from March to July 2007. Four samplings (n = 4) were carried out at regular intervals, approximately every 40 days, at both the LOW- and HIGH-HYDRO sites. Specimens were collected with a 1 cm mesh seine net (50 × 6 m) deployed for three replicate hauls from a small fishing boat at the same depth (about 9—12 m) and at the same time (between 10h00 and 13h00 GT). For each seine haul, the total number (N) of *C. chromis* captured were recorded directly on-board. All individuals collected were frozen at −20 °C in the field and transported back to the University of Palermo Experimental Ecology laboratory for further examination. Once in laboratory, for each individual fish, standard length (SL) was measured with a Vernier caliper (nearest to 0.05 mm), and total wet weight (TW) with a Mettler Toledo balance (nearest to 0.1 g). The sagittal otolith was used to estimate the annual age (y) of a subsample (n = 207 and n = 164 in LOW- and HIGH-HYDRO, respectively) (Secor et al., 1995). Discrimination of light and dark bands (annuli) was made with a stereo microscope LEICA EZ 4D (12.5× magnification) with reflected light. The whole otolith was positioned in immersion oil on a dark surface to increase the contrast between annuli. Two authors independently counted in blind the annuli and agreement between readers determined the final age estimate. A subsample of individuals of a total of 120 individuals (n = 30 in March and n = 30 in July from the two studied sites; tot = 120 individuals analyzed) were chosen randomly to investigate if fish from two hydrodynamics were morphometrically different (Fig. 2). All individuals were pinned with the fins extended in the standard position and photographed with a compact digital camera CANON *Power shot* fixed on a tripod. The fish measuring board was equipped with a ruler as a reference scale and illuminated by a direct light. We measured the 16 morphometric traits (Dulcic, 2005 − Fig. 2) using

TpsDig 2 software (http://life.bio.sunysb.edu/morph/).

2.3. Data analyses

To test whether different hydrodynamics generated changes in functional trait's with potential repercussions on life history traits, we used some descriptors of growth performance that are classically adopted in fish biology as follows.

#### 2.3.1. Allometry and body condition

The length-weight relationship was described by the following allometric equation (Gould, 1966; Dulcic and Kraljevic, 1995): TW = a * SL^b which was linearized through base −10 logarithms). The parameter b in the linearized form was taken as an allometric coefficient which usually ranges around 3 in most organisms (*sensu* Gould, 1966). Differences in length-weight relationships were tested by comparing slopes of allometric regressions (ANCOVA; Zar, 1999; Sarà and Mazzola, 2004). The Body Condition Index (BCI; Nash et al., 2006; Bracciali et al., 2012) *per* each SL class (SLc; 5 mm each) was computed as follows: BCI = TW/SL^3. Differences in BCI were tested by ANOVAs (Zar, 1999) according to SL (7 levels; 5 mm steps) and hydrodynamics (2 levels: low *vs.* high). When the variance was not homogeneous tested through the Cochran's C test (i.e. p < 0.05), we did not transform it but we lowered the significant value level from α = 0.05 to 0.01 (Ruiz et al., 2010).

2.3.2. Body growth

Growth of *C. chromis* was expressed through a linear growth model of length at age (Green et al., 2004; Nyamweya et al., 2010): LS = a + b * Age, where the slope b was considered as the growth coefficient. Differences in growth rates between sites were tested by using the ANCOVA (Sarà and Mazzola, 2004).

2.3.3. Body shape

All morphometrics showed a strong correlation with the SL (Table 2) allowing us to eliminate the individual size effect (Agnese et al., 1997; Dulčić, 2005). SL of LOW- and HIGH-HYDRO specimens was compared with a T-test. The coefficient of variation (CV) of each morphometric was calculated. The relationship between the body height and the SL was analyzed to assess: i) seasonal differences between sampling periods within each site; and ii) differences between sites (LOW- *vs* HIGH-HYDRO) according to the individual
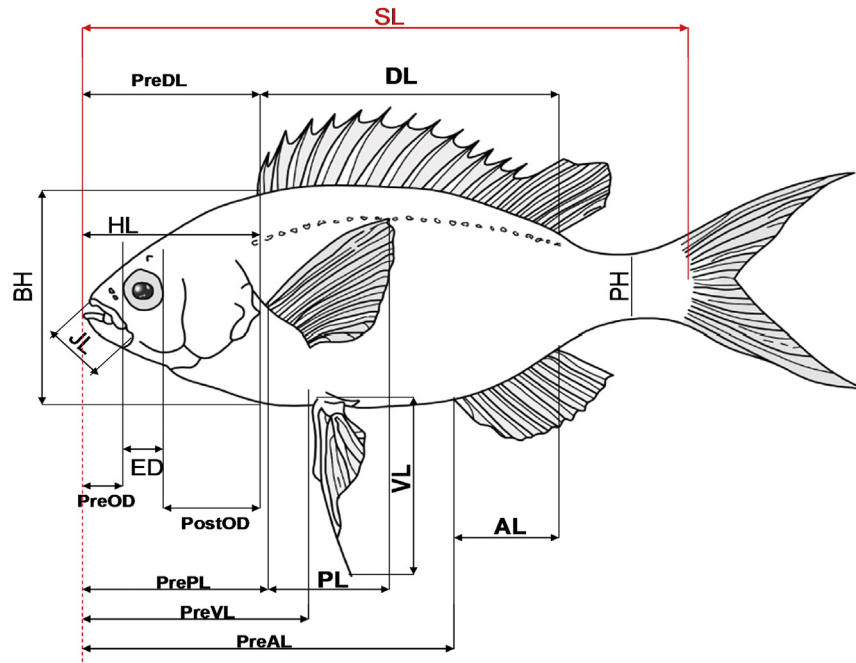
Biometrics: standard length (SL), head length (HL), jaw length (JL), eye diameter (ED), preocular distance (PreOD), postocular distance (PostOD), dorsal fin length (DL), predorsal length (PreDL), pectoral fin length (PL), prepectoral length (PrePL), ventral fin length (VL), preventral length (PreVL), anal fin length (AL), preanal length (PreAL), body height (BH), peduncle height (PH).

Fig. 2. Representation of morphometric measurements on *Chromis chromis* (Dulcic, 2005).

Table 2
Correlation values of each morphometric at standard length increase (SL).

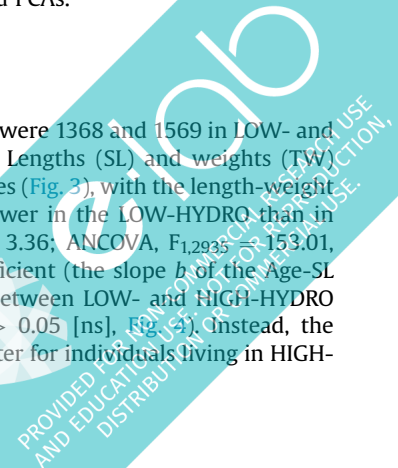| Morphometrics-SL relationship			
Morphometrics	R	N	P
Head length (HL)	0.92	120	<0.0001
Jaw length (JL)	0.61	120	<0.0001
Eye diameter (ED)	0.77	120	<0.0001
Preocular distance (PreOD)	0.50	120	<0.0001
Postocular distance (PostOD)	0.86	120	<0.0001
Dorsal fin length (DL)	0.96	120	<0.0001
Predorsal length (PreDL)	0.93	120	<0.0001
Pectoral fin length (PL)	0.89	120	<0.0001
Prepectoral length (PrePL)	0.93	120	<0.0001
Ventral fin length (VL)	0.72	120	<0.0001
Preventral length (PreVL)	0.93	120	<0.0001
Anal fin length (AL)	0.86	120	<0.0001
Preanal length (PreAL)	0.96	120	<0.0001
Body height (BH)	0.81	120	<0.0001
Peduncle height (PH)§	0.95	120	<0.0001

Table 3
Student-Newman-Keuls *post hoc* comparison test results of the BCI analysis. SLc = SL class; LOW = LOW-HYDRO site of Cammello Bay; HIGH = HIGH-HYDRO site of Punta Bassana.

SLc	Site	LOW	LOW	LOW	LOW	LOW	LOW	LOW
<50.00	HIGH	***						
50.00—54.95	HIGH		***					
55.00—59.95	HIGH			***				
60.00—64.95	HIGH				ns			
65.00—69.95	HIGH					**		
70.00—74.95	HIGH						***	
>75.00	HIGH							ns

size (small, <60.00 mm SL; medium, 60.00—64.95 mm SL; and large, ≥65.00 mm SL; see body condition results). In both cases, body height-SL relationships were compared using the ANCOVA. The relationships between each morphometric variable and the SL were also tested by using the ANCOVA where the slope b was considered as the allometric coefficient. When there were no significant differences between slopes, the intercept a was used as index of morphometric traits length at recruitment time at the school. Lastly, a Principal Component Analysis (PCA) was performed as an ordination tool of morphometrical traits (Flury, 1988) with respect to hydrodynamic conditions, after to have removed the size effect (Elliott et al., 1995). To test if hydrodynamics can have effect on morphometrics, a Permutational Multivariate Analysis of Variance (PERMANOVA) was used considering hydrodynamic condition as a fixed factor (HYDRO; 2 levels; high vs. low). The log-transformed matrix of sixteen morphometrical variables was used to estimate the Euclidean distances, all p-values were calculated using 9999 permutations of the residuals under a reduced model (Anderson, 2001). STATISTICA rel. 10.0 software (StatSoft Inc., USA) was used to perform ANOVAs and PCAs.

3. Results

The total damselfish captured were 1368 and 1569 in LOW- and HIGH-HYDRO sites, respectively. Lengths (SL) and weights (TW) were highly correlated at both sites (Fig. 3), with the length-weight regression slopes significantly lower in the LOW-HYDRO than in the HIGH-HYDRO sites (2.78 vs. 3.36; ANCOVA, $F_{1,2935} = 153.01$, $P < 0.05$ [***]). The growth coefficient (the slope b of the Age-SL relationship) was not different between LOW- and HIGH-HYDRO fish (ANCOVA, $F_{1,370} = 0.17$, $P > 0.05$ [ns], Fig. 4). Instead, the intercept a was significantly greater for individuals living in HIGH-
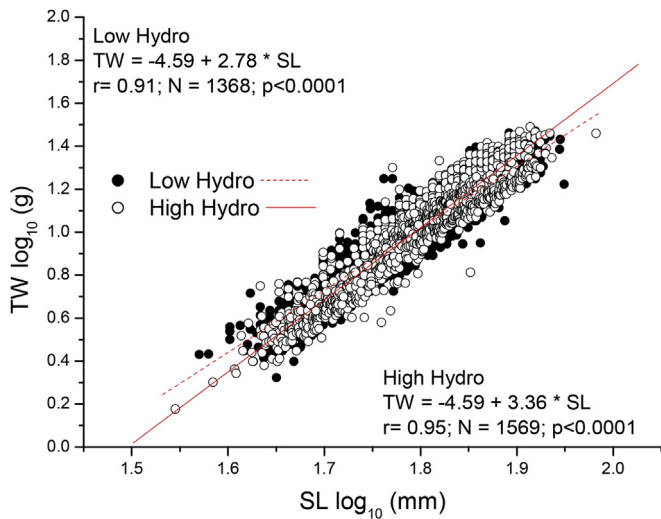
Fig. 3. Length-weight relationship in the linearized form TW $= a + b$ * SL for LOW- and HIGH-HYDRO populations.
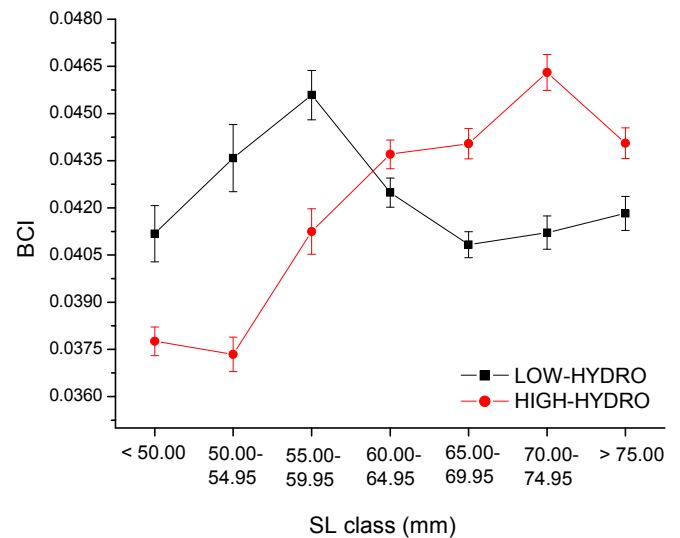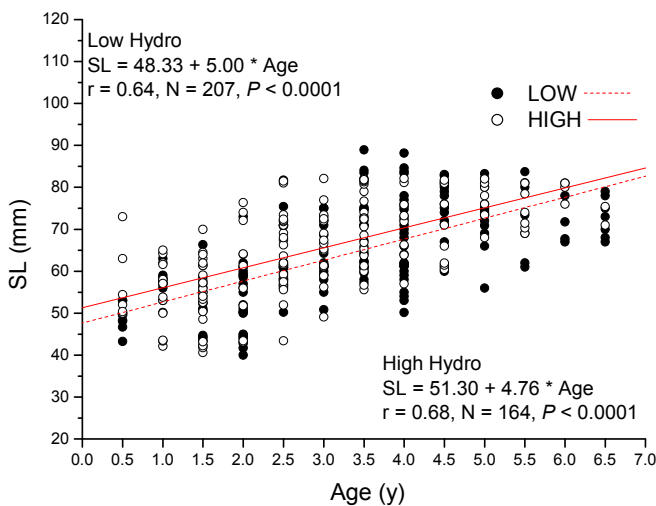

Fig. 4. Mean ($\pm$s.e) Body Condition Index (BCI) of *C. chromis* at different standard length (SL) class living in LOW- and HIGH-HYDRO site.

Fig. 5. Standard length (SL) at age (y) of *C. chromis* in low and high hydrodynamics.

Table 4). Body length (deriving from the sum of traits such as post-ocular distance, pre-dorsal fin length, and pre-anal fin length) was significantly greater in relation to the standard length in HIGH- than in LOW-HYDRO specimens (see Table 4). The two populations were morphometrically different as showed by the PERMANOVA performed on the whole biometrical matrix (p < 0.05). PCA showed that the first principal component (PC1 = 75%) represented most variables linked to the body size such as PH, HL, DL and BH; the PC2 (7%) was explained by the negative correlation of mouth size variables (JL and preOD) and by the positive correlation with eye's size (Fig. 6). Thus, from the visualization of our point-fish distributed on PC1−PC2 axis plan, we show that most low-hydro fish (Cammello) were significantly smaller but with larger eyes, and in contrast, high-hydro fish (Basana) were larger with large mouth and smaller eyes.

4. Discussions

Analysis of morphometric traits of fishes and the study of statistical relationships among them has been largely exploited across the current literature for taxonomic studies, to investigate morphological features linked to prey capture and intake to maximize feeding performances (*sensu* Pitcher and Hart, 1982). Such an information is useful in many fields of marine environmental research as for instance in fishery and resource management (e.g. Moutopoulos and Stergiou, 2002). Here, the power of morphometric analysis allowed us to show how local ecological factors may be able to drive functional differences in that local hydrodynamics was able to influence shape and size of *C. chromis*, on a short spatial scale of only few kms (sensu Antonucci et al., 2009). Morphological traits changed under two different hydrodynamics and this seemed to have rebounds on body size and growth performances. Local hydrodynamics, through a modification of food supply, affected the energy budget (the scope for growth) of specimens of this species. Under LOW-HYDRO conditions, weaker flow velocity currents would determine lower suspended food supply per unit time (*sensu* Mann, 1988; Sarà, 2006). The resulting conditions may be represented by patchily distributed food which can influence both the food intake and the searching for food and in turn the scaled functional response of fish (Sarà et al., 2014). This was consistent with the hypothesis that slower water current velocities supported smaller fish that need

HYDRO (51.22 *versus* 48.33, ANCOVA, $F_{1,370} = 11.34$, $P < 0.05$ [***], Fig. 4). Body condition index (BCI) was different as a function of size classes (ANOVA, $F_{6,2923} = 11.84$, $P < 0.05$ [***]) and sites (ANOVA, $F_{6,2923} = 24.31$, $P < 0.05$ [***]) (Table 3). BCI was greater for *C. chromis* living under LOW- than HIGH-HYDRO conditions up to 60.00 mm and viceversa after this size (Fig. 5). Sizes (SL) were not significantly different between *C. chromis* of LOW- (65.47 $\pm$ 0.97 mm) and HIGH-HYDRO (66.92 $\pm$ 1.46 mm) sites (T-test, t = 0.8377, df = 118, $P > 0.05$ [ns]), while coefficients of variation (CV) of morphometrical traits were overall greater in HIGH-HYDRO for almost all measured traits (Table 4). The regression between SL and all morphological variables was used as a tool to investigate the shape of animals under two conditions. Smaller fish had not significantly different slopes of the body height-SL relationships under two conditions (ANCOVA, $P > 0.05$ [ns]). In contrast, larger individuals showed a body height proportionally greater in the LOW-HYDRO site (ANCOVA, $P < 0.05$ [*]). HIGH-HYDRO *C. chromis* were generally more fusiform as they had longer head and jaw length and longer dorsal and anal fins (see

Table 4

Chromis chromis body shape in LOW- and HIGH-HYDRO site. In order: i) allometry by ANCOVA (*a* = intercept; *b* = slope); ii) descriptive statistics (mean ± s.e.) of each morphometric trait and the coefficient of variation (CV); iii) comparison between means and T-test results.

Morphometrics -SL relationships greater in HIGH-HYDRO										
Differences in angular coefficient — ANCOVA					Descriptive statistics				CV	
Morphometrics	Coefficient	LOW	HIGH	P	Mean LOW	± s.e.	Mean HIGH	± s.e.	LOW	HIGH
Postocular distance (PostOD)	b	0.13	0.17	0.0207	8.91	0.15	8.47	0.28	0.13	0.25
	a	−0.05	−1.87	<0.0001						
Predorsal length (PreDL)	b	0.28	0.37	0.0003	21.25	0.31	21.49	0.57	0.11	0.20
	a	−0.05	−1.47	0.2586						
Preanal length (PreAL)	b	0.62	0.69	0.0564	42.03	0.65	42.90	1.02	0.12	0.18
	a	−0.05	−1.51	0.7510						
Peduncle height (PH)[a]	b	0.13	0.15	0.0669	9.47	0.14	9.84	0.23	0.12	0.18
	a	−0.01	0.01	0.0677						
Differences in intercept — ANCOVA										
Morphometrics	**Coefficient**	**LOW**	**HIGH**	**P**	**Mean LOW**	**± s.e.**	**Mean HIGH**	**± s.e.**	**LOW**	**HIGH**
Head length (HL)	b	0.24	0.27	0.1362	17.83	0.26	17.75	0.43	0.11	0.19
	a	0.03	0.38	0.0192						
Jaw length (JL)	b	0.08	0.06	0.2462	6.28	0.13	6.82	0.14	0.16	0.15
	a	0.07	2.30	0.0041						
Eye diameter (ED)	b	0.06	0.08	0.0759	6.16	0.09	5.89	0.15	0.11	0.19
	a	0.05	0.88	0.0004						
Preocular distance (PreOD)	b	0.05	0.03	0.2644	2.94	0.07	3.40	0.11	0.19	0.25
	a	0.01	0.76	0.0006						
Dorsal fin length (DL)	b	0.56	0.51	0.1364	35.40	0.57	36.73	0.77	0.13	0.16
	a	0.03	1.32	0.0310						
Anal fin length (AL)	b	0.17	0.15	0.2938	12.05	0.19	12.92	0.25	0.12	0.15
	a	0.07	2.39	0.0001						
Morphometrics -SL relationships greater in LOW-HYDRO										
Differences in angular coefficient — ANCOVA										
Morphometrics	**Coefficient**	**LOW**	**HIGH**	**P**	**Mean LOW**	**± s.e.**	**Mean HIGH**	**± s.e.**	**LOW**	**HIGH**
Body height (BH)	b	0.28	0.20	0.0050	21.23	0.32	23.01	0.35	0.12	0.12
	a	0.23	7.55	<0.0001						
Pectoral fin length (PL)	b	0.36	0.27	0.0003	21.37	0.38	23.45	0.42	0.14	0.14
	a	0.05	3.07	<0.0001						
Differences in intercept — ANCOVA										
Morphometrics	**Coefficient**	**LOW**	**HIGH**	**P**	**Mean LOW**	**± s.e.**	**Mean HIGH**	**± s.e.**	**LOW**	**HIGH**
—	—	—	—	—						
Morphometrics -SL relationships not significantly different between sites										
Morphometrics	**Coefficient**	**LOW**	**HIGH**	**P**	**Mean LOW**	**± s.e.**	**Mean HIGH**	**± s.e.**	**LOW**	**HIGH**
Prepectoral length (PrePL)	b	0.26	0.23	0.1446	18.74	0.12	19.20	0.36	0.12	0.15
	a	0.11	3.04	0.5173						
Ventral fin length (VL)	b	0.17	0.19	0.5454	13.61	0.27	14.08	0.37	0.15	0.20
	a	0.05	1.56	0.5436						
Preventral length (PreVL)	b	0.31	0.34	0.3388	22.05	0.34	22.24	0.52	0.12	0.18

[a] *P* value near to the significance.

less intake of energy and characterized by morphometric traits to explain high maneuverability movements (Fulton, 2007). In contrast, specimens inhabiting HIGH-HYDRO sites, encountering currents of greater intensity, could rely on higher food supply being able to sustain greater biomass even though they should be subjected to higher energetic costs to get food with respect to LOW-HYDRO fishes. However, overall allometric coefficients from Marettimo populations, falling well in the normal range for this species (e.g. Stergiou and Moutopoulos, 2001; Karakulak et al., 2006), indicated that weight increments in HIGH-HYDRO were higher (3.36 g per cm) than those recorded under LOW-HYDRO (about 1/3 lesser; 2.78 g per cm) suggesting that HIGH-HYDRO conditions assured greater energy supply. Interestingly, under this local hydrodynamics, the balance between the energy required to live contrasting higher hydrodynamics to get food in open sites and the available energy to grow appears positive. Thus, behavioral strategies adopted by *C. chromis* to get energy in order to persist over time under such environmental conditions allowed damselfish to maximize the energy intake. For example, lower body height observed in HIGH-HYDRO which may resemble a more fusiform body, is a trait to allow more performing exploitation of resources under quicker conditions of water current velocities. Thus, the morphometric traits reflecting behavioral choices, resulted in morphological adaptations bringing an advantage under HIGH-HYDRO conditions: the fish may better control the perturbations and physical disturbances coming from the surrounding water flux (Webb, 2002). In HIGH-HYDRO, there was more available food per unit of time, but individuals should be able to respond to the hydrodynamic forces and remain stable in the water column to catch prey (Sfakiotakis et al., 1999; Webb, 2002). As a main consequence of this, the dorsal and anal fins and the peduncle of our *C. chromis* were more developed under HIGH-HYDRO conditions. Fins are directly employed in swimming activity, and different types of propulsion and swimming modes occur depending on how the fish use them (Sfakiotakis et al., 1999; Drucker and Lauder, 2001; Pulcini et al., 2008). *C. chromis* is described as a non-body/caudal fin-locomotion species (Webb, 1994; Fulton, 2007), but it is obvious that it may change locomotion mode according to the environmental variability (*sensu* Sfakiotakis et al., 1999). For example, in high hydrodynamic habitats, it is more difficult to control the pectoral fins because of their great flexibility (Drucker and Lauder, 2001), whereas longer anal fins should aid to balance pitch and yaw
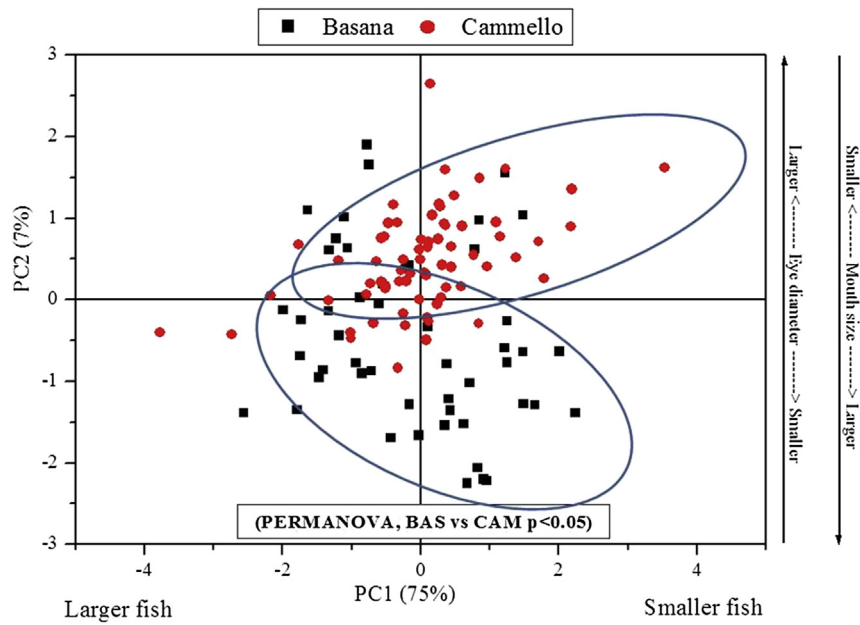
Fig. 6. Principal component analysis carried out on morphometric matrix.

(Lauder and Drucker, 2004) and contrasting recoil (Webb, 2002). On the contrary, under LOW-HYDRO hydrodynamics, *C. chromis* was characterized by greater body height and longer pectoral fins. The latter body structures are used in median/paired fin-locomotion (Webb, 1994) particularly adopted by species that need finer movements assuring greater maneuverability for their demersal lifestyle (Fulton, 2007). Without a relative strong current able to provide food, *C. chromis* have to more actively search prey by implementing body movements of pitch and yaw. Jaw length and eye diameter were both greater in LOW-HYDRO specimens, that is quite possibly related to trophic and light variability (Pulcini et al., 2008). As we do not have direct information on zooplankton resources, nor on light intensity within the two sites, we can only speculate about these aspects. We can hypothesize on the possible role of hydrodynamics in the selection of jaw and eye characteristics. The high current velocity concurrently should increase both the prey encounter rates, modifying the quantity, quality and distribution of the trophic resource. As a result, *C. chromis* in LOW-HYDRO have be able to better detect prey, and from that eyes may be larger. Differences in both jaw length and eye diameter suggested that only individuals with specific morphometric properties are recruited in schools living in the HIGH-HYDRO site. The new recruits should be more adapted to survival as they are capable of a selective food choice (Piet, 1998).

In conclusions, our results may suggest that morphological differences can occur at smaller spatial scale than 10 km due to the local hydrodynamics. Unfortunately, we cannot consider here possible effects deriving from genetic differences between two populations due to lack of genetic data. Nonetheless, some differences in functional morphometrics support the idea that hydrodynamics at small spatial scale plays the role of a primary environmental controlling factor (Losos et al., 2004) able to shape fish both directly and indirectly and affecting fish body condition state with possible rebounds in terms of life history traits.

Author's contribution

CB elaborated data, wrote the paper and with GG carried out the field and lab parts of this study; CG, JMD and GS lead the writing and provided facilities and funds for the CB Ph.D. project.

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