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Variation in Brain Organization of Coral Reef Fish Larvae according to Life History Traits

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Key Words
Allometry · Comparative brain morphology · Coral reefs · Ecomorphology · Fish larvae · Recruitment

Abstract
In coral reefs, one of the great mysteries of teleost fish ecology is how larvae locate the relatively rare patches of habitat to which they recruit. The recruitment of fish larvae to a reef, after a pelagic phase lasting between 10 and 120 days, depends strongly on larval ability to swim and detect predators, prey and suitable habitat via sensory cues. However, no information is available about the relationship between brain organization in fish larvae and their sensory and swimming abilities at recruitment. For the first time, we explore the structural diversity of brain organization (comparative sizes of brain subdivisions: telencephalon, mesencephalon, cerebellum, vagal lobe and inferior lobe) among larvae of 25 coral reef fish species. We then investigate links between variation in brain organization and life history traits (swimming ability, pelagic larval duration, social behavior, diel activity and cue use relying on sensory perception). After accounting for phylogeny with independent contrasts, we found that brain organization covaried with some life history traits: (1) fish larvae with good swimming ability (>20 cm/s), a long pelagic duration (>30 days), diurnal activity and strong use of cues relying on sensory perception for detection of recruitment habitat had a larger cerebellum than other species. (2) Fish larvae with a short pelagic duration (<30 days) and nocturnal activity had a larger mesencephalon and telencephalon. Lastly, (3) fish larvae exhibiting solitary behavior during their oceanic phase had larger inferior and vagal lobes. Overall, we hypothesize that a well-developed cerebellum may allow fish larvae to improve their chances of successful recruitment after a long pelagic phase in the ocean. Our study is the first one to bring together quantitative information on brain organization and the relative development of major brain subdivisions across coral reef fish larvae, and more specifically to address the way in which this variation correlates with the recruitment process.

Introduction

Most fish species on coral reefs have stage-structured life histories, with a largely sedentary benthic stage (usually juveniles and adults), preceded by a pelagic larval

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stage with the capacity for long-distance dispersal [for review, see Leis and McCormick, 2002]. After the pelagic phase, fish larvae must return to reef habitat to continue their development into juvenile and adult stages. This transition from the pelagic oceanic environment to a benthic reef environment (i.e. recruitment phase) represents a key period in the life history of coral reef fish [Lecchini, 2005]. During the recruitment phase, fish larvae are subjected to strong selective pressure to choose a suitable reef habitat that will promote survival and growth of individuals after recruitment [for review, see Doherty, 2002]. Up to 90% of fish larvae may be removed by predation during the first week after recruitment if they do not select a suitable habitat [Doherty et al., 2004; Lecchini et al., 2007a]. Thus, many fish species show marked selectivity in the habitats they choose at recruitment based on the presence of specific substrates and/or conspecifics, and on the absence of predators or competitors for food and space [Doherty, 2002]. However, as it is unlikely that successful recruitment is solely a matter of chance, fish larvae may use their swimming and sensory abilities to detect suitable habitat on which conspecifics are already settled and to avoid predators or competitors [for review, see Arvedlund and Kavanagh, 2009].

Researchers continue to be surprised by the sensory and swimming abilities of larval-stage fish of many species [for review, see Leis et al., 2011]. Irisson and Lecchini [2008] showed that fish larvae in 20 of 27 species recorded from Moorea Island (French Polynesia) swam actively to find a suitable habitat during the night of recruitment. Leis and Carson-Ewart [1999] showed that coral trout larvae (Serranidae) could swim against oceanic currents and that their swimming depth varied according to the distance to the reef: >1 km from Lizard Island (Australia) fish larvae swam at a depth of 20 m, while near reefs (<100 m) fish larvae swam at average depths of 2–4 m. They accorded this variation in swimming depth to the presence of predators: fish larvae could detect predators by visual cues 3–6 m away and stopped or changed depth or direction to avoid them [Leis and Carson-Ewart, 2000]. Similarly, Lecchini et al. [2005a] have studied the sensory abilities of 18 coral reef fish species at the larval stage. They found that 13 species detected their recruitment habitat by visual, chemical and/or acoustic cues emitted by conspecifics or habitat. Thus, the swimming abilities of some larval reef fish may facilitate their reaching of suitable recruitment habitats from long distances [Leis et al., 2011]. Moreover, visual, olfactory and acoustic cues may also play an important role in directing pelagic larval-stage fish to a suitable reef to which they can recruit [Arvedlund and Kavanagh, 2009]. Overall, identifying the ecological, behavioral and neurobiological mechanisms by which coral reef fish larvae recruit to a suitable habitat is critical for understanding evolution, population biology and community dynamics [for review, see Lecchini and Galzin, 2003]. Several recent studies have thus highlighted the role of larval sensory and swimming mechanisms in patch identification and patch selection, including the detection of visual, chemical and sound cues from conspecifics, habitats or predators [for reviews, see Arvedlund and Kavanagh, 2009; Leis et al., 2011]. However, no information is available about the relationship between brain organization in coral reef fish larvae and their sensory and swimming abilities at recruitment.

There are large quantitative datasets on brain organization of many teleost fish, although considerably less ecomorphological data are available for marine fish than for some taxa of freshwater fish [for review, see Ridet and Bauchot, 1990; Kotrschal et al., 1998; Salas et al., 2008]. Fish brains exhibit the serial arrangement of subdivisions typical of most vertebrates [see figure 1 in Kotrschal et al., 1998; Northcutt, 2002]. For example, Rodriguez et al. [2005] reported the functional similarity between the mammalian and the fish cerebellum in learning and cognition. Broglio et al. [2005] showed that the telencephalic lateral pallium in fish could be considered as homologous to the hippocampus of mammals and birds. Thus, typical features of teleostean brains are a large rhombencephalon, a large unpaired cerebellum, two pronounced tectal halves located dorsal to the midbrain tegmentum and diencephalon, a large, paired hypothalamic inferior lobe bulging out on the ventral brain surface, a relatively small, everted telencephalon and relatively large olfactory bulbs [Nieuwenhuys et al., 1998]. In despite of this constant neuroanatomical pattern, there is a much higher morphological diversification in teleost fish compared with that of other vertebrates [Ito, 1978; Kotrschal et al., 1998; Nieuwenhuys et al., 1998; Ito et al., 2007]. For example, Wagner [2002] showed that the mesopelagic population of teleost fish (slickheads, eels and grenadiers) has reduced olfactory bulbs, a larger optic tectum and an octavolateralis area more than twice as large as in the demersal population. In their review on fish brains, Kotrschal et al. [1998] stated that tropical reef fish had a bigger brain size and a more developed telencephalon than pelagic fish (i.e. interspecific comparison). Gonda et al. [2011] also showed that the telencephalon of nine-spined sticklebacks *(Pungitius pungitius)* is larger in marine than in pond populations (i.e. intraspecific comparison).

This huge variation in the fish brain organization could be mainly explained by phylogeny and/or various ecological, behavioral and social processes [Ridet and Bauchot, 1990; Kotrschal et al., 1998; Salas et al., 2008]. After accounting for phylogeny with independent contrasts [Pollen et al., 2007], several strong correlations have been found between brain patterns of fish (relative volume of telencephalon, mesencephalon, cerebellum, vagal lobe and inferior lobe) and various ecological, behavioral and social processes, such as diet, feeding habits, habitat complexity, increased sociality or cognitive skills [Huber et al., 1997; Lisney and Collin, 2006; Gonda et al., 2011; Kotrschal et al., 2012]. For example, Huber et al. [1997] examined the brains of 189 species of cichlids obtained from the three largest African Great Lakes and demonstrated a close relationship between the relative sizes of various brain structures and variables related to the utilization of habitat and prey. Pollen et al. [2007] showed that environmental and social factors differentially affect the brain in cichlid fish, with environmental factors showing a broader effect on a range of brain structures compared to social factors. For example, the telencephalon showed a trend towards a positive correlation with habitat size, while monogamy was associated with a smaller hypothalamic size [Pollen et al., 2007]. In salmon, Kihslinger et al. [2006] demonstrated that simply adding a few rocks in the rearing tanks resulted in increased cerebellum size of *Oncorhynchus mykiss* alevins, while structural complexity of the abiotic environment affected the rate of cell proliferation in the telencephalon of *Oncorhynchus kisutch* juveniles [Lema et al., 2005; Kotrschal et al., 2012]. A growing collection of significant relationships between aspects of brain morphology and species' ecology indicate that fish brains also evolve adaptively in response to cognitive demands [Gonzales-Voyer and Kolm, 2010]. For example, Wagner [2002] showed that the cerebral morphology in slickheads, eels and grenadiers (deep-sea fish) reflected specializations of their sensory systems. For olfaction and vision in shallow-water fish, Meek and Nieuwenhuys [1997] reported correlations between the surface area of the peripheral sensory epithelium and the olfactory lobe or the optic tectum.

Overall, teleost fish represent the largest and most diverse vertebrate radiation, with a considerable amount of variation in brain organization which has arisen adaptively in response to cognitive demands, and environmental and social pressures along phylogenesis [Ridet and Bauchot, 1990; Kotrschal et al., 1998; Ito et al., 2007; Salas et al., 2008]. However, no data are available in this link between neuroanatomical organization and ecological, behavioral and social aspects in coral reef fish [Bauchot et al., 1977]. Moreover, the debate about why sizes of brain regions vary in vertebrates is still open [Jerison, 1991; Finlay and Darlington, 1995; Pollen et al., 2007; Jacobs, 2012]. In the present paper, the structural diversity of brain organization (telencephalon, mesencephalon, cerebellum, vagal lobe and inferior lobe) among larval stages of 25 coral reef fish species captured from Moorea Island, French Polynesia, was explored for the first time. The aim of the study was to link variation in brain organization of fish larvae to their life history traits (use of cues requiring sensory perception, swimming ability, pelagic larval duration, social behavior and diel activity) and/or the phylogeny of species.

Materials and Methods

Specimen Collection

Fish larvae were captured daily from February to April 2011 with crest nets set on the west coast of Moorea Island (17°31′7.38 S, 149°55′20.89 W). This technique samples fish larvae in the process of recruitment to the reef [Lecchini et al., 2004, 2006; Lo-Yat et al., 2011]. Catches were sorted and fish were identified at species level. Three larvae of each of the 25 most common species that were captured were used for the description of brain morphology (table 1).

Brain Mass

Once captured, larvae were deeply anesthetized in 0.4 g/l of MS222 (m-aminobenzoic acid ethyl ester, methanesulfate salt) in seawater. Once unconscious, each fish was blotted, weighed to the nearest 0.001 g and measured (standard length) to the nearest 0.1 mm. Then, larvae were fixed in 10% formalin for 24 h. After 24 h, the larvae were dissected to remove the brain. Each brain was detached from the spinal cord caudal to the fossa rhomboidea in the region of the first complete cervical spinal nerve, according to the recommendations of Yopak et al. [2007]. Each brain was blotted and weighed to the nearest 0.001 g.

Brain Organization – Five Main Subdivisions

Once each brain was removed from the fish body and weighed, the five main subdivisions of the brain (telencephalon, mesencephalon, cerebellum, inferior lobe and vagal lobe; fig. 1) were photographed (digital camera Nikon D300) microscopically in ventral, dorsal and the two lateral views using the SigmaScan® image analysis program (Systat Software Inc., Richmond, Calif., USA). External brain forms are mostly organized by these five subdivisions that can be observed from the outside. To delimit the boundary between the different brain subdivisions, we used the recommendations of Broglio et al. [2003] and Pollen et al. [2007]. (1) Telencephalon: because the boundary between the preoptic area and the telencephalon is not visible from the lateral or ventral views, we used the anterior commissure and the boundary between the dorsal and ventral telencephalon as landmarks to define an ellipsoid for the preoptic area. This preoptical ellipsoid was then

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Table 1. Standard length, body mass, brain mass, and relative volume of the five major brain subdivisions in the 25 coral reef fish species captured at the larval stage on Moorea Island (French Polynesia)

Family	Species	Species abbreviation	PLD, days	Social behavior	Swimming abilities, cm/s	Sensory abilities	Diel activity	Standard length, mm ± SD	Body weight, g ± SD	Brain weight, g ± SD	Tel volume, mm^3 ± SD	Mes volume, mm^3 ± SD	Cb volume, mm^3 ± SD	Vl volume, mm^3 ± SD	IF volume, mm^3 ± SD
Apogonidae	*Apogon coockii*	AC	20	school	v < 20	no attraction	nocturnal	15.7±0.9	0.11±0.01	0.002±0.0001	0.25±0.04	0.47±0.07	0.04±0.01	0.06±0.03	0.29±0.14
	Gymnapogon spp.	Gsp	35	alone	v < 20	no attraction	nocturnal	21.7±0.9	0.14 ±0.01	0.003±0.0001	0.22 ±0.01	0.34±0.07	0.08 ±0.02	0.04±0.003	0.08±0.002
	Ostorhinchus angustatus	OA	18	school	v < 20	cue attraction	nocturnal	14.6±1.4	0.07±0.03	0.002±0.0001	0.23±0.13	0.30±0.13	0.03±0.01	0.04±0.01	0.11±0.009
	Pristiapogon exostigma	PE	34	school	v < 20	cue attraction	nocturnal	26.2±1.5	0.38±0.05	0.008±0.0001	1.79 ±0.80	1.87±0.33	0.07±0.03	0.39±0.17	0.41±0.18
Acanthuridae	*Acanthurus lineatus*	AL	42	school	v > 40	cue attraction	diurnal	32.0±1.3	1.13 ±0.11	0.026±0.002	4.75±0.55	9.21±0.97	9.71±1.49	0.51±0.03	1.69±0.29
	Acanthurus nigricauda	AN	44	alone	v > 40	cue attraction	diurnal	28.9±1.2	0.81±0.08	0.021±0.002	5.93±0.84	6.33±1.12	6.11±0.37	0.46±0.17	0.85±0.18
	Acanthurus triostegus	AT	44	school	v > 40	cue attraction	diurnal	25.8±3.3	0.69 ±0.14	0.024±0.007	4.24±1.64	6.22±1.47	9.74±3.69	0.35±0.13	0.16±0.05
	Ctenochaetus striatus	CSt	39	alone	v > 40	cue attraction	diurnal	35.5±2.1	1.40±0.20	0.028±0.001	3.20±0.76	6.42±0.54	3.58±0.59	0.42±0.03	1.25±0.25
	Naso vlamingii	NV	78	alone	v > 40	cue attraction	diurnal	28.1±2.9	1.68±0.41	0.032±0.003	7.13±2.56	11.41±3.03	2.43±1.59	0.62±0.26	1.68±0.64
Balistidae	*Rhinecanthus aculeatus*	RA	43	alone	v > 40	cue attraction	diurnal	19.9±1.3	0.52±0.08	0.011±0.001	2.97±0.72	3.55±0.18	0.81±0.26	0.67±0.14	1.47±0.21
Chaetodontidae	*Chaetodon citrinellus*	CC	51	school	v > 40	cue attraction	diurnal	27.1±1.1	0.85±0.11	0.023±0.004	3.71±0.74	7.41±1.37	3.82±1.05	0.16±0.04	1.14±0.023
	Chaetodon ephippium	CE	39	school	v > 40	cue attraction	diurnal	13.5±1.3	0.17±0.05	0.003±0.001	0.98±0.34	2.12±0.96	1.95±0.35	0.05±0.006	0.22±0.09
Fistulariidae	*Fistularia commersonii*	FC	46	alone	20 < v < 40	no attraction	nocturnal	118.4±3.1	0.56±0.09	0.012±0.002	0.87±0.33	4.16±0.71	0.08±0.04	0.02±0.01	2.69±0.30
Gobiidae	*Valenciennea strigata*	VS	38	alone	v < 20	no attraction	diurnal	28.3±0.6	0.29±0.03	0.007±0.001	0.45±0.06	0.62±0.09	1.59±0.13	0.23±0.01	0.87±0.15
Lethrinidae	*Monotaxis grandoculis*	MG	34	alone	v > 40	no attraction	nocturnal	42.3±1.2	1.47±0.16	0.025±0.002	5.58±0.13	6.51±0.23	10.49±1.35	0.66±0.24	1.89±0.20
Mullidae	*Mulloidichthys flavolineatus*	MF	46	school	v > 40	cue attraction	diurnal	87.2±4.8	8.86±2.03	0.096±0.016	15.03±2.66	27.25±1.35	6.46±2.92	6.61±1.71	29.99±11.03
	Parupeneus multifasciatus	PM	47	school	v > 40	cue attraction	diurnal	56.6±2.3	2.75±0.41	0.050±0.007	9.74±2.34	16.35±1.67	0.11±0.001	2.98±1.05	12.85±3.13
Pomacentridae	*Abudefduf sexfasciatus*	Ase	25	alone	v > 40	no attraction	diurnal	10.7±0.3	0.06±0.004	0.001±0.0001	0.36±0.02	0.66±0.14	0.11±0.01	0.03±0.003	0.12±0.03
	Chromis viridis	Cvi	21	school	v < 20	cue attraction	diurnal	8.1±0.1	0.02±0.001	0.001±0.0006	0.11±0.004	0.21±0.009	0.06±0.01	0.02±0.01	0.05±0.002
	Chrysiptera glauca	CG	23	school	20 < v < 40	no attraction	diurnal	13.7±0.4	0.07±0.004	0.001±0.0004	0.44±0.04	0.51±0.13	0.06±0.009	0.01±0.004	0.09±0.01
	Chrysiptera leucopoma	CL	26	school	20 < v < 40	no attraction	diurnal	13.6±0.5	0.08±0.009	0.002±0.001	0.57±0.21	1.08±0.47	0.11±0.02	0.10±0.03	0.14±0.04
Synodontidae	*Saurida gracilis*	SG	40	alone	v < 20	no attraction	nocturnal	32.4±0.5	0.22±0.02	0.005±0.001	0.18±0.02	1.22±0.24	0.01±0.002	0.02±0.004	0.42±0.06
Tetraodontidae	*Canthigaster bennetti*	CB	47	school	20 < v < 40	no attraction	diurnal	21.9±1.4	0.44±0.06	0.015±0.003	1.67±0.24	2.87±1.28	0.35±0.08	0.18±0.03	0.88±0.10
	Canthigaster solandri	CS	47	school	20 < v < 40	no attraction	diurnal	13.3±0.7	0.21±0.05	0.006±0.001	1.00±0.16	1.64±0.41	0.18±0.05	0.19±0.03	0.41±0.10
	Canthigaster valentini	Cva	47	school	20 < v < 40	no attraction	diurnal	10.9±0.5	0.10±0.01	0.003±0.001	0.463±0.06	0.92±0.08	0.07±0.007	0.07±0.03	0.25±0.06

The life history traits of the 25 species are also given [cue use relying on sensory ability, swimming ability, pelagic larval duration (PLD), social behavior and diel activity]. Tel = Telencephalon; Mes = mesencephalon; Cb = cerebellum; Vl = vagal lobe; IF = inferior lobe.

subtracted from the whole appearance of the telencephalic ellipsoid to obtain a real telencephalic ellipsoid. The olfactory bulb was included in the telencephalon. (2) Mesencephalon: the whole mesencephalon or midbrain was the subject of the study. (3) Cerebellum: in order to delimit the boundary between the corpus cerebelli and the ventrally positioned other rhombencephalic structures in the lateral view, we used the midpoint of the mesencephalic height as a consistent approximation. Therefore, 'cerebellum' in this study meant only corpus cerebelli, and the valvula cerebelli was excluded. (4) Inferior lobe or hypothalamic inferior lobe: the inferior lobe did not include the vascular sac and hypophysis. (5) Vagal lobe: the whole external form of the vagal lobe was the subject of the study.

Measurement

Following the methods of Pollen et al. [2007] and Kotrschal et al. [2012], the widths of each brain subdivision were determined from dorsal and ventral views, whereas lengths and heights were taken from lateral views. The width was defined as the maximal extension of each brain subdivision perpendicular to the anatomical midline. The length and the height were defined as the maximal extension of each brain subdivision, respectively, in parallel or perpendicular to the estimated projection of the brain. The volume of each brain subdivision was determined according to an ellipsoid model [van Staaden et al., 1995]. For paired structures such as the telencephalon or mesencephalon, the estimated volume of the structure was doubled. Overall, the relative volumes of telencephalon, mesencephalon, cerebellum, vagal lobe and inferior lobe were expressed as percentages (i.e. volume of each brain subdivision over the sum of volumes of the five brain subdivisions), which were then used for further analysis (fig. 2).

Allometric Analysis

A regression line was used to describe the allometric relationship between log10-transformed brain and body masses: $Y = aX^b$ where Y = brain mass, X = body mass, a is the allometric coefficient, and b is the allometric component. However, to obtain a regression equation independent of phylogenetic constraints, independent contrasts were obtained by log10 transforming the data and analyzing brain mass and body mass together using the CRUNCH algorithm within the CAIC software package [Purvis and Rambaut, 1995; Yopak et al., 2007]. For further investigations about allometric analysis and to determine if each brain subdivision could contribute in the same way to this allometry, a multivariate analysis was performed on the different brain subdivisions, body and brain masses. Thus, mass and brain organization variables were subjected to a principal component analysis, computing the correlations between the different variables, after data were log10 transformed to meet the assumption of normal distributions.

Phylogenetic Analysis

A phylogenetic tree of the 25 species used in this study was built based on the phylogeny of Li et al. [2009]. Because the branch lengths for many species are unknown, it was assumed that all branch lengths were equal [Purvis and Rambaut, 1995]. Thus, our aim was to compare phylogenetic relationships with brain organization and life history traits because closely related species often exhibit many common characters [Harvey and Pagel, 1991]. To investigate these relationships, a spatial-autocorrelation correlogram (Moran and Geary test) was used with the univariate and multivariate data on brain organization and life history traits. The Moran and Geary test is particularly well suited for phylogenetic and/or spatial links as it tests whether data are spatially autocorrelated (whether a variable is correlated with itself through space) with the null hypothesis that there is no spatial autocorrelation [Cliff and Ord, 1973; Gittleman and Kot, 1990]. This test allows one to apply a model-independent measure of autocorrelation for estimating whether cross-taxonomic trait variation is related to phylogeny. If nearby or neighboring variables in the tree are more alike, there is a positive spatial autocorrelation and random patterns exhibit no spatial autocorrelation. In our study, the Moran and Geary test allowed us to determine the extent to which adjacent observations of the same life history traits in the phylogenetic tree were correlated.

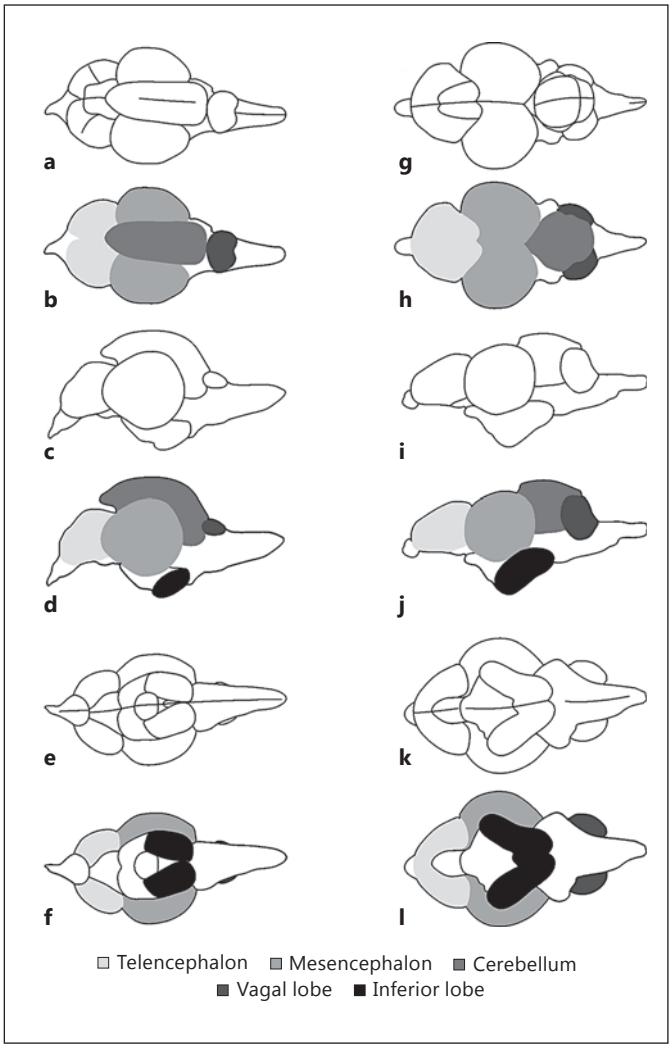
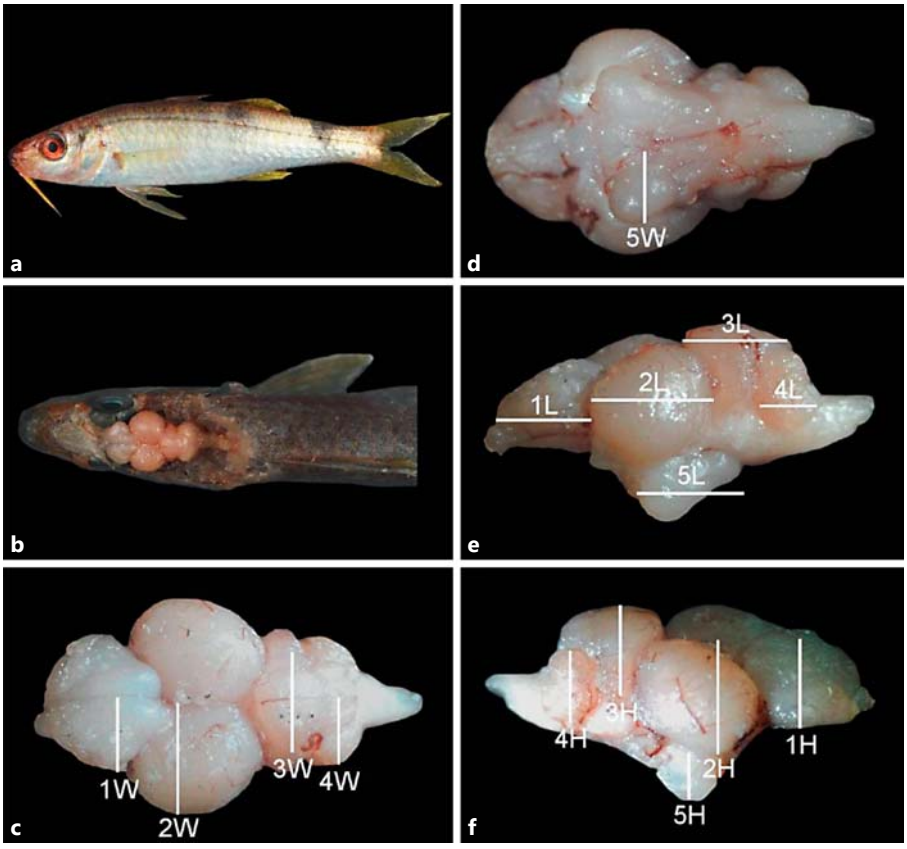


Fig. 1. Dorsal, lateral and ventral views of brains of the coral reef fish *C. striatus* (**a–f**) and *P. multifasciatus* (**g–l**), illustrating the five major subdivisions identified in this study (telencephalon, mesencephalon, cerebellum, vagal lobe and inferior lobe). Brains are not to scale.



Color version available online

Fig. 2. Photographs of an entire fish (**a**) and a fish after opening the cranium (**b**) of *P. multifasciatus* (standard length = 57 ± 2 mm). Photographs of the measurements taken from dorsal (**c**), ventral (**d**) and lateral (**e**, **f**) images to determine the size of various brain structures. W = width; H = height; L = length; 1 = telencephalon; 2 = mesencephalon; 3 = cerebellum; 4 = vagal lobe; 5 = inferior lobe.

Analysis of Life History Traits

In order to relate brain organization to fish ecology, fish species were grouped according to their lifestyle at larval stage, based on published information [Stobutzki and Bellwood, 1994; Kinsgford et al., 2002; Leis and McCormick, 2002; Lecchini and Galzin 2003, 2005; Lecchini et al., 2005, 2007b; Arvedlund and Kavanagh, 2009; Leis et al., 2011]. We used the five most studied life history traits from these seven papers in our study. Some life history traits are nominal variables (social behavior, cue use and diel activity). We split these variables into two groups (1/0 – e.g. fish species with diurnal or nocturnal activity). For the other life history traits as ordinal variables (swimming abilities and pelagic larval duration), we decided to split them into three groups according to the frequency distribution of these variables. For example, when we plotted log 'swimming speed' versus frequency (computed for the 25 fish species), the histogram could be separated into three equal parts: < log (20) = 3, and > log (40) = 3.7. Thus, the variable 'swimming ability' was split into three groups: 1: v < 20 cm/s, 2: 20 cm/s < v < 40 cm/s and 3: v > 40 cm/s. Overall, each trait was split into two (nominal variables) or three groups (ordinal variables): Pelagic larval duration (i.e. time spent in the ocean between hatching and reef recruitment – ordinal variable 1: <30 days, 2: 30–45 days and 3: >45 days); social behavior (i.e. whether fish larvae lived in a school with conspecifics or were solitary – nominal variable: school or alone); swimming ability (i.e. swimming speed of fish larvae at recruitment stage – ordinal variable: swimming speed 1: v < 20 cm/s, 2: 20 cm/s < v < 40 cm/s and 3: v > 40 cm/s); cue use (i.e. response to the chemical, acoustic or visual cues emitted by conspecifics, habitats or predators – nominal variable: no attraction or attraction), and diel activity (nominal variable: nocturnal or diurnal).

The relative size of each brain subdivision, after normalization by an arcsine square root transformation of the data, was compared between different species and life history traits using a multiple factor analysis (MFA) [Escoffier and Pagès, 1994]. MFA extracts the main factors or components that account for interrelations in observed data, thereby reducing correlational data to a smaller number of explanatory dimensions or factors. The relative size of the five main subdivisions of the brain and the five life history characteristics were used as the first and second sets of variables for this analysis. The different clusters identified according to life history characteristics provided resultant components that were analyzed by ANOVA and a post hoc Tukey's test for multiple comparisons. All statistical analyses were performed in R 2.15.0.

Results

Allometric Relationships and Brain Organization of Coral Reef Fish Species at Larval Stage

The 25 fish species belonging to 11 families exhibited wide variations in standard length (from 8.1 mm for *C. viridis* to 118.4 mm for *F. commersonii*), body mass (from

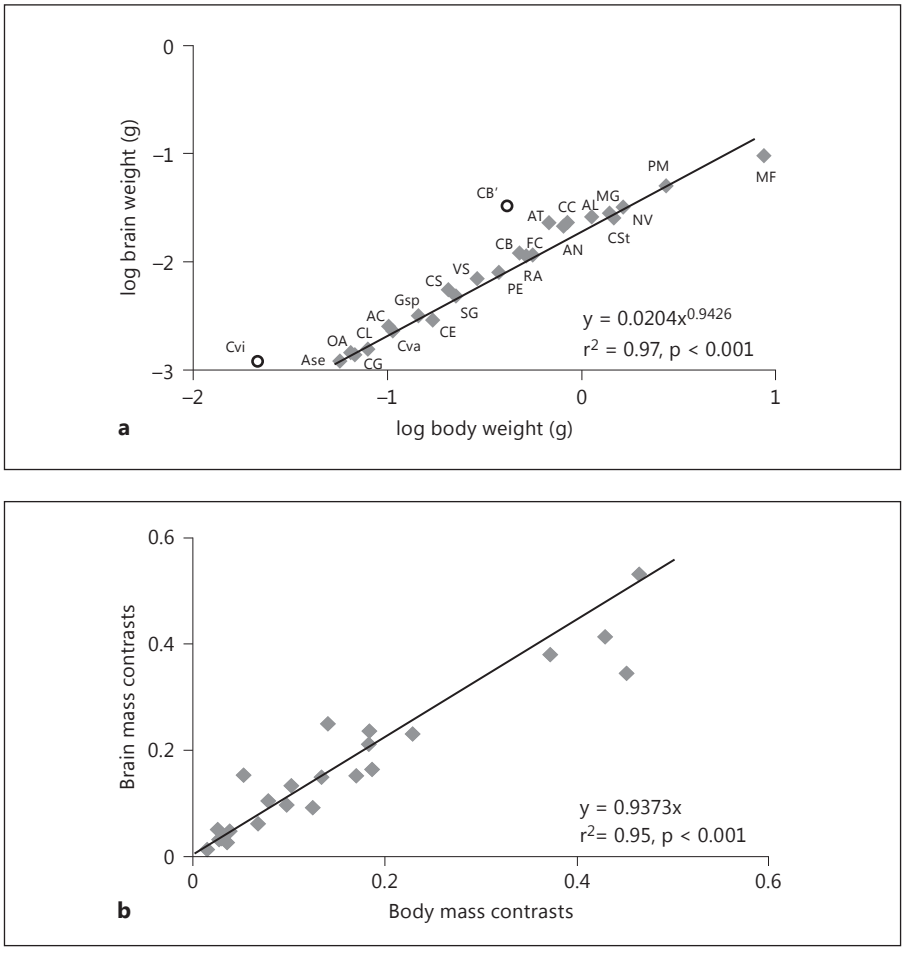


Fig. 3. Scaling of brain mass with body mass in the coral reef fish species captured on Moorea Island using species as independent data points (**a**) and phylogenetically independent contrasts (**b**). The equation, the r^2 value and the p value were given for each regression. The species *C. viridis* and 1 of the 3 individuals of *C. bennetti* were considered as outliers in the analysis. The abbreviations of fish species are given in table 1.

0.02 g for *C. viridis* to 8.8 g for *M. flavolineatus*) and brain mass (from 0.001 g for *C. glauca* to 0.09 g for *M. flavolineatus*; table 1). The allometric analyses showed that brain mass (y) increased with body mass (x) according to the equation: $y = 0.02x^{0.94}$ using fish species as independent data points (fig. 3a), and $y = 0.93x$ using independent contrasts (fig. 3b). In the principal component analysis, the volume of each brain subdivision was correlated in the same way as brain and body weights along axis 1 (87% of variance; fig. 4a). A significant regression was highlighted for 5 of the 11 fish families ($r^2 = 0.88$, $p < 0.001$; fig. 4b). Mullidae and Acanthuridae had the heaviest body and brain (e.g. *M. flavolineatus*: mean body weight = 8.86 g, mean brain weight = 0.09 g) while Synodontidae, Apogonidae and Pomacentridae had the lightest body and brain (e.g. *C. glauca*: mean body weight = 0.07 g, mean brain weight = 0.001 g). Principal component 2 (explaining 5% of variance) showed that fish larvae, independently of their weight, had disproportionately sized brain subdivisions: vagal lobe and inferior lobe opposed to telencephalon, mesencephalon and cerebellum (fig. 4a). Among the five brain subdivisions and the 11 fish families, a significant regression was highlighted for the cerebellum of 6 fish families ($r^2 = 0.82$, $p < 0.001$; fig. 4b). Gobiidae, Synodontidae and Mullidae have the smallest cerebellum (e.g. *V. strigata*: 4% of total brain volume), while Pomacentridae, Chaetodontidae and Acanthuridae have the largest cerebellum (e.g. *A. nigricauda*: 31% of total brain volume).

Phylogenetic Relationship with Brain Organization

As longer and bigger fish larvae had heavier brains (fig. 3, 4), further analysis of brain organization used the relative volumes of telencephalon, mesencephalon, cerebellum, vagal lobe and inferior lobe, eliminating the size effect. Moran and Geary tests showed no significant relationship between the phylogenetic tree and the relative volume of the five brain subdivisions (test number = 10, permutation number = 999, $p > 0.05$; fig. 5). For example,

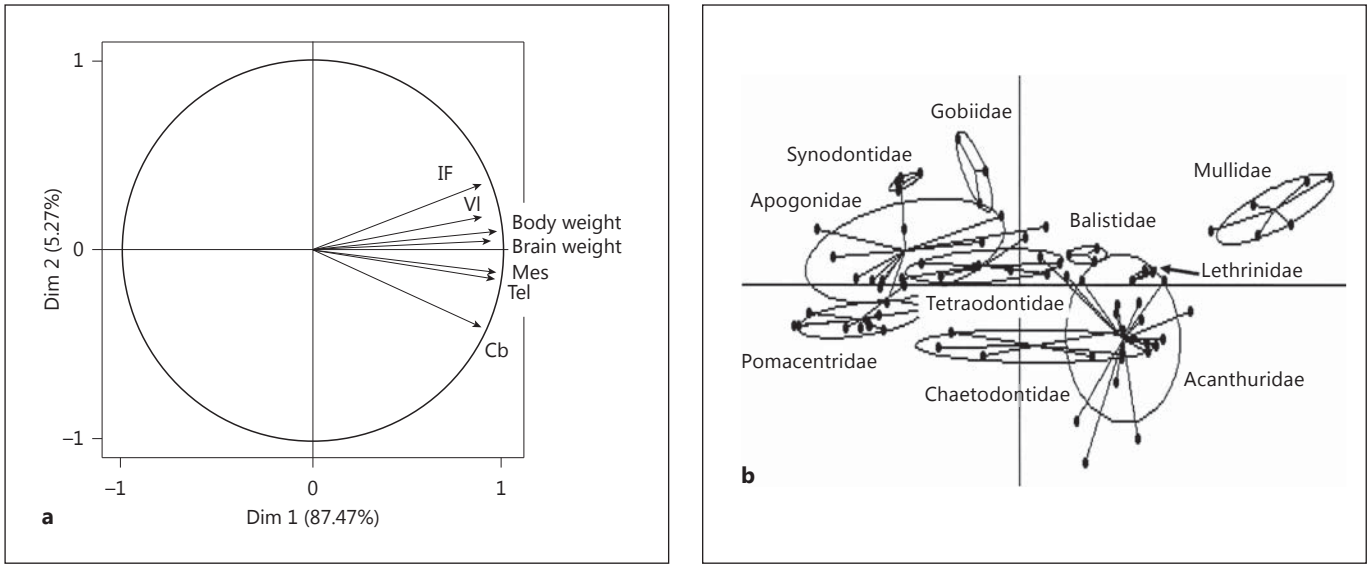


Fig. 4. Correlation circle (**a**) and family representation (**b**) on the first two axes of the principal component analysis conducted on the brain and body weights and the volume of all brain subdivisions. Tel = Telencephalon; Mes = mesencephalon; Cb = cerebellum; Vl = vagal lobe; IF = inferior lobe. **a** Correlation circle showing a projection of the initial variables (volume of each brain subdivision, brain weight and body weight) in the factor space. When variables are far from the center and are close to each other, they are significantly and positively correlated (r close to 1). The length of arrows represents the strength of the link between initial variables and the corresponding axis. **b** Scatter diagram of data on the two-dimensional map with representation of point classes related by segments from the gravity center of the family and an ellipse of a 95% confidence region. The ellipses were calculated for each family and the points correspond to each fish species within this family (the lines link the points to the gravity center of each family).

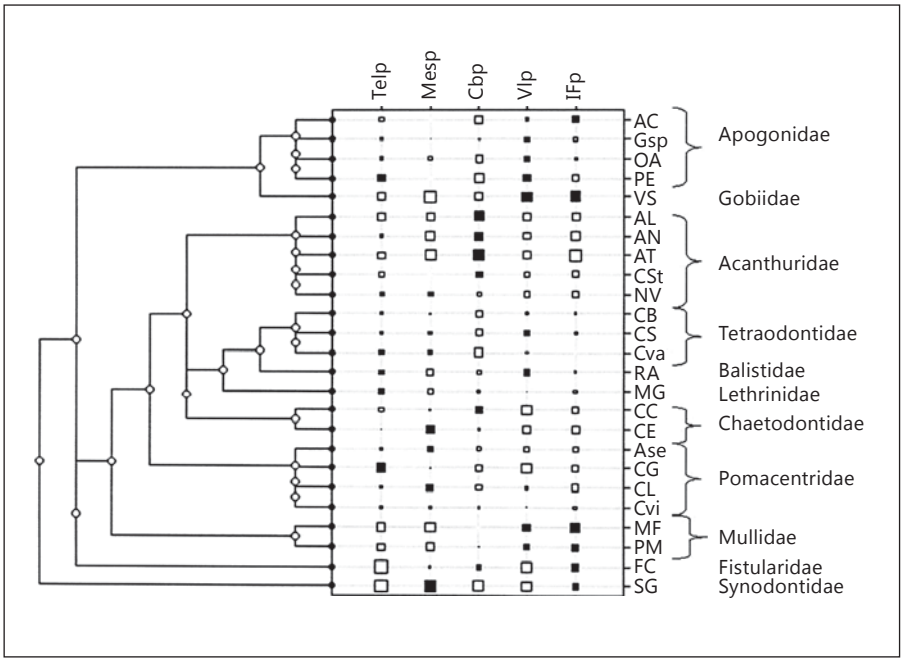
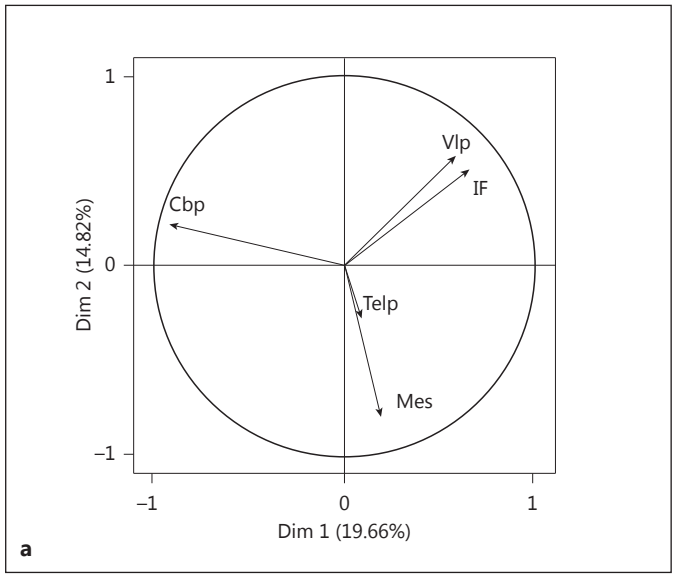
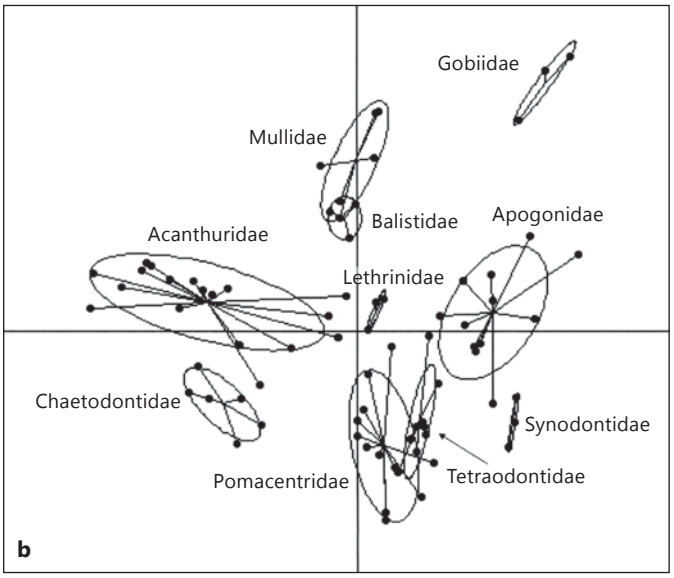
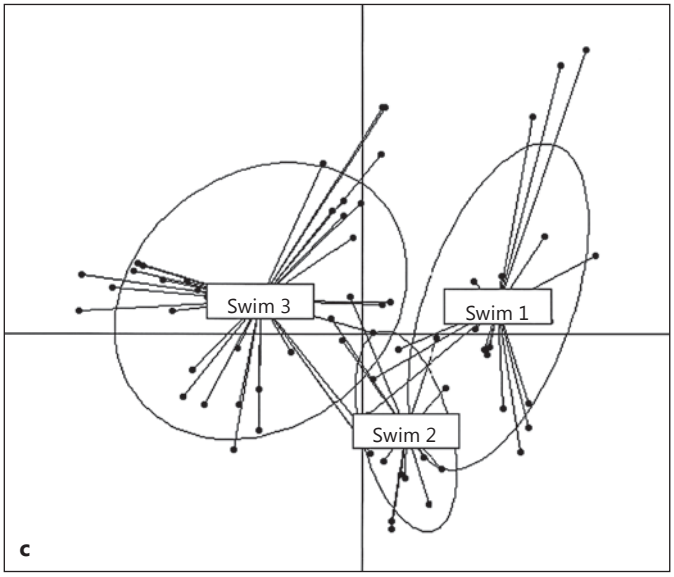


Fig. 5. Spatial-autocorrelation correlogram between phylogenetic data and relative volumes of the five brain subdivisions. The abbreviations of fish species are given in table 1. A 'p' (for proportion) was added to the brain subdivision abbreviations (see legend in fig. 3) to indicate that we were concerned with the relative volumes. Black squares indicate that the volume of brain subdivision for a given species is superior to the mean volume of the brain subdivision calculated on the 25 fish species (mean volume and standard deviation of telencephalon = 26 ± 6.2%; mesencephalon = 43 ± 6.5%; cerebellum = 13 ± 8.6%; vagal lobe = 4 ± 2.1%, and inferior lobe = 14 ± 7.5%). White squares indicate that the volume of species is inferior to the mean volume. The size of squares is proportional to the (positive or negative) difference between the mean value and the species' value.







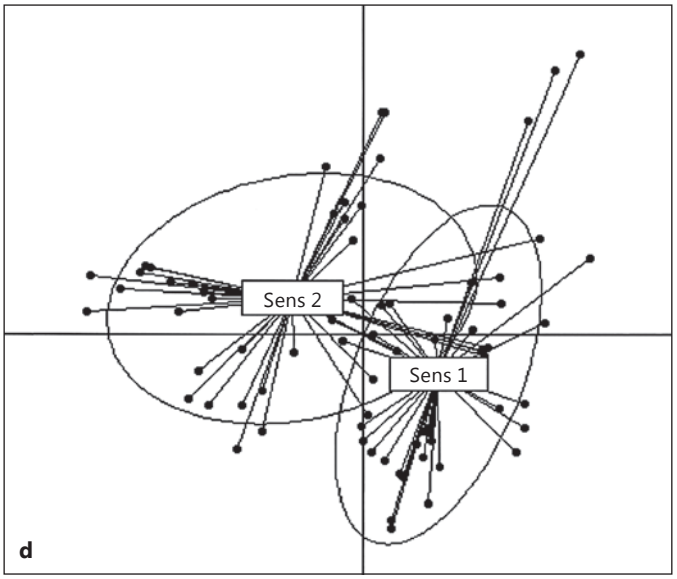
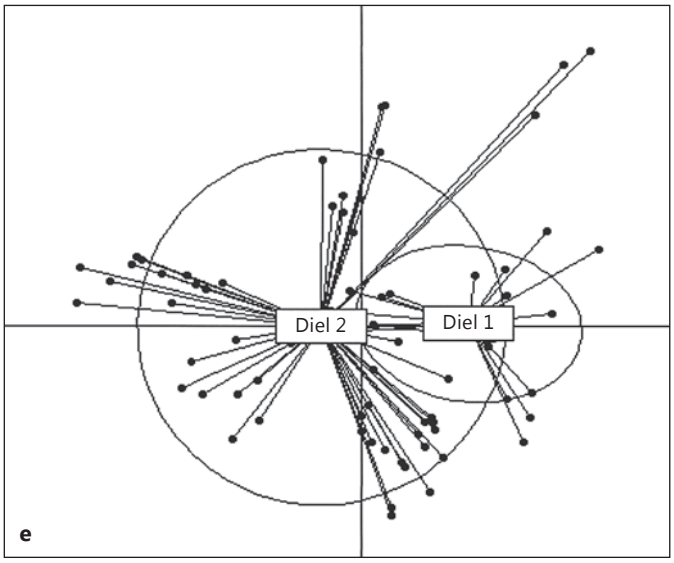
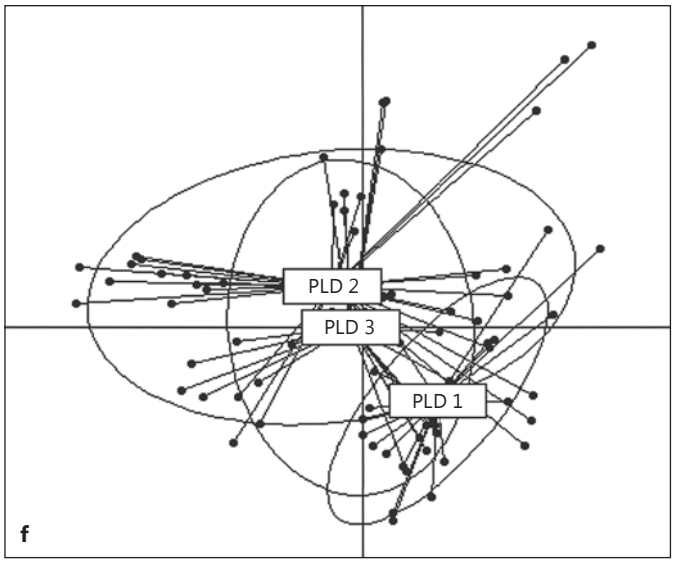
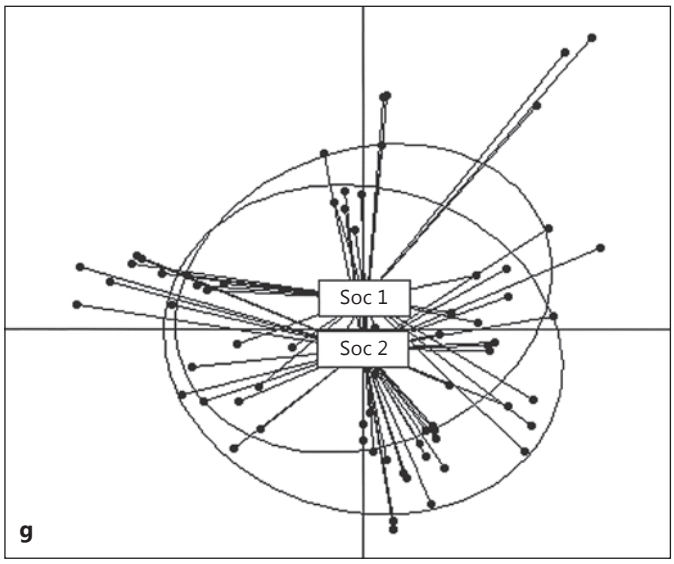


Fig. 6. MFA computed on brain subdivisions' (**a**), fish families (**b**) and life history traits (**c–g**) variables. The five life history traits were coded as follows: Swim 1, 2 and 3 for swimming speed v < 20 cm/s, 20 cm/s < v < 40cm/s and v > 40 cm/s; Sens 1 and 2 for no cue use relying on sensory ability and cue use relying on sensory ability; Diel 1 and 2 for nocturnal and diurnal activity; pelargic larval duration (PLD) 1, 2 and 3 for oceanic phase <30, 30–45 and >45 days, and Soc 1 and 2 for solitary and schooling behavior, respectively. **a** MFA showed a projection of the initial variables (relative volume of each brain subdivision) in the factor space. When variables are far from the center and are close to each other, they are significantly and positively correlated together (r close to 1). The length of arrows represents the strength of the link between initial variables of each species and the corresponding axis. **b–g** Results of MFA showing a projection of family or life history trait data on the two-dimensional map with representation of point classes related by segments from the gravity center and an ellipse of a 95% confidence region. The ellipses were calculated for each family or life history trait and the lines correspond to each fish species.

(For Fig. 6e–g, see next page.)







V. strigata (Gobiidae) was more close to *P. exostigma* (Apogonidae) than *M. flavolineatus* (Mullidae) in the phylogenetic tree (fig. 4). Yet, *V. strigata* had a larger vagal lobe (11% of total brain volume) and inferior lobe (29%) in comparison to the average for all fish species observed here (mean volume of vagal lobe for the 25 fish species: 4%; inferior lobe: 14%). Similarly, *M. flavolineatus* had a larger vagal lobe (8%) and inferior lobe (34%). In contrast, *P. exostigma* had a smaller inferior lobe (8%), and a larger vagal lobe (8%) and telencephalon (39%; mean volume of telencephalon for all species: 26%). Thus, species that were closely related did not share more characteristics of brain organization than distantly related species. Therefore, much of the interspecific variation in brain organization was independent of phylogenetic position, and species could be treated as independent data points to investigate the link between brain organization and life history traits.

Variation in Brain Organization according to Life History Traits of Fish Larvae

MFA, computed on brain subdivision and life history trait variables, showed a separation between the cerebellum and the other four brain subdivisions along axis 1 (explaining 20% of variance; fig. 6a). The second axis (explaining 15% of variance) demonstrated a separation between telencephalon and mesencephalon versus vagal lobe and inferior lobe (fig. 6a). Thus, three clusters were highlighted on the first two axes of the MFA: vagal lobe and inferior lobe; telencephalon and mesencephalon, and cerebellum (fig. 6a). The distribution of the 11 fish families according these three clusters showed that Gobiidae had (proportionally) the largest vagal lobe and hypothalamus, Pomacentridae and Tetraodontidae the largest telencephalon and mesencephalon, and Acanthuridae the largest cerebellum (fig. 6b). The overlap between ellipses encompassing members of the same family was low, suggesting that the variation in brain organization was smaller among fish species within a family than between fish families.

The first axis of the MFA discriminated three of the five life history traits (swimming ability, diel activity and cue use) in relation to cerebellum volume (fig. 6a, c–e). For example, *A. triostegus* larvae (Acanthuridae) could swim up to 47 cm/s [Stobutzki and Bellwood, 1994], could detect their recruitment habitat by visual, chemical and acoustic cues [Lecchini et al. 2005] and showed diurnal activity [Lecchini and Galzin, 2005]. This species had a larger cerebellum (36% of total brain volume) in comparison with all other species (mean volume of cerebellum: 13%). In contrast, *O. angustatus* larvae (Apogonidae) could swim at speeds reaching 19 cm/s [Stobutzki and Bellwood, 1994],

did not respond to sensory cues indicating recruitment habitat [Lecchini et al., 2005a] and was nocturnally active [Lecchini et al., 2007b]. This species had a small cerebellum (4% of total brain volume). One-way ANOVA (three categories of swimming ability and relative volume of cerebellum; table 1) indicated that an increase in swimming speed was linked with the proportional size of the cerebellum (ANOVA and Tukey's test, all values of $p < 0.001$): faster fish had a larger cerebellum than slower fish (fig. 6c). Similarly, fish with high use of cues requiring sensory ability to detect their recruitment habitat (fig. 6d) and with diurnal activity (fig. 6e) had a larger cerebellum than the other species (ANOVA and Tukey's test, all $p < 0.001$).

The second axis of the MFA discriminated the two other life history traits: pelagic larval duration (fig. 6f) and, to a lesser extent, the social behavior (fig. 6g). In fish species with shorter pelagic duration (<30 days), mesencephalon and telencephalon were more developed than in species with a long pelagic duration (ANOVA and Tukey's test, $p < 0.001$). For example, *C. glauca* (Pomacentridae) had a short pelagic duration (23 days) and *P. multifasciatus* (Mullidae) had a long pelagic duration (47 days). Their brain organizations (proportional volumes) were, respectively, as follows: 39 and 20% for telencephalon, 44 and 33% for mesencephalon; 5 and 13% for cerebellum, 2 and 6% for vagal lobe and 8 and 26% for inferior lobe. Thus, the telencephalon and mesencephalon were proportionally larger in species with short pelagic durations, while cerebellum, vagal lobe and inferior lobe were proportionally larger in species with long pelagic durations. Lastly, MFA showed that the solitary fish (e.g. *V. strigata*; table 1) had a reversed proportion with a mean volume that was substantially greater for inferior and vagal lobes than telencephalon and mesencephalon (ANOVA, $p = 0.049$).

Discussion

In ray-finned fish, there is a wide variety of brains in terms of both external form and internal structure [for review, see Kotrschal et al., 1998]. Such variations in brain morphology among teleost species are often correlated with their behavior and niches [Lissner, 1932; Evans, 1940; Ito et al., 2007]. Moreover, several studies have shown that the importance of cytoarchitecture and fiber connections in the functions of the different brain subdivisions in fish [e.g. cerebellum, Montgomery et al., 2012]. However, to date, no data exist on the variation in brain morphology (for both external form and internal structure) of larval-stage coral reef fish.

Allometric Relationship and Brain Organization

While there has not been any previous work on the brain organization of coral reef fish larvae, our results fit with previous research on adult fish and the patterns observed in changes in allometric slope in mammals through ontogenetic stages: Bauchot et al. [1977] showed that the allometric slope between brain mass and body mass in adult tropical fish was 0.44 for intraspecific comparison, 0.50 for intrafamiliar comparison and 0.66 for broad interspecific comparison; evidence from mammals also shows that the allometric slope is higher in prenatal than adult stages [Lande, 1979]. In our study (interspecific comparison), the slope was 0.94 (fig. 3a), which is in close accordance with a decreased allometric slope compared to adult coral reef fish [Bauchot et al., 1977]. However, a large amount of variation in the relative volumes of different brain subdivisions was observed between the 25 fish species studied (table 1). For example, the relative volume of the cerebellum ranged from 4% for *V. strigata* to 36% for *A. triostegus*. Atema et al. [1988] attributed the large variation in relative volumes of different fish brain subdivisions to a higher number of potential sensory modalities in aquatic environments, due to the physical properties of water, compared with that available to terrestrial animals such as birds and mammals. Indeed, aside from vision, olfaction and hearing, fish exhibit an extensive array of additional 'aquatic' senses, including mechanosensory lateral line, different schemes for external taste (taste buds and solitary chemosensory cells) and a range of electroreceptor systems [for review, see Myrberg and Fuiman, 2002]. Therefore, compared with mammals, brain structure in fish is more likely to escape a variety of spatial and developmental constraints [Atema et al., 1988; Kotrschal et al., 1998; Lisney and Collin, 2006; Gonda et al., 2011]. In our study, this variation in brain organization of coral reef fish was related more to ecology than phylogeny (fig. 5). A significant link was highlighted between the relative volumes of different brain subdivisions and life history trait variables (fig. 6). (1) Fish larvae with good swimming ability (>20 cm/s), use of cues requiring good sensory abilities to detect their recruitment habitat, diurnal activity and a long pelagic duration (>30 days) had a larger cerebellum than the other species. (2) Fish larvae with a short pelagic duration (<30 days) and nocturnal activity had larger mesencephalon and telencephalon. Lastly, (3) fish larvae with solitary behavior during their oceanic phase had larger inferior and vagal lobes.

The link between the relative volume of different brain subdivisions and life history traits of fish species should be, nevertheless, taken with caution. The debate about

why the sizes of different brain regions vary is still open [Jerison, 1991; Finlay and Darlington, 1995]. For example, Jacobs [2012] showed that the link between the size of the olfactory bulb and the function of olfaction is not evident in vertebrates. In contrast, other studies have shown a strong link between the size of a specific brain subdivision and a function [Metzner 1991: inferior colliculus and nocturnal behavior in bats; Van Hooser and Nelson, 2006: superior colliculus and visual abilities in squirrels; Schinazi et al., 2013: hippocampal size and cognitive function in humans]. For example, Mehlhorn and Rehkamper [2009] showed that homing pigeons have larger brains in comparison to other nonhoming pigeon breeds and particularly show an increased size of the hippocampus. Mehlhorn and Rehkamper's result underlines the hypothesis that there is a relationship between hippocampus size and spatial ability. Overall, our study is not a functional analysis, but an attempt to discern ecological patterns within a neuroanatomical framework. Our present approach rests on the assumption that the relative size of a brain subdivision is a measure of the relative importance of a particular sensory faculty in the orientation of individuals, life history stages or species. However, the available literature does indicate that this assumption is often valid in fish, making the relative size of brain subdivisions a reliable predictor of their relative importance [Broglio et al., 2003; Yopak et al., 2007; Kotrschal et al., 2012].

Relationship between Brain Organization and Life History Traits of Fish Larvae

The overall objective of our study was to highlight the relationship between brain organization in fish larvae and the recruitment process. Although all brain subdivisions are interconnected, our study highlighted that the relative volumes of cerebellum, mesencephalon and telencephalon (and not inferior and vagal lobes) varied with a strong association with swimming ability, cue use and pelagic duration of coral reef fish larvae (fig. 6). Thus, fish larvae with a short pelagic duration (<30 days) had larger mesencephalon and telencephalon regions, while fish larvae with a long pelagic duration (>30 days) had a larger cerebellum, and these species also had stronger swimming ability and cue use relying on sensory ability. The teleost telencephalon contains essential components of the neural network that underlies map-like spatial memories in fish, and the mesencephalon enables the fish to visually identify moving objects, such as prey or predators [for review, see Salas et al., 2008]. Therefore, a well-developed mesencephalon and telencephalon are likely to be essential for the oceanic dispersion of fish larvae, even if they have a short pelagic duration [Kotrschal et al., 1998; Myrberg and Fuiman, 2002; Salas et al., 2008].

The main pertinent result of our study highlights that fish larvae with a long pelagic duration (> 30 days) had a larger cerebellum (fig. 6). Fish larvae with a long pelagic duration move further from their natal reef than fish with a short pelagic duration [Leis and McCormick, 2002]. These larvae need stronger swimming and sensory abilities, firstly, to survive longer in the ocean (to avoid predators and to find prey during a period >30 days) and, secondly, to come back to a reef from a greater distance [Leis and McCormick, 2002; Arvedlund and Kavanagh, 2009]. In vertebrates, the cerebellum is one of the most variable brain parts in terms of shape and size [Butler and Hodos, 1996]. However, despite the notable macroanatomical variability, the cerebellum of teleost species plays an important role in monitoring incoming sensory information and in providing online adaptation of not only motor but also nonmotor functions to perform contextually relevant behaviors, even spatial cognition [Imura et al., 2003; Salas et al., 2008]. Thus, we hypothesize that a well-developed cerebellum allows fish larvae to improve their chance of successful recruitment after a long pelagic phase in the ocean. Sol and Price [2008] showed that large brains in birds were associated with increased cognitive skills, enabling animals to use new environments and resources more successfully. Therefore, a larger cerebellum in coral reef fish larvae may allow them to survive better in the ocean during a longer period (>30 days), the ocean being considered a novel environment for fish originating from reefs [Leis and McCormick, 2002]. Such behavioral flexibility is theoretically expected to have macroevolutionary consequences [Sol and Price, 2008]. In the classical concept of metapopulations, the long-term persistence and stability of fragmented marine populations depend on the effects of dispersal rates and recruitment success [Hanski and Gilpin, 1997]. A well-developed cerebellum would allow this long-term persistence and stability of fish populations in coral reefs. Indeed, firstly, fish larvae with long pelagic durations should more easily become established in new locations, increasing opportunities for allopatric speciation and decreasing chances that the species as a whole becomes extinct. Secondly, the ability to use new resources due to a well-developed cerebellum should place new selection pressures on populations, promoting adaptive diversification, a process termed 'behavioral drive'.

Other explanations are, however, possible to explain the link between the development of different brain sub-

divisions and life history traits of fish species. For example, nocturnal fish larvae had a larger mesencephalon than diurnal species [Kotrschal et al., 1998]. Lastly, we have no hypothesis to explain the relationship between the development of inferior and vagal lobes in fish larvae and the recruitment process. Other studies have stressed that a strong connection between the inferior lobe and the vagal lobe [Yoshimoto and Yamamoto, 2010], and the size of the inferior lobe in teleost fish was unaffected by social environment [Gonda et al., 2009; Kotrschal et al., 2012].

Next Steps

Future studies should examine adult fish stages to establish whether brain proportions are similar to those of presettlement larvae, which would resolve the question of ontogenetic changes associated with age rather than functional need of larvae (i.e. larval brain adaptations). Indeed, if adult brains are similar to larval brains, then the brain proportions are difficult to ascribe solely to behavior and survival needs in the larval stage, since they may have been selected for adult life. No information is currently available on brain organization in adult-stage coral reef fish. Thus, a fruitful avenue for future research could explore the external form (relative size of telencephalon, mesencephalon, cerebellum, vagal lobe and inferior lobe) and internal structure (cytoarchitecture and fiber connections) of adult coral reef fish brains.

Conclusion

Although detailed and descriptive illustrations of brain morphology from a number of fish species have provided evidence of substantial interspecific variation of component parts [for review, see Kotrschal et al., 1998; Salas et al., 2008], our study is the first one to bring together quantitative information on brain organization and the relative development of major brain subdivisions across coral reef fish larvae, and more specifically, to address the way in which this variation correlates with the recruitment process. We hypothesize that a well-developed cerebellum would allow fish larvae to improve their chance of successful recruitment after a long pelagic phase in the ocean. Nevertheless, additional behavioral and (psycho) physiological studies should be conducted in the future to address the functions of the cerebellum, mesencephalon and telencephalon in coral reef fish larvae.

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