Presettlement schooling behaviour of a rocky fish in a shallow area. Is it related to local environmental conditions?

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Summary: This study evaluates the swimming behaviour of pre-settled fish larvae of the triplefin *Helcogrammoides chilensis* (Tripterygiidae) in relation to local environmental conditions. Larval aggregations were recorded on rocky reefs off central Chile during the austral summer of 2014 and 2016 to describe their swimming behaviour (i.e. solitary, shoaling, schooling) and relate it to in situ water temperature, wind stress, wind speed and turbulence. Shoaling and solitary behaviour were influenced only by wind-induced turbulence in 2014 and by seawater temperature and wind stress in 2016. Schooling behaviour was not influenced by any of the environmental variables. In situ swimming behaviour of fish larvae has been little investigated, and this work proposes a non-invasive in situ methodology for studying fish larval behaviour.

Keywords: shoaling; reef fish; settlement; seawater temperature; local winds; turbulence.

Comportamiento del cardumen de preasentados de un pez rocoso en aguas someras. ¿Está relacionado con las condiciones ambientales?

Resumen: Este estudio evalúa el comportamiento natatorio de larvas pre-asentadas del trombollito de tres aletas *Helcogrammoides chilensis* (Tripterygiidae) en relación con las condiciones ambientales locales. Para describir su comportamiento natatorio (i.e. solitario, agregación y cardumen) los grupos de larvas fueron grabadas en video en el intermareal rocoso en Chile central, durante el verano austral de 2014 y 2016. Luego, estas conductas fueron relacionadas con la temperatura del agua de mar in situ, estrés y velocidad del viento y turbulencia. Los comportamientos solitarios y agregados fueron afectados solamente por la turbulencia inducida por el viento en el 2014, y por la temperatura del agua de mar y estrés del viento en 2016. El comportamiento de cardumen no fue influido por ninguna variable ambiental. El comportamiento natatorio in situ de larvas de peces ha sido escasamente estudiado, por lo tanto, este trabajo propone una metodología no invasiva in situ para estudiar el comportamiento de las larvas de peces.

Palabras clave: agrupación; peces de arrecife; asentamiento; temperatura agua de mar; vientos locales; turbulencia.

INTRODUCTION

Aggregations are groups of individuals that form a coherent and cohesive whole (Parrish et al. 1997), ranging from two to millions of individuals. Aggregation behaviour occurs in a wide variety of organisms, from unicellular bacteria to whales (Parrish and Edelstein-Keshet 1999), and has been described in at least 50% of all marine and freshwater fish species (López et al. 2012). Two types of aggregations have been described for fish: (1) schools, synchronized and self-organized swimming groups formed by individuals that display coordinated movement patterns; and (2) shoals, passive aggregations of individuals that may not be actively attracted to these aggregations but are grouped because of physical processes (e.g. light or food) or for social reasons (individuals interact within the group). The former has a structure measured in polarity and synchrony, while the latter has no implications of structure or function (Hoare et al. 2000, López et al. 2012, Miller and Gerlai 2012).

Many fish species switch between polarized schools and loosely organized shoals (even competitive aggregations) following a change in the risk of predation (Magurran 1990). Consequently, the stability of fish aggregations can be influenced by ecological factors. However, recent studies have demonstrated that environmental variables (e.g. water quality or physical disturbances) can act as powerful stressors that decrease the fitness of fish aggregations and are expressed as a change in their behaviour. Therefore, environmental conditions may lead to immediate modification of swimming behaviour, i.e. between schooling and shoaling behaviour (Hasler et al. 2009, Miller and Gerlai 2012, Sadoul et al. 2014).

In central Chile, intense upwelling-favourable conditions driven by southwesterly winds are present throughout the year but are more intense during the austral spring and summer (Shaffer et al. 1999, Narváez et al. 2004). At a local scale, central Chile is characterized by a micro-tidal dynamic and wind-induced currents (Aiken et al. 2007). Local winds have a strong seasonal and diurnal signal, the latter marked mostly by the sea breeze during the austral spring and summer, which is described as an afternoon intensification of onshore winds (Narváez et al. 2004).

In the nearshore, temperatures can change abruptly in response to wind forcing, since these variables are strongly and significantly correlated (Narváez et al. 2004). Hence the question arises: can changes in local winds and/or water temperature influence the swimming behaviour of fish larvae prior to settlement? The aim of this study is to describe in situ swimming behaviour of larval aggregations of the triplefin *Helcogrammoides chilensis* (Cancino, 1960) in subtidal rocky reefs of central Chile and to evaluate whether local environmental conditions may alter their behaviour. We postulate that events of intense local wind may disrupt schooling behaviour into a more dispersed and lose shoal, while in calm conditions aggregation of organisms will be favoured.

MATERIALS AND METHODS

Model species

Triplefins (family Tripterygiidae), particularly *Helcogrammoides chilensis*, are small-bodied, cryptobenthic fish characterized by a bipartite life cycle. They spawn benthic eggs and show parental care up until a planktonic larva with pigmented eyes, small yolk sacs and open mouth hatches (Ruck 1973, 1980). Their pelagic larval duration is approximately 2 to 4 months (Mansur et al. 2014), after which they settle as juveniles in the rocky exposed shores (McDermontt and Shima 2006).

Helcogrammoides chilensis inhabits the coast of Chile from 20°18′S to 36°45′S in the southern Pacific, in shallow waters near the coast (Williams and Springer 2001, Cancino et al. 2010). It has carnivorous habits, with a diet mostly composed of copepods and amphipods (Muñoz and Ojeda 1998). Its pelagic larval stages are found throughout the year in nearshore waters (Hernández-Miranda et al. 2003, Landaeta et al. 2009, 2015), with maximum abundances between October and April (Palacios-Fuentes et al. 2014). *H. chilensis* larvae have a long pelagic larval duration (78-113 days; Mansur et al. 2014) given their slow growth rates (~0.15 mm day^{-1}; Palacios-Fuentes et al. 2014).

H. chilensis can be considered a model species due to its life history traits, which are similar to those of other cryptobenthic species that inhabit rocky or reef shores in temperate waters (e.g. benthic eggs, parental care, carnivorous, pelagic larvae and slow growth) (Caie and Shima 2019). Recently, Tripterygiids have been considered part of a group of cryptobenthic reef fishes (species shorter than 5 cm in length) which fuel reef trophodynamics, owing to their unique larval dynamics (high abundance, rapid growth and extreme mortality) (Brandl et al. 2019).

Study area

The subtidal rocky reefs of the semi-protected area of Montemar, Valparaíso Bay, central Chile (32°57′S, 77°33′W) (Fig. 1A), are characterized by their shallow depth (~1 m during neap tide, ~3 m during spring tides) and moderate swell. These reefs are subject to seasonal and diurnal oceanographic changes generated by events such as coastal storms that occur in winter, sea breeze in summer and daily tidal variation. The region is dominated by a semidiurnal tidal regime that explains 98% of the sea level variability (Díaz-Astudillo et al. 2017). Sea level in the very nearshore is dominated by both tides and surge waves, but there is no information about sea level variability in intertidal or subtidal pools of central Chile. The seafloor is mostly lithic, composed of coarse sand and eroded shells. These reefs are the habitat of small and medium-size cryptobenthic fish species (Stepien 1990), housing large abundances of *H. chilensis* which settle preferentially on lithic substratum (Pérez-Matus et al. 2016).
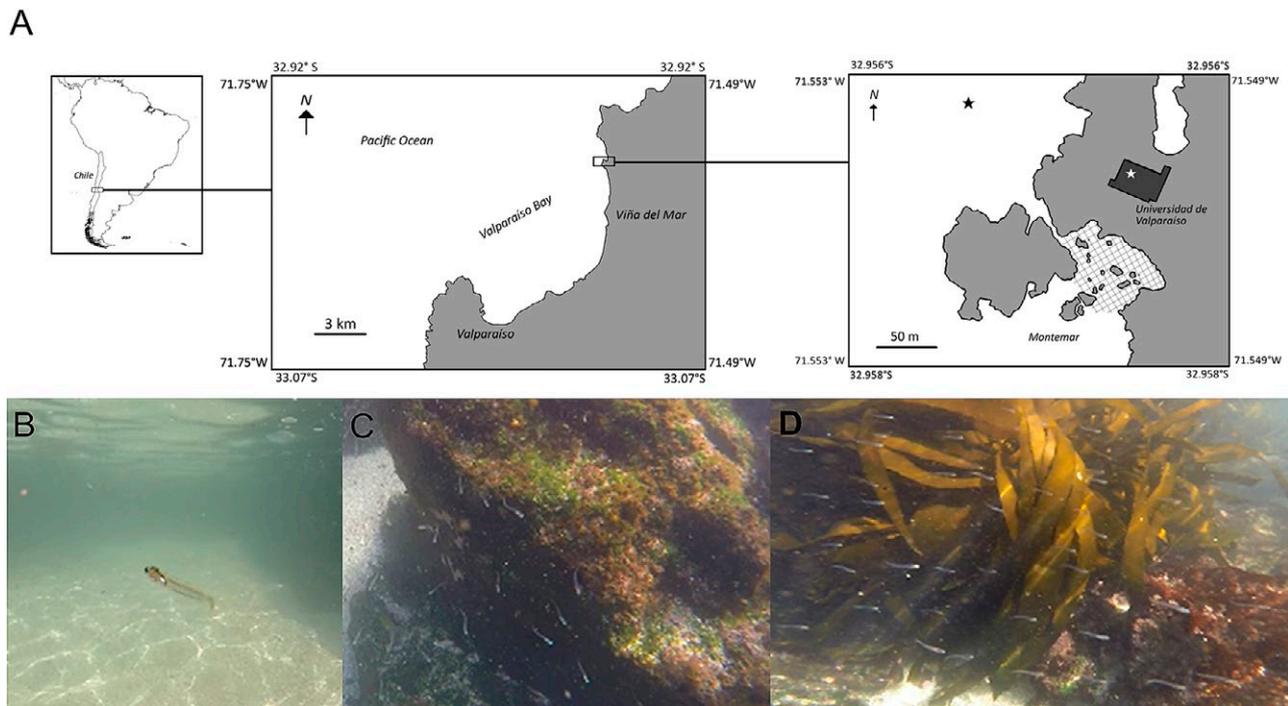
Fig. 1. – Studied sampling location and types of behaviour of larval triplefin *Helcogrammoides chilensis*. A, the shaded area represents the analysed subtidal pool in Montemar. The black star represents the temperature logger mooring and the white star the meteorological station. B, solitary individuals were considered solitary behaviour; C, loose and directionless movements were defined as shoaling behaviour; and D, dense and coordinated aggregations were described as schooling behaviour.

Field work

During the late austral summer and early autumn, larval fish aggregations from intertidal rocky reefs nearby Montemar (Fig. 1A) were video-recorded (1080 p resolution) with a GoPro Hero3+ Black Edition camera (2014, 32 recordings from 19 February to 16 April) and a GoPro Hero4+ Silver Edition camera (2016, 29 recordings from 3 January to 15 March). The larvae were recorded by three observers (PPF, MFL, MAR) each day between 10:00 and 14:00 h, a similar time frame to that used in previous studies (e.g. Leis et al. 2014) and suitable considering our study's aim to determine inter-daily behavioural responses.

Larval fish aggregations were recorded as long as they could be followed underwater and at an appropriate distance to avoid major disturbances in fish behaviour (~20 cm). In situ observations of *Helcogrammoides* larvae, juveniles and adults show that the presence of the diver does not generate significant differences in fish pool abundances (Javier Polanco, pers. comm.). Recordings were not available for weekends or days of extremely high tides or dangerous surges (2014: 3 days; 2016: 6 days).

Haphazard individuals were captured periodically with hand nets (10×13 cm, 2 mm mesh opening), then sacrificed in 1 mL of benzocaine BZ-20 (20 mg per 100 mL) dissolved in 1 L of seawater and immediately preserved in 96% ethanol. Then individuals were observed and photographed with a camera Moticam 2500 (5 Mpx) attached to an Olympus ZS-61 stereomicroscope (Olympus Corporation, Shinjukuku, Tokyo, Japan), and later identified as the triplefin

Helcogrammoides chilensis (Cancino, 1960) according to Pérez (1979).

Video analyses

The length of each video segment in which larvae appeared was determined to estimate sampling effort in seconds (s). Each video was examined to count the number of fish larvae in the aggregations per frame every 10 s (higher frequency than proposed by Hoare et al. 2004 to obtain a finer temporal scale). The final abundance was considered as the maximum observed value. A second revision was conducted to establish the time (in seconds) that the aggregations of fish larvae spent in schooling (i.e. when individuals were grouped, swimming polarized and coordinated in the same direction), shoaling (i.e. when individuals were grouped and stayed together as a whole, but with each larva swimming in its own direction), or solitary behaviour (i.e. when a single larva was found per frame) (Fig. 1B-D). This time was then standardized using the sampling effort (s) to obtain comparable measurements. If there was more than one video segment containing larvae per day, the information was pooled together so that each day contained only one data value. Days without larval aggregations were not considered for further analysis.

Meteorological and oceanographic data acquisition

Wind speed and direction were measured every 5 minutes from 6 January to 20 April 2014 and from 3 January to 15 March 2016 with a Davis Vantage Pro2

meteorological station installed ~20 m away from the subtidal pool of the study (Fig. 1). Wind speeds under 1 m s^{-1} were assigned by the station as "calm winds". To estimate the along-shore and cross-shore wind stress (τ), the wind vector was separated into its orthogonal components u (east-west) and v (north-south). A constant drag coefficient (C_D) of 1.3 10^{-3} and a constant air density (ρ_A) of 1.2 kg m^{-3} were used, following Shaffer et al. (1997). The kinetic energy dissipation rate (ε, W m^{-3}) was derived from wind speed as a proxy of wind-induced turbulence following the model developed by MacKenzie and Leggett (1993), using Z=2 m (mean water depth of the aggregations), C_D=1.3 10^{-3}, ρ_A=1.2 kg m^{-3}, a seawater density of ρ_w=1025 kg m^{-3} and a von Karmann constant of 0.4. Wind stress components and wind-induced turbulence were then plotted through time to detect any temporal patterns that may influence the behaviour of larval fish.

In 2014 water temperature (°C) was measured directly from the intertidal pools during each sampling day using a Hanna HI9828 multiparameter probe. In 2016 a HOBO data logger anchored 50 m away from the pool was used to determine the water temperature at 3 m depth during the sampling period (Fig. 1A).

Statistical analyses

To explore relations between the observed behaviours and environmental variability, a principal component analysis (PCA, using correlation matrix) was performed using a biological matrix containing the proportion of time spent in each behaviour per date and an environmental matrix with four explanatory variables: water temperature, u- and v- wind stress and wind-induced turbulence. Spearman correlations were performed between larval behaviour proportions and the four environmental variables. Prior to analysis, proportional data were transformed using an arcsine function. Differences in environmental variables between each year were evaluated using Mann-Whitney U tests. Statistical analyses were performed using the Past 4.0 software (Hammer et al. 2001).

RESULTS

Larval fish aggregations

In 2014, larval fish observations varied between 1 and 148 individuals (mean 37.82±41.09) (Fig. 2A), with two main peaks of +60 individuals, the first on 28 February and the second during the first fortnight of April. In 2016, abundances ranged between 1 and 70 individuals (28.52±15.69) (Fig. 2B), with only one peak which started in mid-January and lasted until early February. Larval abundances were more variable in 2014 than in 2016 (Levene test, F=1.63, P<0.01).

All types of behaviour were observed. In 2014 (Fig. 2C), schooling behaviour was dominant from 19 February to 11 March, later changing into a solitary condition until 26 March, followed by predominate shoaling behaviour until 16 April. In contrast, in 2016 (Fig. 2D) a dominant schooling period was observed between 5 January and 10 February, later shifting into solitary behaviour until 9 March.
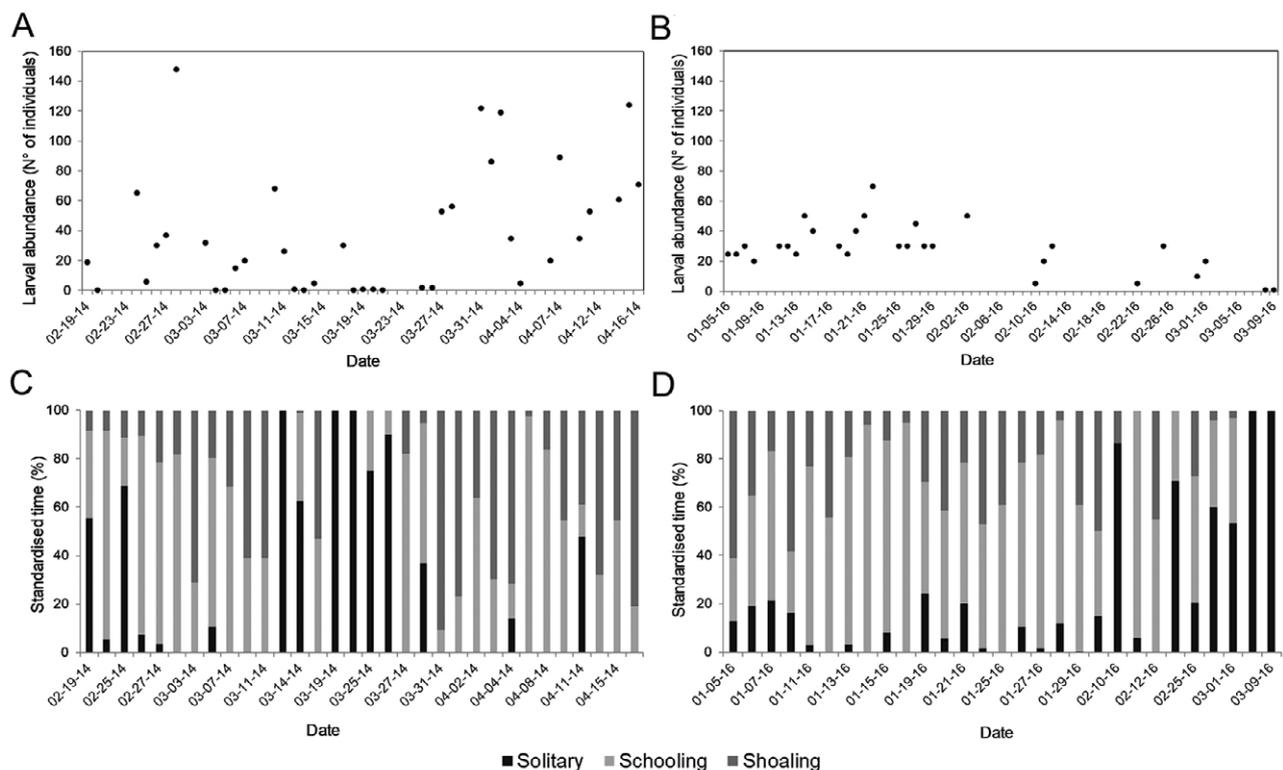

Fig. 2. – Larval fish aggregations abundance during the study period in 2014 (A) and 2016 (B). The standardised time that larval fish aggregations spent in solitary, schooling and shoaling behaviour for each sampling date in 2014 (C) and 2016 (D).
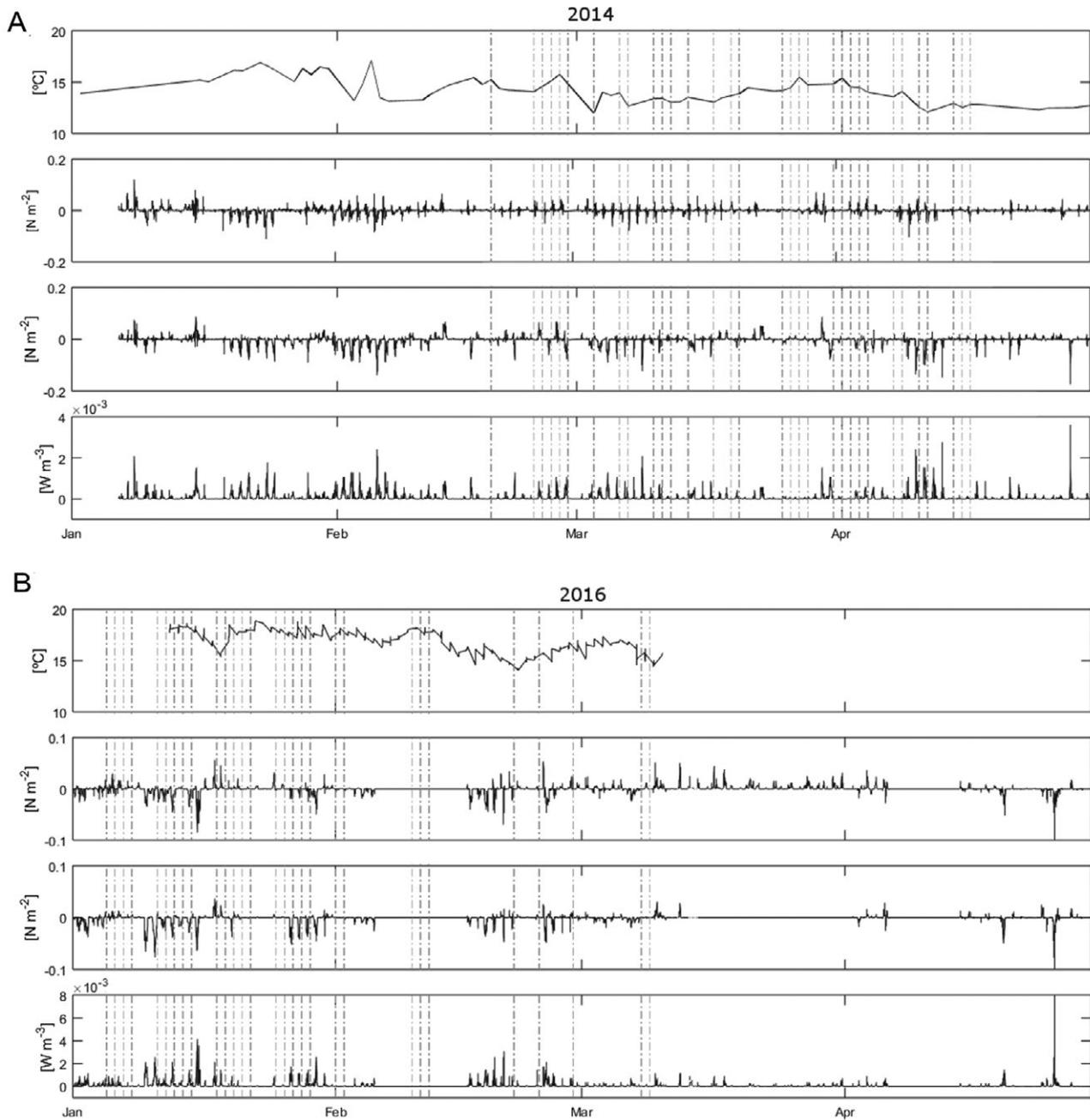
Fig. 3. – Water temperature (°C), v- and u-wind stress (N m^{-2}, N-S and E-W components, respectively) and turbulent dissipation rate (W m^{-3}) for 2014 (A) and 2016 (B). The vertical dashed lines represent the diving and recording dates.

In both years, the majority of individuals observed in solitary behaviour were large (~3.7 cm) and had highly pigmented bodies, corresponding to juveniles of *H. chilensis*.

Environmental conditions

In 2014 water temperatures decreased gradually over the course of the study period, fluctuating between a maximum of 17.12°C on 5 February and a minimum of 11.98°C on 3 March (mean 14.23±1.26°C) (Fig. 3A). Strong fluctuations of about 4°C over periods of less than three days during the first week of February, the first days of March and the

second week of April can be associated with strong southwesterly wind events (Fig. 3A). Wind stress in the v component (maximum v-stress of 0.08 N m^{-2}, minimum of –0.11 N m^{-2}) showed lower variation than the u component (maximum u-stress of 0.02 N m^{-2}, minimum of –0.17 N m^{-2}), illustrating the high variability of cross-shelf winds and the lower kinetic energy of meridional winds. Westerly winds were more intense than easterly winds during summer. Turbulent dissipation rates showed a similar pattern to wind stress, fluctuating between 0 and 0.004 W m^{-3} (mean of 7.9 10^{-5}±0.0002 W m^{-3}), with high turbulence events during the first week of February and the second week of April.

Table 1. – Principal component analysis for both study periods, displaying the main contributors (in bold) to the variability of each axis.

		PC 1 (26.68%)	PC 2 (22.61%)	PC 3 (16.29%)	PC 4 (13.31%)	PC 5 (10.72%)	PC 6 (10.01%)	PC 7 (0.38%)
2014	u–stress	**0.357**	0.076	0.279	**0.689**	–0.191	**–0.526**	–0.032
	v–stress	–0.063	0.098	**0.802**	0.129	–0.014	**0.572**	–0.013
	turb	**0.322**	0.210	–0.418	0.480	**0.455**	0.489	0.034
	temp3	0.100	**0.489**	0.270	–0.309	**0.670**	–0.365	–0.001
	Sol	**0.641**	–0.290	**0.105**	**–0.282**	–0.028	0.050	0.641
	Sch	–0.214	**0.697**	**–0.128**	0.027	**–0.394**	0.033	0.543
	Sh	**–0.546**	–0.362	0.067	**0.320**	**0.389**	**–0.143**	0.540

		PC 1 (38.44%)	PC 2 (28.61%)	PC 3 (16.4%)	PC 4 (11.54%)	PC 5 (4.24%)	PC 6 (0.5%)	PC 7 (0.27%)
2016	u–stress	**0.475**	**0.371**	**0.156**	–0.278	0.220	**0.407**	**–0.567**
	v–stress	**0.455**	**0.397**	0.134	–0.342	0.057	–0.388	**0.589**
	turb	0.267	0.260	0.137	**0.888**	0.223	–0.041	0.054
	temp3	**–0.510**	0.208	0.034	–0.125	**0.821**	–0.050	0.061
	Sol	**0.344**	**–0.559**	–0.069	–0.019	0.355	**0.513**	**0.418**
	Sch	–0.181	**0.517**	–0.554	**0.045**	–0.205	**0.510**	0.299
	Sh	–0.292	0.119	**0.791**	–0.006	–0.239	0.396	0.246

In 2016 water temperatures fluctuated between a minimum of 14°C on 22 February and a maximum of 18.9°C on 22 January, with a mean of 16.8±1.17°C. A gradual decrease of the temperature was observed, given that higher temperatures were observed during late January and lower ones in mid-March (Fig. 3B). Winds were predominantly from the southwest and highly variable in intensity, with temporary windows of up to 8 days of calm winds (<1 m s⁻¹) between events of intense winds. Similar values of wind stress were observed in both components, varying between –0.13 N m⁻² and 0.04 N m⁻² in the east-west component and between –0.13 N m⁻² and 0.06 N m⁻² in the north-south component (Fig. 3B). Two particularly strong southwest wind events were observed in mid-January and late February, causing abrupt decreases in water temperatures. Turbulent dissipation rates were generally low, except during windows of strong winds in mid-January, late February and late April. They varied between 0 and 0.008 W m⁻³, with a mean of 7.5 10⁻⁵±0.0002 W m⁻³.

Water temperatures were significantly higher in 2016 than in 2014 (Mann-Whitney U=26, P<0.001), while no differences were found in u-wind stress (Mann-Whitney U=353, P=0.322) and v-wind stress (Mann-Whitney U=326, P=0.161) between the years. Nonetheless, wind-induced turbulence was significantly higher in 2014 (Mann-Whitney U=247.5, P=0.004).
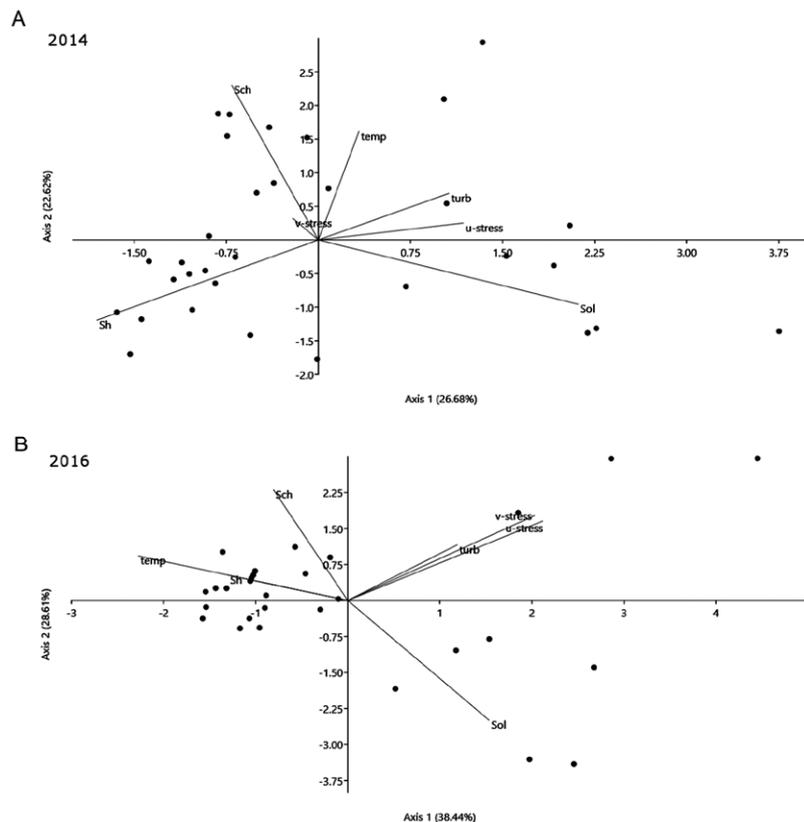

Fig. 4. – Principal component analysis (PCA) for 2014 (A) and 2016 (B), including larval behaviour (sol, solitary; sch, schooling; sh, shoaling) and environmental variables (temp, water temperature; turb, turbulent dissipation rate; u-stress, zonal wind stress; v-stress, meridional wind stress).

Table 2. – Spearman correlation values between larval behaviour (solitary, schooling and shoaling) and environmental factors (seawater temperature at 3 m deep, wind stress and wind-induced turbulence) for 2014 and 2016. Significant values are in bold.

		v-stress	u-stress	turb	temp3	Sol	Sch	Sh
2014	v-stress		0.099	0.532	0.786	0.663	0.748	0.623
	u-stress	0.297		0.063	0.868	0.720	0.700	0.852
	turb	–0.115	0.333		0.613	**0.010**	0.901	**0.011**
	temp3	–0.052	–0.032	0.096		0.577	0.209	0.277
	Sol	0.080	0.066	0.447	0.106		0.006	0.060
	Sch	–0.059	0.071	–0.022	0.236	–0.478		0.737
	Sh	0.090	–0.034	–0.446	–0.205	–0.706	–0.062	
		u–stress	v–stress	turb	temp3	Sol	Sch	Sh
2016	u-stress		0	0.077	0.009	0.040	0.584	**0.020**
	v-stress	0.835		0.007	0.019	0.105	0.997	**0.037**
	turb	0.353	0.516		0	0.155	0.355	0.412
	temp3	–0.553	–0.507	–0.756		**0.011**	0.068	**0.035**
	Sol	0.405	0.326	0.271	–0.512		0	0.027
	Sch	–0.113	–0.001	–0.178	0.378	–0.699		0.465
	Sh	–0.452	–0.412	–0.158	0.431	–0.411	–0.141	

Biophysical interactions

The PCA for 2014 explained 65.6% of the variability in the first three axes (Fig. 4A), with the first accounting for 26.7% of the variance, which mainly showed a positive (negative) correlation between u-wind stress and wind-induced turbulence with solitary (shoaling) behaviour. The second axis (22.6% of the variance) illustrated a positive relationship between the water temperature and schooling behaviour, while the third axis explained 16.3% of the variance and showed a positive (negative) correlation between v-wind stress and solitary (schooling) behaviour (Table 1). In 2016, the first three axes of the PCA explained 83.5% of the variability (Fig. 4B). Axis 1 (38.4%) showed a positive correlation between wind stress (in both components) and wind-induced turbulence with solitary behaviour, and a negative correlation between water temperatures and solitary individuals. Axis 2 (28.6%) showed a positive (negative) relation between u- and v-wind stress and schooling (solitary) behaviour. Axis 3 (16.4%) showed a positive correlation between u-wind stress and shoaling behaviour (Table 1).

The Spearman correlations showed that in 2014 wind-induced turbulence showed a significant correlation with solitary (positive correlation, $\rho=0.45$, $P<0.05$) and shoaling (negative correlation, $\rho=–0.44$, $P<0.01$) behaviour, meaning that when turbulence was high the proportion of solitary fish increased while aggregations in the form of shoals decreased. In 2016 water temperatures were correlated negatively with solitary behaviour ($\rho=–0.51$, $P<0.05$) and positively with shoaling behaviour ($\rho=0.43$, $P<0.05$). Shoaling was also correlated negatively with wind stress in both the u- ($\rho=–0.45$, $P<0.05$) and v- ($\rho=–0.41$, $P<0.05$) components. (Table 2).

DISCUSSION

Social aggregations are mainly studied as ecological responses to food stimuli or reproduction tactics (López et al. 2012, Maury 2017). Hence, behaviour patterns associated with physical forcing have been scarcely explored. This is the first attempt to study larval fish aggregation behaviour in Chilean waters, and one of the few that relate larval aggregations with environmental conditions using in situ observations. Most of the previous fish swimming behaviour studies have been performed with adult individuals of demersal and pelagic fish under controlled conditions (Leis 2010, López et al. 2012, Santana-Garcon et al. 2014, and references therein), which may not completely reflect the behaviours that would be observed in natural conditions (López et al. 2012). Therefore, in situ studies associated with physical forcing can provide significant information to support experiment- and model-based assumptions about fish behaviour. In this study, only a fraction of collective behaviour (i.e. shoaling and solitary) was influenced by environmental variables.

Schooling behaviour, which requires a complex level of interaction among individuals and energy resources to swim together in a synchronized and self-organized manner (Miller and Gerlai 2012), did not respond to the environmental variables selected for this study. Schooling is a density-dependent regulation in marine metapopulations that is adopted when the benefits of increased survival outweigh the costs of increased competition among individuals (López et al. 2012), fulfilling an important ecological function and response of auto-organized groups (Maury 2017). Thus, it is possible that the environmental conditions found during the study period were not sufficiently stressful to induce the schooling behaviour.

However, shoaling and solitary behaviour showed a different interaction with local meteorological and oceanographic conditions. Long-term time-series of water temperature data have proven that Montemar, along with the rest of the central Chilean coast, is directly influenced by mesoscale upwelling (Aravena et al. 2014), resulting in the entrance of colder water into nearshore areas. This probably occurred in 2014, when higher wind-induced turbulence and a cooler water column were observed than in 2016, although no differences were found in local wind stress. Additionally, the austral summer of 2016 was influenced by a positive ENSO phase, which warmed up the nearshore waters of central Chile, reducing the intensity of coastal winds (Díaz-Astudillo et al. 2019).

During the austral summer of 2014, higher wind-induced turbulence was observed along with an increase in the frequency of solitary individuals and a reduction in shoaling aggregations. Accordingly, a peak of solitary individuals (possible presettled specimens due to their size and intense pigmentation) was observed during the second and third week of March (i.e. early autumn), coinciding with the lowest larval abundances, decreasing water temperatures and moderate to high turbulence. Studies of fish larvae swimming speeds have shown that they increase with ontogeny (Leis 2006), meaning that bigger larvae have better swimming abilities. Therefore, it is expected that older and bigger (solitary) individuals will be found during periods of high turbulence, as was observed in 2014. Wellenreuther and Clements (2008) described that active processes (i.e. behaviour) can highly affect settlement, in which larval conduct plays an important role in determining the settlement location. Therefore, presettled triplefin larvae, which show better swimming skills, are expected to have a greater impact on settlement and the ecological processes of this species. A similar scenario was observed in 2016, when a peak in solitary individuals between mid-February and the first days of March (i.e. late summer), coincided with a high turbulence event, decreasing temperatures and lower larval abundances. However, these relationships were not significant, probably due to the lower magnitude of wind-induced turbulence. Some triplefin species from temperate waters around New Zealand have their maximum recruitment during the late austral summer and autumn (i.e. between February and April) (Wellenreuther and Clements 2008), suggesting that solitary behaviour in triplefins may occur prior to settlement on rocky reefs. Accordingly, the pre-settlement larvae of *H. chilensis* showed solitary behaviour before settlement, coinciding with the transition between the austral summer and autumn, along with a decrease in seawater temperatures.

When studying the in situ swimming behaviour of temperate fish, Hindell et al. (2003) found that the movement of postlarvae was a result of both swimming and local currents. Though coastal currents were not assessed in this study because of the lack of subtidal circulation data, evidence shows that mesoscale circulation in Valparaíso Bay is driven by regional winds (Aiken 2008), suggesting that coastal currents in the subtidal rocky reefs of Montemar are probably controlled by local winds. In this study, shoaling behaviour was inversely related to wind-induced turbulence in 2014 and to wind stress in 2016. A possible reason for this is that higher winds might suppress fish shoals by generating currents that 1) are strong enough to transport fish outside the reefs, or 2) encourage fish to hide in rock cracks as a form of protective conduct. In either case the proportion of shoals would diminish, but further in situ observations are needed to clarify the underlying mechanism, which should incorporate local currents and sea level as additional environmental variables. By contrast, in periods of weaker or calm winds, shoaling was the prevailing behaviour.

In a broader context, given the correlation found between environmental variables and some aggregated behaviours, what would the implications regarding future survival or recruitment be? Early life experiences of fish can shape an individual's fitness (Caie and Shima 2019), a concept known as the carry-over effect (Pechenik 2006). Juvenile survival and metapopulation connectivity can be moderated by larval growth rates (*Paralabrax clathratus*, Shima and Findlay 2002) and larval quality (*Forsterygion lapillum*, Shima and Swearer 2009), respectively, both of which can be influenced by biotic factors and environmental conditions. Hence, the changes in the environmental conditions observed in our study were perceived by larvae (shown by a correlated change in their behaviour) and are expected to have an effect on how many individuals can settle in the rocky intertidal zone and/or on post-settlement survival.

Nevertheless, in situ studies, like this one, still have some limitations. Firstly, it is challenging and expensive to increase the sampling period, which forces us to limit the study objective to a certain time of the day and/or of the year. Future studies should strive to increase diving hours to address diurnal (Leis et al. 2014) and annual variability in fish larval behaviour. This also implies more time to analyse videos and data. Secondly, the very nature of the data limits the variety and power of the statistical analysis that can be performed. Either way, any future attempts to carry out in situ behavioural studies will have to improve the methodological logistics and explore, or develop, statistical methods which better suit the data, possibly leading to more generalized conclusions. Although the data presented in this study about the influence of wind-induced turbulence on fish schools will set a basis for studying the future of rocky reef fishes, especially taking into account the recent increase in extreme coastal storms, which erode the coasts of central Chile (Martínez et al. 2018). Also, in future studies, this oceanographic influence on fish larval behaviour ought to unveil its impact beyond the pelagic larval stage, as well as its carry-over effects on fitness and the dynamics of juvenile and adult populations.

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