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Predicting the structure of larval fish assemblages by a hierarchical classification of meteorological and water column forcing factors

L. Carassou · D. Ponton · C. Mellin · R. Galzin

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Abstract The first step in building predictive models of larval fish assemblages is to identify the main environmental parameters which influence their spatial and temporal structure. In this study, multivariate regression trees (MRT) were used to classify hierarchically the effects of large-scale meteorological factors and small-scale water column factors on pre-settlement larval fish assemblages at two sites in the lagoon at New Caledonia, southwest Pacific. The environmental conditions at one site were highly variable spatially and temporally, but varied little at the other. In spite of these differences, MRT models revealed that identical forcing factors influenced the structure of larval fish assemblages at both sites, with a similar hierarchy, but a different statistical efficiency. At a large spatial scale, the seasonal variabilities in sun hours and wind (speed and/or direction) explained 14% and 64% of the structure of larval fish assemblages at the sites of high and low variability, respectively. At a small spatial scale, the seasonal variability in mean surface water temperature, followed by the concentration in Chl *a*, explained 22% and 62% of the structure of assemblages at the sites of high and low variability, respectively. The Dufrêne–Legendre index matched characteristic families of larvae to each set of environmental conditions, and illustrated the role of sheltered, Chl *a* enriched, coastal waters in producing a families-rich assemblage of fish larvae, some species of which are targeted by

fishing. This study shows that it may be possible to use environmental data, and predictions computed from MRT to design spatially explicit models of larval fish distribution in coral-reef lagoons.

Keywords Reef fish · Larvae · Environmental parameters · Predictive models · Southwest Pacific · New Caledonia

Introduction

Over recent decades, coral reef ecosystems have undergone widespread changes largely caused by increasing demographic pressure and the exploitation of marine resources, particularly fishes (Hughes et al. 2003). The abundance and diversity of fish species mainly depend on recruitment success, which is characterized by important spatio-temporal variations (Doherty 2002). Understanding these variations in specific locations and under various environmental conditions is thus a crucial challenge in reef fish conservation strategies. The success of recruitment is known to depend upon the survival rate of larvae in the water column and of juveniles in benthic habitats (Leis and McCormick 2002). Moreover, the abundance of newly settled juveniles in a specific location partly depends on the environmental conditions encountered by larvae just before their settlement (Milicich et al. 1992; Hoey and McCormick 2004). Designing models which predict the structure of pre-settlement larval fish assemblages in specific habitats holds much promise, and may contribute to improve the efficiency and sustainability of resources management (Fuiman and Werner 2002).

The selection of predictor variables is crucial in designing an appropriate procedure for model selection (Guisan and Zimmermann 2000). The variables which

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determine the structure of larval fish assemblages at a specific location include environmental factors acting at different spatial scales, and the behavioural responses of larvae to these factors (Boehlert 1996; Doherty 2002; Werner 2002). The major environmental factors known to influence the structure of larval fish assemblages include lunar and tidal cycles (Sponaugle and Cowen 1996; Kingsford and Finn 1997), meteorological conditions (Milicich 1994; Bergenius et al. 2005) such as wind speed and direction (Wilson and Meekan 2001), local currents (Shenker et al. 1993; Milicich and Doherty 1994), water temperature (Meekan et al. 2003; Sponaugle et al. 2006) and the concentration of chlorophyll *a*, or the density of zooplanktonic prey (Meekan et al. 2003, 2006). However, the relative contributions of each of these factors at various spatial scales remain unknown, since in most of the studies mentioned above, only a few environmental variables were examined simultaneously, and the hierarchy of their relative influences on larval fish assemblages was not investigated.

The lagoon at New Caledonia is characterized by a subtropical to temperate climate with a warm and wet period from mid-November to mid-April, and a cool and dry period from mid-May to mid-September (ORSTOM 1981). The lagoon extends over ~19,000 km², with the barrier reef being up to 65 km from the coast. The water in embayments is characterized by significant terrigenous inputs (Tenório et al. 2005), high chlorophyll *a* concentration (Bujan et al. 2000), high phytoplankton biomass (Pinazo et al. 2004) and high zooplankton densities (Champalbert 1993). In contrast, the lagoonal water is mainly under the oligotrophic oceanic water influence (Pinazo et al. 2004).

This wide variation in environmental conditions in the lagoon at New Caledonia provides an ideal opportunity to examine the spatial hierarchy of meteorological and water column factors and their role in the structure of larval assemblages. The ultimate use of these hierarchical classifications is to parameterize spatially explicit predictive models of the structure of larval fish assemblages in different water masses in the lagoon, which will help to identify, and predict, the conditions in which a high abundance of specific larval fish families may be found.

The aim of this study was to assess how different environmental factors contribute to the structure of larval fish assemblages along an inshore-offshore and water quality gradient in the lagoon. The specific objectives were to: (1) hierarchically classify the meteorological and water column factors which contribute to structure pre-settlement larval fish assemblages, at different spatial scales; (2) identify the families of fish larvae which are characteristic of specific meteorological and/or water column conditions; (3) present and discuss the potential application of these results for designing spatially explicit models of the structure of larval fish assemblages.

Material and methods

Study sites and time period

In order to sample a range of the environmental conditions, fish larvae were collected from two sites in the South-West lagoon of New Caledonia that differed in geomorphology and distance from the barrier reef (Fig. 1). The first site, hereafter named “Ouano”, extended from the coast to the barrier reef (Fig. 1a). The second site, hereafter named “Dumbéa”, was the Bay of Dumbéa, ~20 km from the barrier reef. Four stations were sampled at Ouano: station O1 in the sheltered muddy Bay of Chambeyron; station O2 in the sheltered Bay of Ouaraï influenced by the La Foa River; station O3 near a lagoonal islet and station O4 on the inner-reef slope, the latter two sites being more exposed to the prevailing South-East trade-winds. Four stations were also sampled at Dumbéa: stations D1 and D4 in the sheltered part of the bay; stations D2 and D3 more exposed to the prevailing South-East trade-winds (Fig. 1b), all four stations being under the influence of the Dumbéa River.

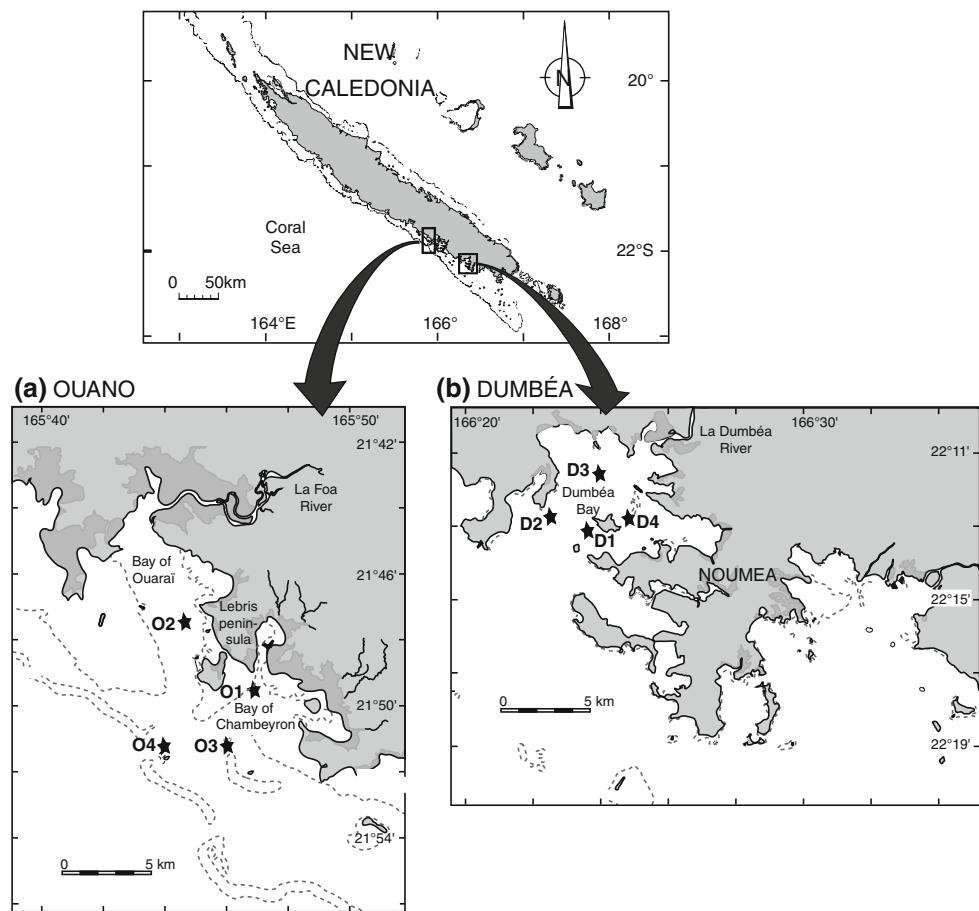
Since the range and variability of environmental conditions were expected to be greater at Ouano than at Dumbéa, the stations at Ouano were sampled four nights per month whereas the stations at Dumbéa were only sampled two nights per month. Sampling occurred between September 2005 and February 2006, during the warm season when fish larvae are most abundant in the lagoon (Carassou and Ponton 2007).

Sampling design

Fish larvae were collected using light-traps (Ecocean Company, Saint-Clément-de-Rivière, France). It is well-known that light-traps selectively attract some taxa (Doherty 1987; Lindquist and Shaw 2005); nonetheless, light-traps have been used extensively to sample fishes at late larval stages in coral reef habitats, since they can be used synoptically to evaluate the spatial patterns in larval fish abundance (Wilson 2001; Sponaugle et al. 2005). Each light-trap consisted of a buoyant water-tight block containing a 6 V battery and a 7 W neon lamp under which a 2 mm mesh size conical net hung vertically. When this net was pulled out of the water, fish were retrieved using a gauze collector (330 µm). The light-traps were placed at the surface just after dusk, and illuminated for 7 h (22:00–05:00 h) each night. All sampling periods were centred on the new moon in order to optimize the efficiency of the light-traps (Wilson 2001). Ouano was always sampled first, followed by Dumbéa on the next two nights. After collection, the fish were anaesthetized in 0.75 g l⁻¹ benzocaine and immediately preserved in 95% alcohol.

Potential prey of fish larvae, represented by micro- and meso-zooplankton (Sampey et al. 2007), were collected at

Fig. 1 Position of the sampling stations (stars) at Ouano and Dumbéa, southwestern New Caledonia. Dark grey zones on the maps indicate the mangroves; dotted lines represent the location of coral reefs



each sampling station when the light-traps were set just after dusk. A plankton-net (60- μm mesh, 1.60-m long and 20 cm diameter) was towed ~ 0.5 m below the water surface by a boat that followed a circular trajectory for 2 min at approximately two knots. A General Oceanic flowmeter provided an estimate of the distance travelled and thus of the filtered volume of water (in m^3) by assuming 100% filtering efficiency. The plankton-net samples were immediately preserved in 10% formaldehyde.

Three water samples were collected at each sampling station with a Niskin bottle, in order to assess the level of trophic enrichment (or eutrophication) by measuring: (1) the concentration of chlorophyll *a* (Chl *a*, $\mu\text{g l}^{-1}$); (2) the relative abundance of pheopigments (pheo, %); (3) the concentration of particulate organic nitrogen (PON, $\mu\text{M l}^{-1}$); (4) the concentration of particulate organic carbon (POC, $\mu\text{M l}^{-1}$) and (5) the carbon/nitrogen ratio (C/N). The water samples were collected at the surface, at mid-depth, and one meter above the bottom. The three samples were then mixed in order to provide a mean value for the water column. Sampling took place at the time the light-traps were recovered at dawn, and the measurements were assumed to correspond to the water in which the larval fish and zooplankton were sampled. The samples were

immediately put in a cooler in which they were kept for a maximum of 2 h at 0°C . Once back on shore, sub-samples varying between 250 and 700 ml were filtered on 25 μm GF/F Whatman filters. The filters were in turn immediately put in a cooler where they were kept at -18°C , and later analyzed following Aminot and K erouel (2004). At each sampling station, the temperature ($^\circ\text{C}$), salinity (psu) and turbidity (FTU) were also recorded from the surface to the bottom using a SBE19 Seabird CTD before and after fish sampling.

Laboratory work

As in the majority of studies focusing on larval fish assemblages ecology (e.g. Sponaugle et al. 2003; Fisher 2004; Sampey et al. 2004; Muhling and Beckley 2007), the fish larvae were sorted by family, since this was the lowest taxonomic level at which all specimens could be identified. Morphological, meristic and pigmentation criteria from Leis and Trnski (1989) and Leis and Carson-Ewart (2000) were used for this purpose. Zooplanktonic organisms were counted under a microscope ($\times 125$) in three sub-samples poured into a 101.8 mm^3 counting cell (ref. n $^\circ$ 9948 Thomas Company, Philadelphia, USA). The density of

zooplankton ($N\ m^{-3}$) was then calculated from the estimated volume of water filtered by the plankton-net. Photographs of the first 30 organisms observed in each subsample (90 organisms per sample) were digitalized using a Scion Corporation digital camera (model CFW-1308 M). For each sample, the mean maximum width with appendages of the zooplanktonic organisms (mm), considered as the critical dimension for the ingestion of prey by fish larvae (Hunter 1984), was then measured using the ImageJ software.

Environmental data

There were two sets of environmental data: one contained meteorological variables that were presumed to influence all the sampling stations at each site, and the other formed the characteristics of the water column at each station. The meteorological data were obtained from the closest Météo-France meteorological stations: La Tontouta for Ouano, and Nouméa for Dumbéa. These data included: daily rainfall ($mm\ d^{-1}$), daily sun hours ($h\ d^{-1}$), corresponding to the number of hours within a day when the sunshine was strong enough to produce a shadow (irradiance $\geq 120\ watts\ m^{-2}$), the daily mean wind speed ($km\ h^{-1}$) and direction ($^{\circ}$) of the maximum wind observed over periods of 10 min. Data for wind direction were converted into the proportion, in number of hours per day, when the wind blew from different sectors (East–North–East, South–South–East, West–South–West and North–North–West) (the sum of the four directions being 24 h). As each sampling period was centred on the new moon, the tide amplitude was low (typically $< 1.5\ m$) and therefore had a minor effect on surface currents compared to the effect of wind (Douillet et al. 2001). As a consequence, the tidal amplitude, or its state at the time of sampling, was not included in the environmental variables. The characteristics of the water column at each station included the mean temperature, salinity and turbidity in the 0–5 m layer obtained from CTD profiles, the five variables used as proxy of trophic enrichment (Chl *a*, pheo, PON, POC, and C/N), and the densities and mean sizes of potential prey.

Data analyses

In order to determine whether there was any temporal lag in the effect of meteorological conditions on the structure of larval fish assemblages, data were analyzed using the values observed on the day of sampling and the means for the four days preceding sampling. This period of 4 days has been shown to correspond to the time it takes for a particular meteorological event, high rainfall or strong wind, to modify water column properties in the lagoon of New Caledonia (Jouon et al. 2006).

The overall structure of the environmental data at each site was first assessed by normed Principal Component Analyses (PCA). For each variable, the differences between sites, sampling periods (months) and sampling stations (water column data only) were examined using non parametric Mann–Whitney and Kruskal–Wallis tests (Scherrer 1984). The differences between days within each sampling period were also assessed using non parametric Kruskal–Wallis tests for water column data (several values per day), or by comparing the within-sampling period and between-sampling period standard deviations (SD) for meteorological data (only one value per day).

Multivariate regression trees (MRT, De’Ath 2002) were then used to classify separately the meteorological and water column variables which contributed to structure the larval fish assemblages. This statistical method has proven efficient for ordering the effects of environmental characteristics on the structure of communities in terrestrial ecosystems (Kallimanis et al. 2007) and marine ecosystems (Claudet et al. 2006), including larval fish assemblages (Sampey et al. 2004; Meekan et al. 2006). This method allows complex ecological data that may include imbalanced and/or missing data, linear relationships between variables and/or high order interactions to be analyzed (De’Ath 2002). MRT rely on very few statistical assumptions, and are very robust to the collinearity of explanatory variables (De’Ath 2002). MRT provide hierarchical clusters of taxa, each cluster, or “leaf”, corresponding to an assemblage associated with the environmental conditions observed at the nodes of the tree (De’Ath 2002). Each tree is characterized by its size, i.e. the number of leaves and nodes, and an overall fit, called the relative error (RE), corresponding to the amount of variation among the samples not described by the tree (De’Ath 2002). The optimal size of a tree is obtained when the cross-validated relative error term (CVRE) reaches a minimum value, i.e. when the variability between leaves is maximized and the variability within leaves is minimized (Breiman et al. 1984). From a statistical point of view, the best tree for a given data set will show the lowest CVRE and RE. However, as in other clustering methods, the level of contribution of a result to the explanation of a given problem does not necessarily reflect its level of statistical performance (Questier et al. 2005). Thus, practically, a compromise has to be found between the statistical performance and the usability of the resulting models (Guisan and Zimmermann 2000). The procedure that was followed to select the best tree was based on three main criteria: (1) statistical scores; (2) parsimony and (3) relevance. The first step was the observation of the RE and CVRE associated with the analysis. The tree providing the minimal RE and CVRE was examined first. Its parsimony was assessed by the number of explanatory variables appearing on the nodes, so that the trees which

were based on a single variable, or in which the same splitting variables appeared several times on different nodes, were excluded (Questier et al. 2005). Relevance was assessed by observing the position of the samples from each leaf on the first factorial plane of a PCA. If the samples from the different leaves were poorly distinguished on this plane, the model was considered as non relevant. The trees associated with increasing RE and CVRE were examined in turn, until the three criteria cited above were satisfied.

As the precision of estimates of larval fish abundances increases with the number of individuals (Pepin and Anderson 1997), only the families that gathered at least 10 fish, i.e. approximately 0.1% of the total number of non-Clupeiformes larvae caught, were included in the analyses. Since a small number of abundant families co-occurred with a high number of rare ones, the abundances were $\log(x + 1)$ transformed prior to any analysis (Legendre and Legendre 1998).

Finally, the Duf re-Legendre index (Duf re and Legendre 1997) was used to identify the families that were characteristic of each leaf, i.e. cluster, of each tree. This index is based on the product of the relative abundance and the relative frequency of occurrence of a family within a cluster. If a family does not occur in a cluster, then its index value is zero, whereas the index is close to one if the family occurs in all the samples of the cluster and does not occur in any other sample (De'Ath 2002). The statistical significance of the index was assessed by using a randomized permutation procedure (Duf re and Legendre 1997).

Mann–Whitney and Kruskal–Wallis tests were performed using Systat version 10.2. PCA, MRT analyses and the calculations of the Duf re and Legendre index were performed using R version 2.2.1 (Ihaka and Gentleman 1996).

Results

Larval fish assemblages

The 88 samples from Ouano and 48 samples from Dumb a resulted in the collection of 21,557 individuals, including 4,326 Engraulidae, 2,965 Clupeidae and 49 unidentified individuals that were all excluded from subsequent analyses. The remaining 14,217 fish larvae belonged to 13 orders and 51 families, among which 23 were represented by at least 10 fish (Table 1). Apogonidae, Pomacentridae, Atherinidae and Lethrinidae were the most abundant at Ouano, whereas Pomacentridae, Lutjanidae, Lethrinidae and Blenniidae were the most abundant at Dumb a.

Table 1 Families of fish larvae (i.e. Clupeiformes excluded) for which at least 10 individuals were caught in the two studied sites (Ouano, $N = 88$ samples, and Dumb a, $N = 48$)

Families	Ouano	Dumb�a	Total
Pomacentridae	479	10,732	11,211
Apogonidae	592	162	754
Lethrinidae	215	286	501
Lutjanidae	17	297	314
Blenniidae	54	248	302
Atherinidae	231	10	241
Carangidae	131	45	176
Siganidae	15	103	118
Syngnathidae	40	25	65
Tripterygiidae	19	40	59
Gobiidae	48	10	58
Plesiopidae	35	0	35
Scorpaenidae	34	0	34
Mullidae	29	5	34
Scaridae	30	0	30
Muraenidae	22	0	22
Nettastomatidae	21	0	21
Haemulidae	8	12	20
Serranidae	19	0	19
Congridae	18	0	18
Labridae	18	0	18
Bothidae	17	0	17
Pseudochromidae	4	6	10

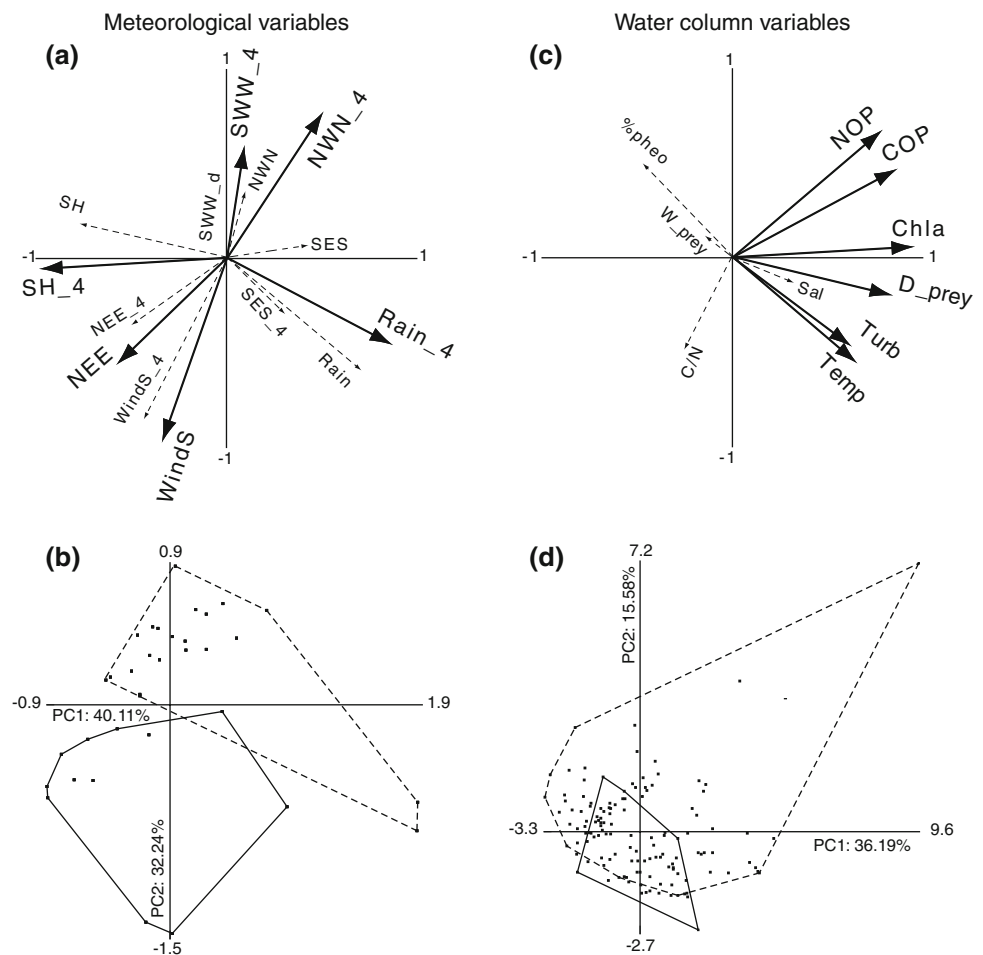
Families are ranked in decreasing order of their total abundance

Temporal and spatial variability in environmental conditions

For each meteorological variable, the within-sampling period standard deviation (SD) was much smaller than the between-sampling period SD. For all the water column variables, except for Chl *a*, POC, PON and prey width at Ouano, and PON and C/N at Dumb a, the differences between sampling periods were significant (Kruskal–Wallis tests, $P < 0.05$). Conversely, within each sampling period, the differences between days were non-significant for 96% of the tests performed. The temporal variability of the meteorological and water column variables was thus driven by monthly variations at each site.

For all the meteorological variables, the values observed on the day of sampling and the values averaged over 4 days before sampling were close (Table 2a), and highly correlated (Fig. 2a). The general meteorological conditions recorded during the study differed between sites, as indicated by the disconnected convex hulls on the first PCA plane (Fig. 2b). More specifically, the mean

Fig. 2 Principal component analyses (PCA) performed on the meteorological (a and b) and water column (c and d) variables. Convex hulls on the 1–2 plane of the PCA indicate the observations for Ouano (dotted lines) and for Dumbéa (black lines). See Table 2 for variables codes



sun hours, rainfall, wind speed and number of hours the wind blew from a given direction differed significantly between sites (Mann-Whitney test, $P < 0.05$). Generally, wind speed was higher at Dumbéa, where the wind blew from the North-East and East more often, while at Ouano the wind was lower and blew more frequently from the South-West and West and the North-West and West (Fig. 2b).

Although all the mean values of the water column characteristics observed at each site were close (Table 2b), their variability was higher at Ouano than at Dumbéa, as indicated by the relative sizes of the convex hulls on the first PCA plane (Fig. 2d). This difference in variability of the water column characteristics was due to the fact that sampling took place in coastal waters alone at Dumbéa, and in both lagoonal and coastal waters at Ouano. As a consequence, except for the C/N ratio and mean width of zooplankton, all the variables differed significantly between sampling stations for each month at Ouano (Kruskal–Wallis tests, $P < 0.05$). In contrast, no significant difference between stations for each month was observed at Dumbéa for any variable (Kruskal–Wallis tests, $P > 0.05$).

MRT with meteorological variables

The MRT performed with the meteorological variables showed better statistical scores for Dumbéa than for Ouano (61–64% as against 13–22% of variation explained, respectively, Table 3). Statistically speaking, the data based on the 4-day averaged values explained the structure of larval fish assemblages better at Ouano, i.e. both RE and CVRE were lower (Table 3). However, the resulting tree was neither parsimonious nor relevant, as only two groups of fish larvae were discriminated by a single splitting variable, i.e. sun hours. At Dumbéa, the measures recorded on the day of sampling appeared to explain the structure of larval fish assemblages a little better (Table 3). As a result, only the MRT based on the measures recorded on the day of sampling were kept for interpretation (Table 3, Fig. 3a, b).

At Ouano, the MRT discriminated four larval fish assemblages based on sun hours and wind direction (Fig. 3a). Sun hours $< 8.0 \text{ h d}^{-1}$ and wind blowing from the South-West to West discriminated larval assemblages characterized by Apogonidae, Lutjanidae and Pomacentridae. Sun hours $\geq 8.0 \text{ h d}^{-1}$, and wind blowing from the

Table 2 Means (\pm SD) of (a) meteorological and (b) water column variables during the sampling periods at Ouano and Dumbéa with corresponding units and codes

Environmental variables	Unit	Code	Ouano	Dumbéa
(a) Meteorological variables				
Sun hours				
day of sampling	h d ⁻¹	SH	7.1 \pm 3.5	7.8 \pm 4.4
4-day average	h d ⁻¹	SH_4	7.1 \pm 2.3	8.7 \pm 2.0
Rainfall				
day of sampling	mm d ⁻¹	Rain	1.1 \pm 3.3	1.9 \pm 3.0
4-day average	mm d ⁻¹	Rain_4	1.3 \pm 3.3	1.1 \pm 1.6
Mean wind speed				
day of sampling	km h ⁻¹	WindS	11.0 \pm 3.0	20.8 \pm 5.5
4-day average	km h ⁻¹	WindS_4	11.4 \pm 2.7	20.9 \pm 3.9
Number of hours on the day of sampling when wind blew from:				
North-East to East	h	NEE	5.5 \pm 3.4	12.8 \pm 8.0
North-West to North	h	NWN	3.2 \pm 2.2	0.3 \pm 0.6
South-East to South	h	SES	11.5 \pm 4.7	8.3 \pm 5.4
South-West to West	h	SWW	3.8 \pm 3.8	2.8 \pm 5.5
Number of hours averaged on four days when wind blew from:				
North-East to East	h	NEE_4	5.9 \pm 1.6	11.7 \pm 4.9
North-West to North	h	NWN_4	3.2 \pm 1.3	0.3 \pm 0.3
South-East to South	h	SES_4	11.9 \pm 2.9	10.3 \pm 3.9
South-West to West	h	SWW_4	3.0 \pm 1.9	1.7 \pm 3.0
(b) Water column variables				
Mean surface temperature (0–5 m)	°C	Temp	24.8 \pm 2.3	25.3 \pm 2.0
Mean surface salinity (0–5 m)		Sal	35.7 \pm 0.6	35.6 \pm 0.6
Mean surface turbidity (0–5 m)	FTU	Turb	1.5 \pm 1.3	2.2 \pm 1.4
Chlorophyll <i>a</i> concentration	μ g l ⁻¹	Chl <i>a</i>	0.5 \pm 0.3	0.6 \pm 0.2
Proportion of Pheophytine	%	%ptheo	31.6 \pm 7.6	28.0 \pm 4.3
Particulate Organic Carbon concentration	μ M l ⁻¹	POC	17.9 \pm 11.8	11.3 \pm 3.2
Particulate Organic Nitrogen concentration	μ M l ⁻¹	PON	2.3 \pm 2.1	1.3 \pm 0.4
Carbon/Nitrogen ratio		C/N	8.7 \pm 2.2	9.0 \pm 1.8
Total density of potential prey $\times 10^4$	nb m ⁻³	D_pre	17.6 \pm 17.0	14.2 \pm 9.7
Mean width of potential prey	mm	W_pre	0.2 \pm 0.1	0.2 \pm 0.0

Values of sun hours, rainfall and mean wind speed are those observed on the day of sampling or values averaged over the 4 days before sampling

South-East discriminated larval assemblages characterized by Blenniidae, Lethrinidae and Syngnathidae. Two other assemblages, for which no characteristic families were identified, corresponded to all the other meteorological conditions.

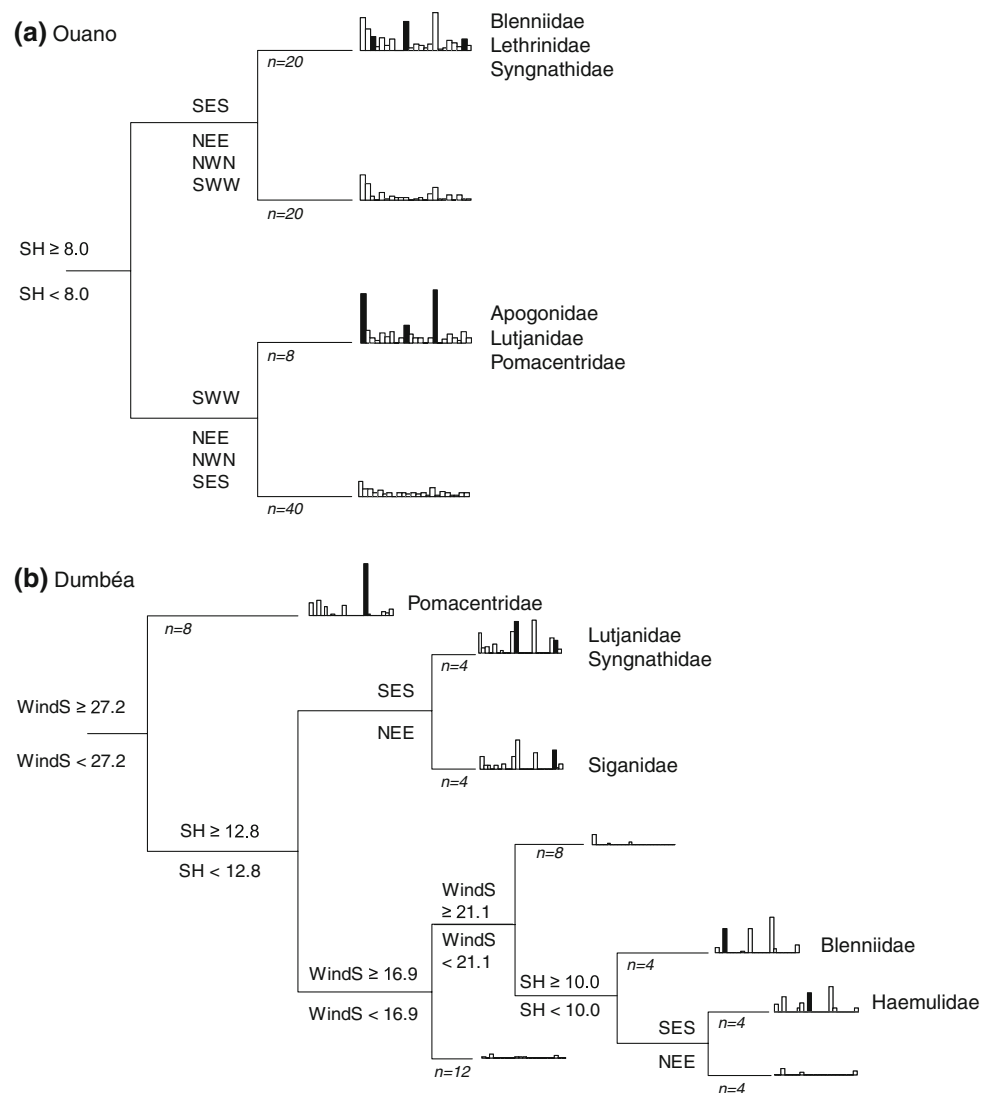
At Dumbéa, the MRT discriminated eight larval fish assemblages based on wind speed, sun hours and wind direction (Fig. 3b). Pomacentridae were characteristic of the assemblages collected when wind speed exceeded 27.1 km h⁻¹. Lutjanidae and Syngnathidae on the one hand, and Siganidae on the other hand, were characteristic of the assemblages sampled when sun hours exceeded 12.8 h d⁻¹ and the wind blew from the South to South-East or from the East to North-East, respectively. Blenniidae were

characteristic of the assemblages collected when sun hours varied between 10.0 and 12.8 h d⁻¹ and wind speed varied between 16.9 and 21.1 km h⁻¹. Finally, Haemulidae were characteristic of the assemblages collected when wind speed was between 16.9 and 21.1 km h⁻¹, when sun hours was <10.0 h d⁻¹, and when the wind blew from the South to the South-East. Three other assemblages, for which no characteristic families were identified, corresponded to all the other meteorological conditions.

MRT with water column variables

The MRT performed with the water column variables showed better statistical scores for Dumbéa than for Ouano

Fig. 3 Graphic representations of multivariate regression trees (MRT) coupling meteorological data (daily values, see Table 2 for abbreviations) and log ($x + 1$) abundances of fish larvae families at Ouano and Dumbéa. Bars represent the abundances of Apogonidae, Atherinidae, Blenniidae, Bothidae, Carangidae, Congridae, Gobiidae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Muraenidae, Nettastomatidae, Plesiopidae, Pomacentridae, Pseudochromidae, Scaridae, Scorpaenidae, Serranidae, Siganidae, Syngnathidae and Tripterygiidae from left to right. Black bars and names correspond to families with significant Dufrene-Legendre index. The n values indicate the number of samples included in each cluster



(62% as against 22% of variation explained by the tree, respectively, Table 3). At Ouano, surface water temperature $\geq 24.1^\circ\text{C}$ and Chl a concentration $< 0.5 \mu\text{g l}^{-1}$ discriminated assemblages that gathered a total of 11 indicator families among which Apogonidae, Atherinidae, Pomacentridae and Syngnathidae presented the highest Dufrene-Legendre index (Fig. 4a). When Chl a concentration reached or exceeded $0.5 \mu\text{g l}^{-1}$, the larval assemblages were characterized by Carangidae, Lethrinidae, Siganidae and Scorpaenidae. When surface water temperature was lower than 24.1°C , no indicator family was identified.

At Dumbéa, the MRT discriminated five larval fish assemblages based on surface water temperature, salinity, and Chl a concentration (Fig. 4b). When surface water temperature was $< 26.9^\circ\text{C}$, salinity ≥ 35.6 and Chl a $< 0.5 \mu\text{g l}^{-1}$, the larval fish assemblages were characterized by Blenniidae, Haemulidae, Lethrinidae, Pomacentridae and Pseudochromidae. When surface water temperature was between 25.1 and 26.9°C , and salinity was < 35.6 , the assemblages

were characterized by Apogonidae, Atherinidae, Lutjanidae, Siganidae and Syngnathidae. The Dufrene-Legendre index for Lutjanidae reached 0.83, indicating that Lutjanidae larvae were abundant in all the samples corresponding to these environmental conditions and nearly absent when the conditions differed. Three other assemblages, for which no characteristic families were identified, corresponded to all the other water column conditions.

Synthesis of MRT analyses

The values of sun hours and surface water temperature vary seasonally in New Caledonia (data not presented here, but see Carassou and Ponton (2007) for an example). Thus, the threshold values detected by MRT analyses with meteorological variables can easily be related to specific months. Similarly, the threshold values detected by MRT analyses with water column variables can be related to sampling stations, i.e. given locations at each site. A tentative synthesis

Table 3 Results of multivariate regression trees (MRT) analyses performed on the meteorological variables (daily value and 4-day average) or the water column and log ($x + 1$) larval abundance for each site

Site	Environmental data set	RE	CVRE	SE	Number of nodes	Number of leaves	Explaining variables
Ouano	Meteorological daily	0.87	1.12	0.12	3	4	SH WindD
	Meteorological 4-day average	0.78	0.99	0.12	4	5	SH_4
	Water column	0.78	0.89	0.10	3	4	Temp Chl <i>a</i>
Dumbéa	Meteorological daily	0.36	0.55	0.07	7	8	WindS SH WindD
	Meteorological 4-day average	0.39	0.54	0.08	5	6	WindS_4 Rain_4 WindD_4 SH_4
	Water column	0.38	0.66	0.14	5	6	Temp Sal Chl <i>a</i>

The relative error (RE), cross-validated relative error (CVRE), standard error (SE), numbers of nodes and leaves and the environmental variables explaining the structure of larval fish assemblages are provided. RE represents the part of the variation among samples not described by the tree. The variables are presented from the first to the last node. See Table 2 for variables abbreviations and Figs. 3 and 4 for graphic representation

of the months, wind regime and location for which different fish families can be observed at the pre-settlement stage in two sites of the lagoon of New Caledonia can be made (Table 4).

The periods of high abundance of Blenniidae, Lethrinidae, Pomacentridae and Syngnathidae determined by sun hours data or by water temperature data largely overlap (Table 4). Blenniidae, Lethrinidae and Syngnathidae appear related to the wind blowing from the South and South-East at both sites, whereas Pomacentridae are associated with the more episodic West wind events (Table 4, Fig. 3). Apogonidae, Atherinidae and Syngnathidae appear associated with lagoon water masses at Ouano and sheltered locations at Dumbéa, indicating that these families can be found in a wide range of Chl *a* concentration and/or salinity. Similarly, Lutjanidae larvae can be observed when the wind is blowing from different directions. Conversely, Siganidae larvae show a consistent affinity for Chl *a* enriched and sheltered coastal water masses at both sites.

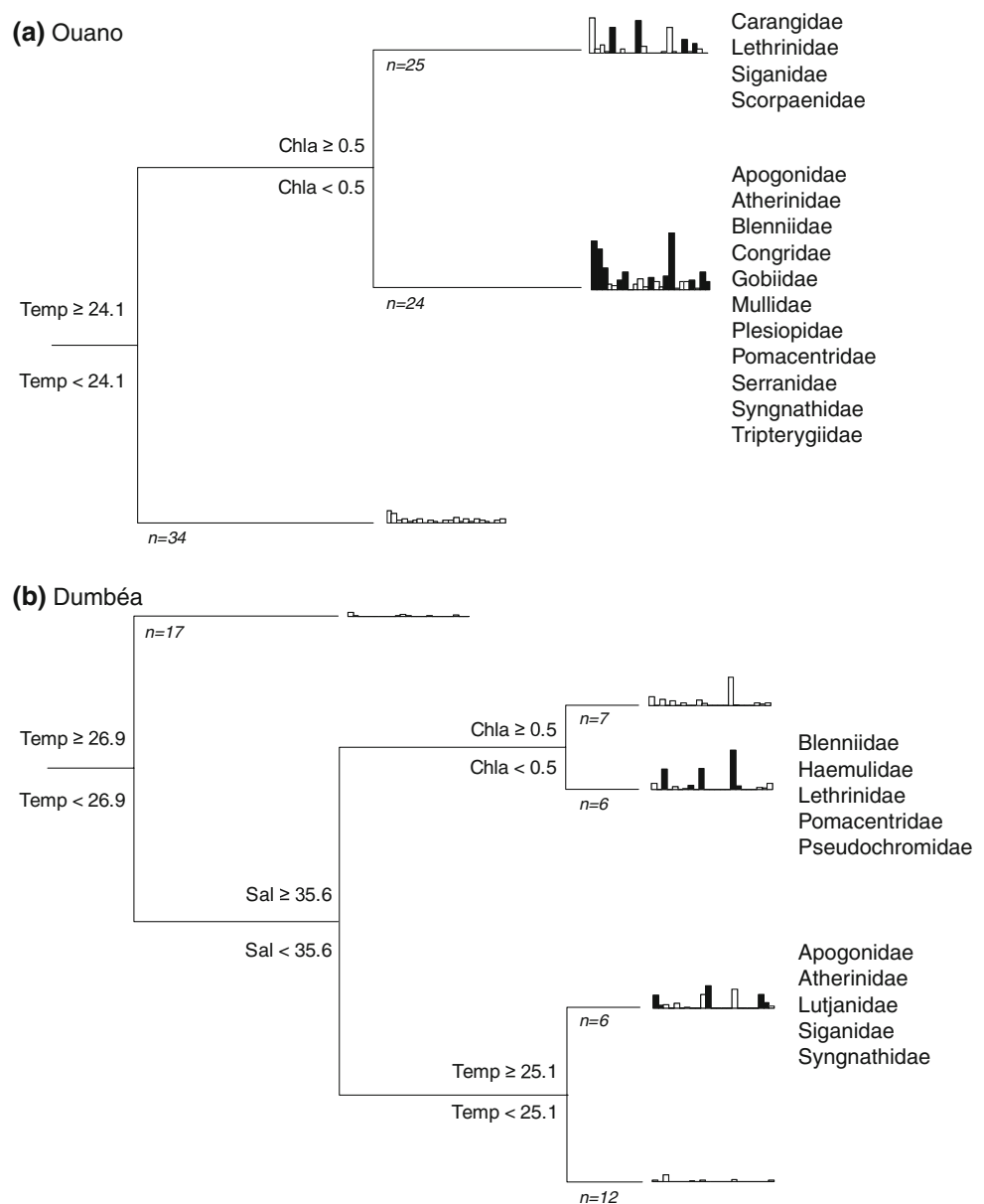
Discussion

This study identified the environmental factors that best explained the structure of larval fish assemblages at two lagoonal sites of New Caledonia by: (1) taking into account the spatial scale at which each of these factors acts on assemblages; (2) providing a hierarchy of their respective influence at each scale and (3) defining, for each factor, a range of

values associated with the occurrence of characteristic larval fish families. Among the 14 variables tested, the meteorological which best explained the structure of assemblages were found to be sun hours, followed by wind conditions (speed and/or direction), and for the water column, water temperature followed by Chl *a* concentration. The hierarchy of these factors was similar at the two sites, although the sites were different in terms of geomorphology and area, and presented different ranges of environmental variability.

Although both the meteorological and water column factors may be considered as good predictors of the structure of larval assemblages in the lagoon of New Caledonia, their predictive power was variable between the two sites. At the embayment site (Dumbéa), both the meteorological and water column variables accounted for over 60% of the variation in the structure of larval fish assemblages. At the coast-to-barrier site (Ouano), the meteorological variables performed less efficiently. This lower performance was probably because the nearest meteorological station was 40 km to the south and therefore, the available data did not reflect the environmental heterogeneity at this site, and only gave an indication of conditions on a broad scale, although wind speed and direction are known to vary locally between the coast and the barrier reef (Jouon et al. 2006) and between different habitats (Milicich 1994). The water column characteristics performed slightly better at Ouano, but the relationship with the larval fish assemblages was still difficult to establish because of a higher spatial and temporal variation in assemblage composition at this site.

Fig. 4 Graphic representations of multivariate regression trees (MRT) coupling water column data (see Table 2 for abbreviations) and $\log(x + 1)$ abundances of fish larvae families at Ouano and Dumbéa. Bars, names and n values as in Fig. 3



This study corroborates the affinities between some families of fish larvae and some environmental factors that have been revealed in previous studies. For example, it is known that in the South-West lagoon of New Caledonia, Siganidae larvae are preferentially found in coastal waters, and Apogonidae larvae are associated with a wide range of water column conditions (Carassou and Ponton 2007). Similarly, wind speed and/or direction has been shown to be an important structuring factor of larval fish assemblages on the Great Barrier Reef (Milicich 1994; Kingsford and Finn 1997), in the Caribbean (Thorrold et al. 1994; Wilson and Meekan 2001) and in the Indian Ocean (Munk et al. 2004).

This study also, however, demonstrates that the influence of some environmental factors (e.g. wind speed and direction) differ depending on the locality and habitat. In

this study, Blenniidae larvae were found to be characteristic of moderate wind speed, but in the Caribbean were found to be positively related to wind speed (Wilson and Meekan 2001), whilst at different sites on the Australian Great Barrier Reef there was considerable variability (Milicich 1994; Kingsford and Finn 1997). This suggests that the effect of the wind on larval assemblages requires a prior understanding of the interaction between wind direction and site geomorphology at different localities.

Sun hours has rarely been mentioned in the literature as a factor that influences the structure of larval fish assemblages. In the present study, larvae of Lutjanidae, Siganidae and Lethrinidae were notably present when sun hours exceeded 12 h per day. In New Caledonia, this value is reached in December, at a time when surface water temperature in the

Table 4 Month, wind regime and location for which fish families can be observed at the pre-settlement stage in the lagoon of New Caledonia

Families	Month						Wind regime			Location	
	S	O	N	D	J	F	SWW	NEE	SES	Ouano	Dumbéa
Apogonidae	s			s	s		x			lagoon	sheltered areas
			t	t	t	t					
Atherinidae			t	t	t	t				lagoon	sheltered areas
Blenniidae	s	s	s	s	s				x	lagoon	–
	t	t	t	t	t	t					
Carangidae			t	t	t	t				bays	–
Congridae			t	t	t	t				lagoon	–
Gobiidae			t	t	t	t				lagoon	
Haemulidae	s								x		
	t	t									
Lethrinidae	s	s	s	s	s				x	bays	–
	t	t	t	t	t	t					
Lutjanidae	s			s	s		x		x	–	sheltered areas
			t								
Mullidae			t	t	t	t				lagoon	–
Plesiopidae			t	t	t	t				lagoon	–
Pomacentridae	s	s	s	s	s		x				
			t	t	t	t				lagoon	–
Pseudochromidae			t	t						–	–
Scorpaenidae			t	t	t	t				bays	–
Serranidae			t	t	t	t				lagoon	–
Siganidae	s			s	s			x		bays	sheltered areas
			t	t	t	t					
Syngnathidae	s	s	s	s	s				x	lagoon	sheltered areas
			t	t	t	t					
Tripterygiidae			t	t	t	t				lagoon	–

Months of occurrence are defined from sun hours (s) or water temperature (t) threshold values determined by MRT. Stations O1 and O2 from Ouano correspond to “bays”; stations O3 and O4 to “lagoon”; stations D1 and D4 from Dumbéa to “sheltered areas”, see Fig. 1 for the location of the sampling stations. With S = September, O = October, N = November, D = December, J = January, and F = February

lagoon reaches the annual maximum (Carassou and Ponton 2007). It is thus difficult to differentiate the influence of sun hours from that of temperature, the latter having been shown to be important for structuring larval fish assemblages in tropical areas (Harris et al. 1999; Wilson and Meekan 2001; Minagawa et al. 2007; this study). As both day length and water temperature are known to affect the reproduction of several coral reef fish species (Robertson 1991), further experimental studies are needed to distinguish the relative importance of water temperature and sun hours. However, for predicting the structure of larval fish assemblages at a given location, water temperature is likely to be a better tool, since remotely sensed and spatially explicit continuous representations of water temperature are now readily available (Ouillon et al. 2005).

In this study, the larval fish assemblages differed depending on the Chl *a* concentration in the water in which they were found. Apogonidae, Atherinidae, Pomacentridae

and Syngnathidae were particularly abundant when Chl *a* concentration was $<0.5 \mu\text{g l}^{-1}$; Carangidae, Lethrinidae, Siganiidae and Scorpaenidae were abundant when Chl *a* concentration reached or exceeded this value. Chl *a* concentrations $<1 \mu\text{g l}^{-1}$ are considered as typical of oligotrophic waters, whereas waters with Chl *a* $>1 \mu\text{g l}^{-1}$ are usually considered as eutrophic (Partensky et al. 1996). The intermediate value of $0.5 \mu\text{g l}^{-1}$ might thus be considered as the dividing line between water masses of different origin along the gradient from oligotrophic oceanic waters and mesotrophic coastal waters (Fichez et al. 2005; Faure et al. 2006). Although Chl *a* has been shown to play a minor role in the northwestern shelf of Australia (Meekan et al. 2006), it seemed to constitute a good predictor of the spatial distribution of larval fish in the lagoon at New Caledonia.

Surprisingly, although the degree of eutrophication in the water column appeared to influence the abundances of some families in this study, the density of their potential

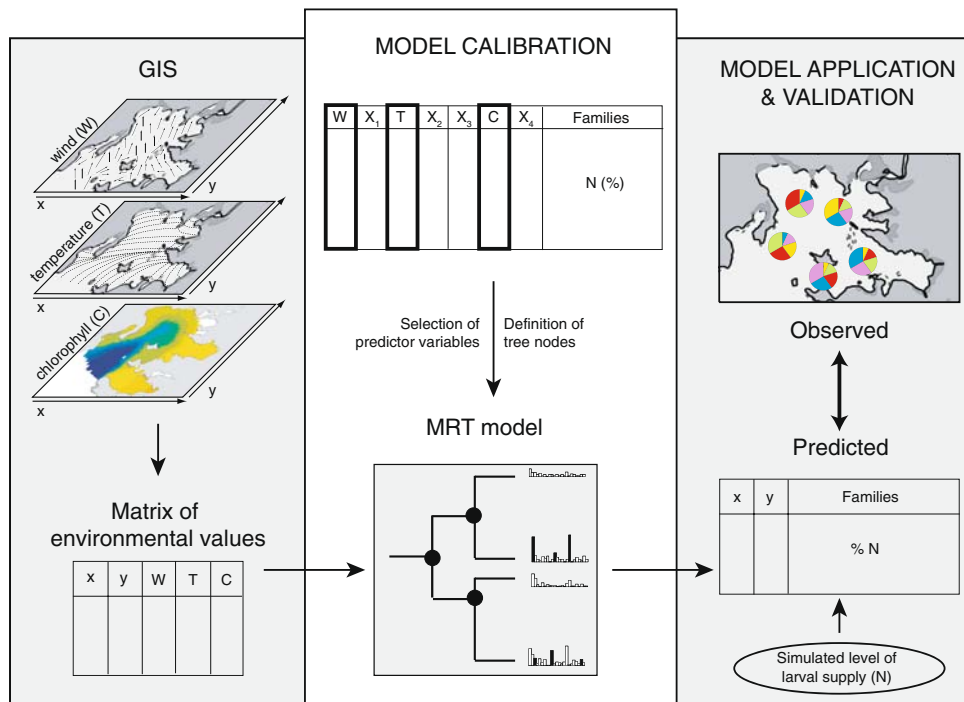


Fig. 5 Methodological steps for spatial modelling of larval fish assemblages based on: (1) a calibration step involving the use of multivariate regression trees (MRT) to select the appropriate environmental predictors (white central panel, this study) and (2) an application and validation step (in grey). Application and validation would involve assigning predictor values to spatial coordinates using a geographic

information system (GIS) (left panel). MRT applied on this independent data set (central panel) would then provide, for a simulated level of larval supply (N), predicted proportions of families (% N) for groups of spatial coordinates (bottom right panel). Finally, predictions of the structure of larval assemblages in various habitats or water masses in the lagoon can be compared with observed values (top right panel)

prey was not detected by MRT as a structuring factor. Sheltered coastal stations are known to present a low water flushing time (Jouon et al. 2006), which is favourable to bacterial and phytoplankton production, and thus to high zooplankton biomass (Torréon et al. 2007). In the present study, the densities of potential prey at the coastal stations (O1 and O2 at Ouano, and D1 and D4 at Dumbéa) were two to three times higher than at the lagoonal stations. The fact that the density of potential prey was not detected as important by MRT may be due to the strong spatial and temporal variability in zooplankton distribution (Omori and Hammer 1982). Nevertheless, a higher zooplankton biomass was observed in the coastal sheltered waters, potentially making these preferential habitats for a large number of fish larvae families, some of which are targeted by fishing activities (Cocheret de la Morinière et al. 2002; Nagelkerken and van der Velde 2004; Islam et al. 2006).

Following on from this study, the next step would be to predict larval assemblages from an independent data set (De'Ath 2002). The MRT obtained in this study represents a calibration step of a spatially explicit model to predict the proportions of different families of larval fish in various habitats, or water masses, in the South-West lagoon of New Caledonia (Fig. 5, central white panel). Using such a predictive approach would involve the integration of the values of

environmental predictors (i.e. wind, water temperature and chlorophyll concentration) into a geographic information system (GIS) (Fig. 5, top left panel), allowing an extensive matrix of environmental values to be built and associated with spatial coordinates in various habitats (Fig. 5, bottom left panel). This matrix could then be used as a new input for the MRT model, to predict the relative abundances of families at each spatial coordinate for a simulated level of global larval supply (Fig. 5, bottom right panel). Predictive maps of the composition of assemblages for various hypothetical levels of larval supply could then be compiled using GIS. Such a procedure would be useful in identifying the abundant families in each type of habitat or water mass. Thus, the next step will be to validate the distribution models obtained in this study at different locations (Fig. 5, top right panel), and for different years (Guisan and Zimmermann 2000), and once the associations between larval fish assemblages and environmental factors have been verified, this technique might then be used more widely to conduct further investigations into the replenishment of fish populations in coral reef lagoons.

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