



Unexpected effects of coastal storms on trophic ecology of two rocky reef fish species

Javier Polanco-Pérez^{1,2} · Francesca V. Search³ · Patricio Winckler^{2,4,5} · María José Ochoa-Muñoz⁶ · Mauricio F. Landaeta^{1,2}

Received: 30 October 2020 / Accepted: 9 January 2021 / Published online: 25 January 2021
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Abstract

Coastal storm risks have been increasing over the last couple of decades, affecting both marine infrastructure and human security. Nevertheless, the ecological impact on intertidal marine fishes has not been addressed yet. We carried out a field experiment during austral summer 2018, using statistical wave parameters, characterizing coastal storms as a factor, and the gut content of two sympatric intertidal triplefins, *Helcogrammoides chilensis* and *Helcogrammoides cunninghami*, as a proxy for trophic interactions. Three locations were sampled before and after the arrival of three consecutive summer coastal storm events. From all gut contents, a total of 16,597 prey items were found. Both species are micro-carnivorous, preying mostly on harpacticoid copepods, amphipods and chironomid larvae, without significant differences in prey composition with the passing of the summer coastal storms. However, after coastal storms, heavier-at-length fish (0.05–0.5 g weight gain) were found in the intertidal. Indeed, after the impact of the coastal storms, *H. chilensis* increased their ingestion of larger prey (amphipods, chironomid larvae), while *H. cunninghami* decreased the number of prey ingested. When compared between species, the feeding success after the passing of coastal storms was greater for *H. chilensis* than *H. cunninghami*. Finally, trophic overlap between species was high, but after the coastal storms passed, it decreased noticeably due to small changes in proportion of large chironomid and gammarid amphipods in the diet. Therefore, summer coastal storms affected the foraging behavior, increasing the weight of two recurrent cryptobenthic rocky reef fish from central Chile. In a broader ecological context, the shift from pelagic (i.e., copepods) to benthic prey (i.e., amphipods, polychaetes) may change the relative contribution and the subsidy production in nearshore habitats via pelagic-benthic coupling.

Responsible Editor: K.D. Clements.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-021-03827-w>.

✉ Mauricio F. Landaeta
mauricio.landaeta@uv.cl

- ¹ Laboratorio de Ictioplancton (LABITI), Instituto de Biología, Facultad de Ciencias, Universidad de Valparaíso, Valparaíso, Chile
- ² Centro de Observación Marino Para Estudios del Ambiente Costero (COSTA-R), Universidad de Valparaíso, Valparaíso, Chile
- ³ Laboratorio de Oceanografía Física y Satelital (LOFISAT), Centro de Observación Marino Para Estudios del Ambiente Costero (COSTA-R), Universidad de Valparaíso, Valparaíso, Chile

Introduction

A major threat to coastal environments is the increasing frequency and intensity of coastal storms. These events can be defined as meteorologically induced disturbances to the local maritime conditions (i.e., waves and/or water levels) which

- ⁴ Escuela de Ingeniería Civil Oceánica, Facultad de Ingeniería, Universidad de Valparaíso, Valparaíso, Chile
- ⁵ Centro de Investigación Para la Gestión Integrada del Riesgo de Desastres (CIGIDEN), Valparaíso, Chile
- ⁶ Fundación CIDEMAR, Valparaíso, Chile

can potentially alter the underlying morphology, exposing the backshore to waves, currents and/or inundation (Harley 2017). Nearshore wave energy is one of the most important triggering factors for erosion and flooding, and is often related to severe damages in infrastructure, property loss and loss of life (Jaranovic et al. 2017).

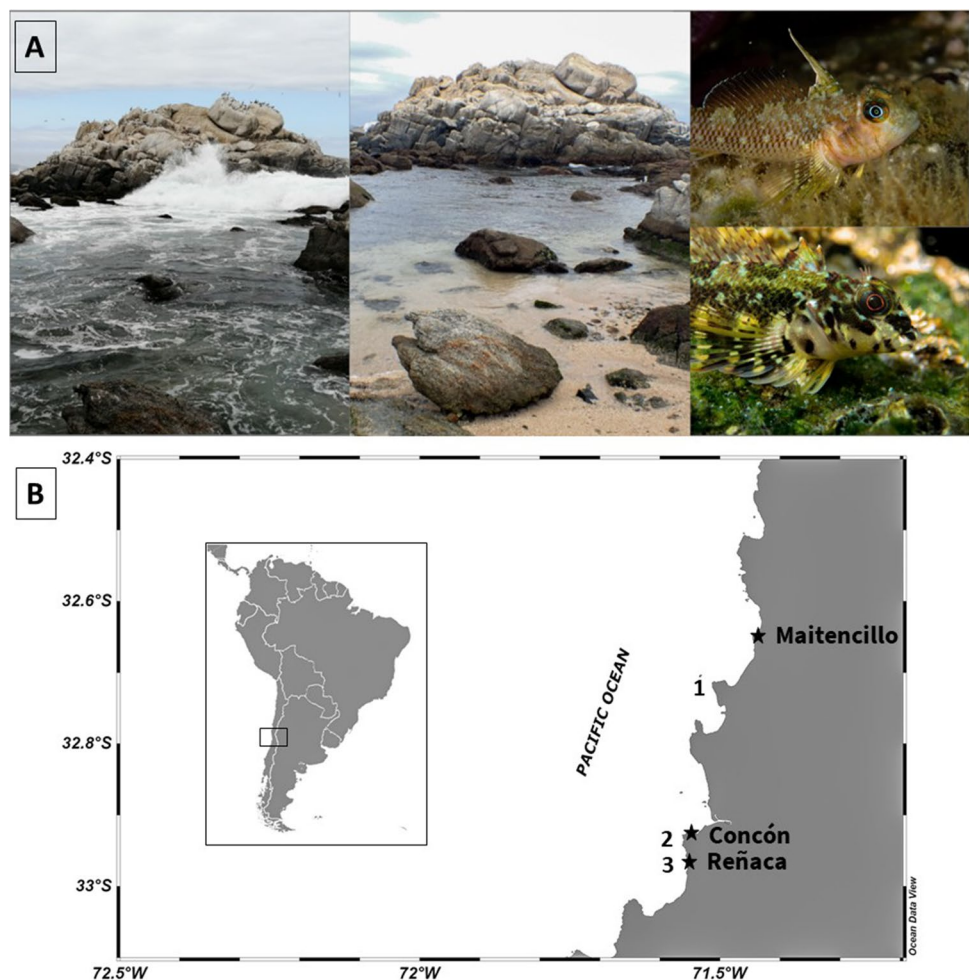
In the southeastern Pacific Ocean, these events are caused by both frontal systems traveling north-eastwards at high latitudes off Chile during the austral winter or long-distance swells generated in the North Pacific over the course of the austral summer. The latter tend to have longer periods and smaller wave heights compared to those generated during the winter months (Becerra 2017), because of wave propagation over thousands of kilometers from their source. In central Chile, extreme events have increased from an average of 5 per year during the middle of the last century to roughly 20 per year in the twenty-first century, and are linked to an increase in coastal erosion (Martínez et al. 2018). Coastal storms have recently caused both damage in coastal infrastructure and civilian casualties within this region. For example, the August 8th, 2015 storm caused damages of US\$7.2 million, 1 casualty and affected 4276 people

(Carvajal et al. 2017; Winckler et al. 2017). Despite these consequences, little information is available on the effect of coastal storms on marine animal survival (see Sepúlveda et al. 2020) and trophic interactions of marine organisms, such as littoral, cryptobenthic fishes.

Cryptobenthic fishes correspond to the “hidden half” of the fish community. Adult fishes are small to medium size, visually or behaviourally cryptic and live near to or even within the seabed (Goatley and Brandl 2017). They have a worldwide distribution and play an important role in energy transfer in tropical waters, producing between 6 and 60% of the consumed reef fish biomass (Brandl et al. 2019; Allgeier and Cline 2019). However, the impact of emergent hazards, such as coastal storms, on the trophic interactions of cryptobenthic fishes has yet to be addressed.

Throughout the Humboldt Current ecosystem, cryptobenthic fishes constitute the largest biomass in nearshore environments (Stepien 1990). Triplefins (genus *Helcogrammoides*) are among the most abundant, occurring from near-surface down to 25 m depth (Pérez-Matus et al. 2016; Winkler et al. 2017; Fig. 1). They comprise two sympatric species, *H. chilensis* (Cancino, 1960), occurring mostly in

Fig. 1 **a** Photographies during coastal storms (left) vs. calm conditions (right) at the rocky shore off Reñaca, central Chile. In addition, adult triplefin *Helcogrammoides cunninghami* (upper panel) and *H. chilensis* (lower panel) are shown. **b** Map showing locations (black stars) studied during austral summer 2018. Numbers indicate the location of the numerical nodes for the estimation of the wave parameters



the intertidal and *H. cunninghami* (Smith, 1898), which both inhabit understory algae at 20–30 m depth (Pérez-Matus et al. 2016) and feed on similar prey items (crabs, gastropods, and harpacticoid copepods, Stepien 1990; Winkler et al. 2017). Their larvae hatch at a small size during spring tides in temperate water off central Chile, growing at slow rates (0.14–0.15 mm day⁻¹) (Palacios-Fuentes et al. 2014). Both species have long pelagic larval durations (95 and 75 days in *H. chilensis* and *H. cunninghami*, respectively, Mansur et al. 2014), and can be dispersed over the continental shelf during spring (Landaeta et al. 2015). Then, during summer, pre-settlement schools move to nearshore waters, after which, settlement occurs (Palacios-Fuentes et al. 2020).

In this work, we addressed the following question: do the summer coastal storms affect the trophic interactions of these two common cryptobenthic fish species in terms of their length–weight relationships, diet composition, feeding success and trophic overlap? Using a field experiment, we tested the hypothesis that after a summer coastal storm passes, both fish species will vary their prey ingestion, affecting their trophic overlap, with a concomitant impact in their weight at a given length.

Materials and methods

Predicted wave height model

To better understand offshore wave conditions between January 1st and February 28th, 2018, we modeled the wave climate of the Pacific Ocean using Wavewatch III (WWIII, Tolman 2014), using parameters adjusted for central Chile (Beyá et al. 2017) and wind fields from NOAA's Global Forecast System GFS database. Wind fields were obtained from GFS, at a height of 10 m and 1/2 degree resolution at hourly intervals (<https://polar.ncep.noaa.gov/waves/download.shtml>). Data available <ftp://ftpprd.ncep.noaa.gov/pub/data/nccf/com/wave/prod/>). A digital elevation model was constructed from ETOPO v.2 global bathymetry (Smith and Sandwell 1997), with 1° × 1° spatial resolution in a Pacific-wide domain, and nautical charts from the Hydrographic

and Oceanographic Service of the Chilean Navy (SHOA 2017). The offshore grid built with WWIII was physically downscaled to a spatial resolution of 10 m × 10 m in Quintero (the closest node to Maitencillo), Concón and Reñaca, (Fig. 1). These three locations were used to collect triplefin. The downscaling was made using SWAN, a spectral wave model capable of simulating near shore processes (The SWAN team 2020). At these locations, triplefin were collected. Statistical wave parameters (significant wave height, wave period, mean direction and wave power) were evaluated from wave spectra covering periods between 4 and 26 s and directions between 180° and 360°.

Locations and field collection of triplefin

During austral summer 2018 (January–February), before and after the arrival of each of three consecutive coastal storms predicted by the model, juvenile and adult specimens of triplefin *Helcogrammoides chilensis* ($n = 178$) and *Helcogrammoides cunninghami* ($n = 129$) were collected during the morning at three separate bays along central Chile, Maitencillo (El Chungungo beach, 32° 39' S, 71° 26' W), Concón (Los Lilenes beach, 32° 55' S, 71° 32' W) and Reñaca (Reñaca beach, 32° 57' S, 71° 33' W) (Fig. 1; Table 1). Fish were collected with hand nets and killed with an overdose of benzocaine (BZ-20[®], Veterquímica, Chile). Later, they were preserved in 96% ethanol.

Laboratory work

In the laboratory, all specimens from the three locations were measured with a caliper (total length, TL, from the tip of the premaxilla to the end of the tail, mm) and weighed (TW, g) using a Precisa analytical scale model Swiss Quality. Following this, a gut content analysis was carried out on each individual specimen. The gut content was observed under an Olympus SZ61 stereomicroscope and all prey were photographed using a Motic camera (5 MPx resolution) for further identification of the major groups, quantification and measuring. The maximum body length and width of each prey item was measured to the nearest 0.01 mm along the

Table 1 Sampling size of triplefin *Helcogrammoides chilensis* (*H.chi*) and *Helcogrammoides cunninghami* (*H.cun*) collected before (B) and after (A) the arrival of coastal storms

Sampling	Date	Maitencillo		Concón		Reñaca		Total	
		<i>H.chi</i>	<i>H.cun</i>	<i>H.chi</i>	<i>H.cun</i>	<i>H.chi</i>	<i>H.cun</i>	<i>H.chi</i>	<i>H.cun</i>
First coastal storm	16–17/01/2018 (B)	10	10	11	4	9	10	30	24
	23–25/01/2018 (A)	10	10	10	1	10	10	30	21
Second coastal storm	29–30/01/2018 (B)	10	10	10	0	10	7	30	17
	03–04/02/2018 (A)	10	10	8	0	10	10	28	20
Third coastal storm	06–07/02/2018 (B)	10	10	10	2	10	10	30	22
	10–11/02/2018 (A)	10	10	10	5	10	10	30	25
Total		60	60	59	12	59	57	178	129

maximum cross-section which the fish had to ingest. The volume of each prey item was estimated using the three-dimensional shape which most closely resembled the item, following Cass-Calay (2003).

Data analysis

Length–weight relationships were estimated separately for both species, before and after the arrival of coastal storms, using allometric models, $TL = aW^b$, where TL = total length (mm), W = weight (g), and a and b are the parameters of the potential model. Later, data were log–log transformed and simple linear regression models were fitted separately for each species, as well as for before/after coastal storms. The linear models before and after the arrival of the coastal storms were compared by means of a one-way ANCOVA, using log TL as the covariate (Supplementary Material 1). TL measurements showed normal distribution (Shapiro–Wilk tests, $P > 0.05$), but they were heteroscedastic (Levene test, $P < 0.05$).

Three indicators of prey preferences were calculated for each specimen separately by species and before/after the coastal storms. First, the frequency of occurrence (%F) of every prey item was calculated as a percentage of the number of individuals with gut contents in relation to the total number of individuals examined; second, the number of individuals in each food category recorded for all stomachs and the total was expressed as the percent of the total number (%N) of diet items which were examined; and third, the total volume of a food category taken by the fish population, was calculated as the percent of volume (%V) of each item out of the total volume of prey items. An index of relative importance (IRI) was calculated as follows: $IRI = (%N + \%V)\%F$. To allow comparisons among prey items, the IRI was then standardized to %IRI for each prey item (Hyslop 1980).

The diet composition was compared between locations and before/after coastal storms using a nested PERMANOVA, with the Bray–Curtis similarity index and the before/after coastal storm as a factor nested for the locations. These analyses were done separately for each species using Primer 6.0 + PERMANOVA.

Comparison of the size (i.e., volume) of the most important prey items (harpacticoid copepods, gammarid amphipods, chironomid larvae, megalopae, and polychaetes) was done using Kruskal–Wallis test, randomly selecting 200 specimens (prey) by each taxonomic group. Post hoc comparisons were made by means of Mann–Whitney tests and Bonferroni-corrected P values.

As proxies of feeding success, the total number of prey items per gut (NPPG), as well as the total volume of prey items per gut (TVPG) were calculated for both species. First, Spearman correlations were tested between TL, NPPG and TVPG for both species, and before and after the

arrival of coastal storms. When correlations were significant ($P < 0.01$), least-square linear regression models were fitted, between log NPPG and TL, and between log (TVPG + 1) and TL. Comparisons were made between species and before/after using one-way ANCOVA, and TL as a covariate. When the correlations were not significant, comparisons were made using Mann–Whitney U tests.

Finally, to estimate the trophic overlap between *H. chilensis* and *H. cunninghami* before and after the arrival of coastal storms during austral summer only fish collected in Maitencillo and Reñaca were used, due to the low number of *H. cunninghami* collected in Concón (12 vs. 59 *H. chilensis*). The simplified Morisita's overlap index was utilized (Wolda 1981; Cortes 1997). This index takes values from 0 to 1, values over 0.6 consider the occurrence of overlapping. Comparisons of the overlap before and after coastal storms were tested using Wilcoxon paired test.

Results

Coastal storm forecast

Three consecutive summer coastal storm events were forecast for central Chile: 16–25 January, 29 January–04 February and 6–11 February 2018 (Fig. 2). In Maitencillo and Reñaca, coastal storm waves came from the south-west and west (Fig. 2a, c), while in Concón, all events consisted in north-westerly swells (Fig. 2b). Larger maximum wave heights were forecast for Maitencillo for the three events (1.7, 1.9 and 1.9 m). The smallest maximums were predicted for Reñaca (1.4 m), for the first coastal storm, and for Concón (0.9 and 0.8 m), for the second and third events. Generally, the greatest forecast maximum power coincided with the locations of the largest wave heights (19.7 W for the second event and 21.9 W for the third), except for the first coastal storm (23.8 W at 1.6 m in Concón). However, lowest maximum predicted powers did not coincide with the smallest wave heights. The longest periods, at all the locations, were forecasted during the first coastal storm (21.9–24.2 s).

Length/weight relationships

A total of 307 specimens were collected, 178 *H. chilensis* and 129 *H. cunninghami* (Table 1). The length/weight relationships are shown in Fig. 3. Intraspecific comparison of the log–log transformed relationships before and after the storms (Supplemental Material 1) indicated that triplefins were heavier-at-length after the coastal storms passed (*H. chilensis*: $F = 14.64$, $P < 0.001$; *H. cunninghami*, $F = 18.98$, $P < 0.001$). Using the models, a fish of 50 mm had a weight gain of 0.056 g and 0.503 g for *H. chilensis* and *H. cunninghami*, respectively.

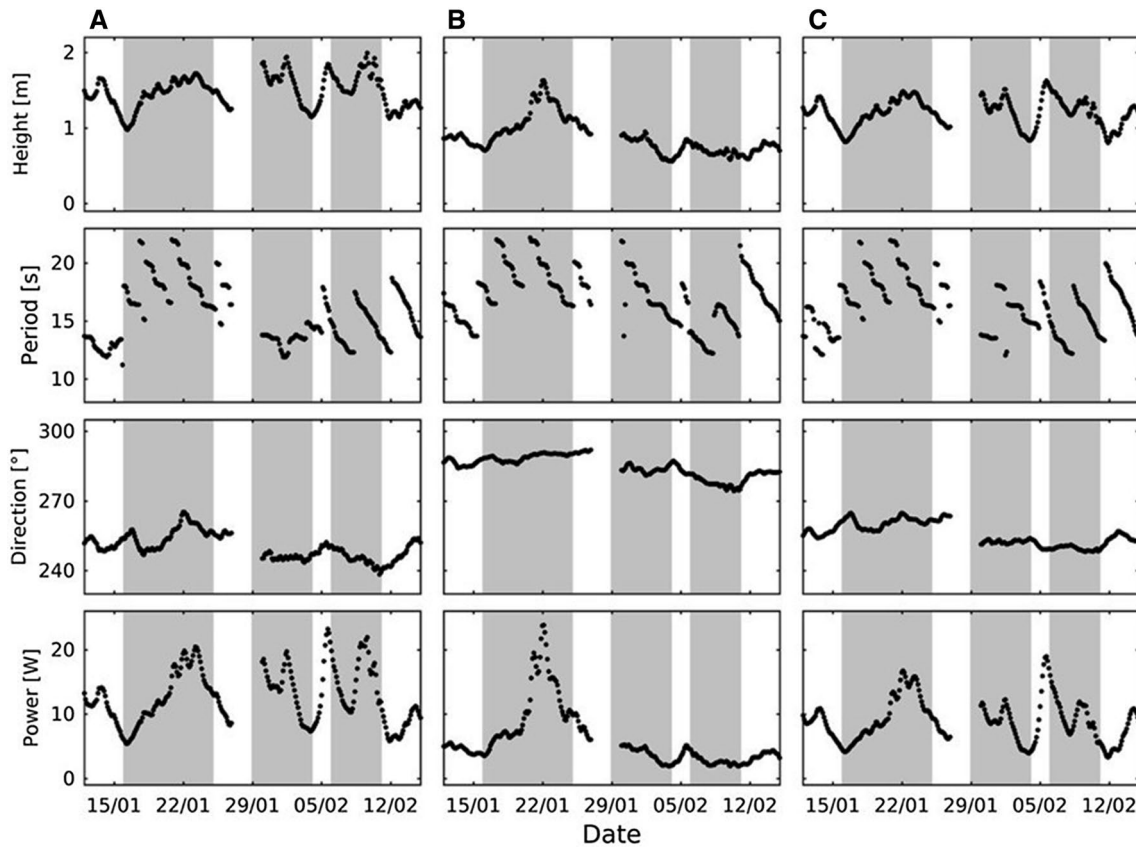


Fig. 2 Wave model results for **a** Maitencillo, **b** Concón and **c** Reñaca (Jan–Feb 2018). The three predicted coastal storm events are shaded

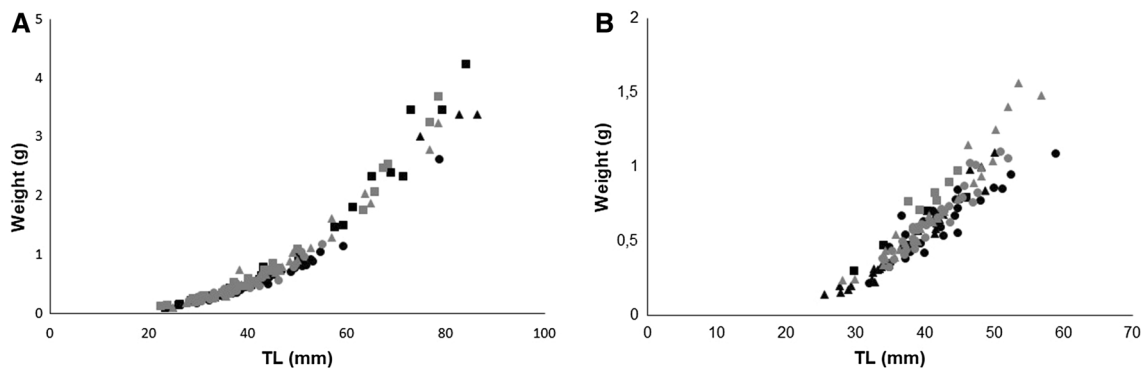


Fig. 3 Length/weight relationships before (black symbols) and after (grey symbols) the arrival of coastal storms. **a** *Helcogrammoides chilensis*, **b** *Helcogrammoides cunninghami*. Triangles, squares, and

circles represent fish collected at Maitencillo, Concón and Reñaca, respectively. The log–log relationships are shown in Supplementary Material 1

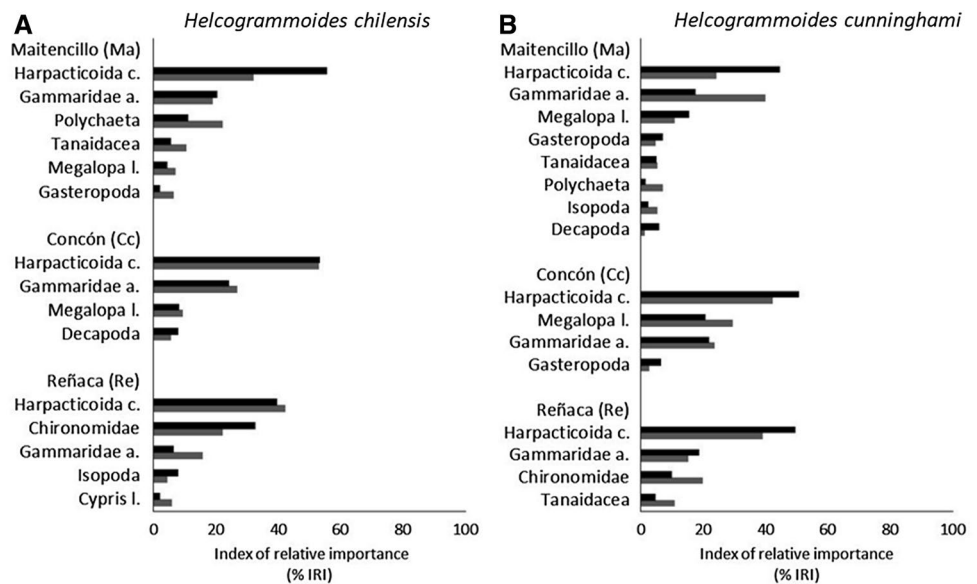
Gut content analysis

From the 307 specimens, 174 (of 178) and 124 (of 129) gut contents were analyzed for *H. chilensis* and *H. cunninghami*, respectively, due to damage to the abdominal section of a few individuals. From all gut contents, a total

of 16,597 prey items were counted, 10,574 in *H. chilensis* and 6023 in *H. cunninghami*.

The most important prey in all the locations was harpacticoid copepods (Fig. 4). This small prey was numerically important as well as highly recurrent in most of the specimens of both species (Supplemental Material 2). At most of the locations, in both species, the relative importance (%IRI)

Fig. 4 Spatio-temporal variation of the diet composition of triplefin, **a** *Helcogrammoides chilensis* and **b** *Helcogrammoides cunninghami* before (black bars) and after (grey bars) the arrival of coastal storms



of harpacticoid copepods decreased after the coastal storms arrived, and this was particularly noticeable in Maitencillo (Fig. 4a, b). In addition, in most cases, there was an increase in the ingestion of Gammaridae amphipods (*H. cunninghami*), polychaetes (*H. chilensis*) or megalopae (both species) after the coastal storms, particularly in Maitencillo and Concón (Fig. 4). In Reñaca, chironomid larvae were also important prey items. Interestingly, the before/after variation showed opposite trends between species: after the coastal storm passed, *H. chilensis* decreased the ingestion of chironomid larvae, while *H. cunninghami* increased it (Fig. 4).

There were differences in ingested prey size in both fish species (Fig. 5), with the harpacticoid copepods being the smallest and polychaetes being the biggest (Kruskal–Wallis test, $H = 675.2$, $P < 0.001$, Fig. 5a, b). Post hoc comparisons (Mann–Whitney test, Bonferroni-corrected P values) indicate that only amphipods and chironomid larvae found in guts had similar size ($P > 0.05$) in both species (Fig. 5).

The nested PERMANOVA detected that the prey composition of *H. chilensis* changed significantly between locations, but this variation was not noticeable before and after coastal storms (Table 2A). On the other side, *H. cunninghami* showed similar prey composition among locations and coastal storm events (Table 2B). Therefore, after the coastal storms passed, diet composition was similar but there was a decrease in the relative importance of small copepods and an increase in the relative importance of relatively larger prey, such as gammarids, megalopae and polychaetes (Fig. 4).

Feeding success and trophic overlap before/after coastal storms

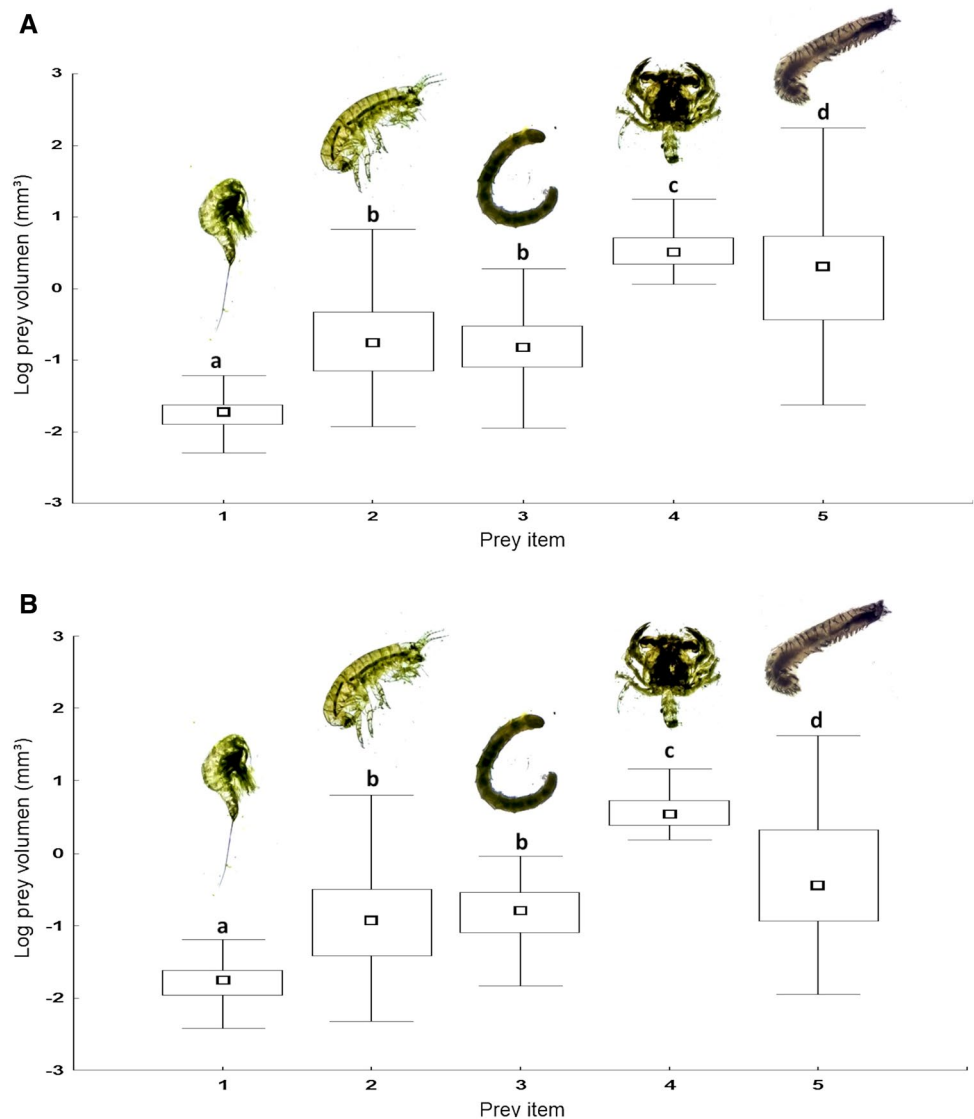
In *H. chilensis*, the TVPG increased as the fish TL increased (Fig. 6a), before (Spearman $r_s = 0.78$, $P < 0.001$) and after

the coastal storms ($r_s = 0.74$, $P < 0.001$). The NPPG varied widely, up to ~400 prey items, being particularly large around 30–50 mm TL. Specimens larger than 50 mm TL contained less than 50 prey items (Fig. 6b). TVPGs were significantly larger (log-transformed data, one-way ANCOVA, $F = 7.69$, $P = 0.006$) after the impact of coastal storms. There was a negative correlation between body size (TL) and the total number of prey ingested in *H. chilensis*, both before ($r_s = -0.43$, $P < 0.001$) and after the coastal storms ($r_s = -0.51$, $P < 0.001$). Nonetheless, no significant differences were noticed in the number of preys ingested before and after the coastal storms in *H. chilensis* (one-way ANCOVA, $F = 0.05$, $P = 0.82$).

The triplefin *H. cunninghami* only showed a positive correlation between the TVPG and the TL before the coastal storms arrived ($r_s = 0.38$, $P < 0.01$), but after the storms passed this relationship disappeared ($r_s = -0.032$, $P = 0.80$) (Fig. 6c). Nevertheless, there was no significant difference in the ingested volume-at-length (one-way ANCOVA, $F = 1.38$, $P = 0.24$). On the other hand, NPPG and TL in *H. cunninghami* were independent before ($r_s = -0.023$, $P = 0.085$) and after the coastal storms ($r_s = -0.044$, $P = 0.73$, Fig. 6d). However, *H. cunninghami* ingested more prey before than after the coastal storms ($U = 1376$, $P = 0.009$).

When comparisons were made between species, both ingested similar prey volumes before the arrival of coastal storms (one-way ANCOVA, $F = 1.08$, $P = 0.30$). However, after the coastal storms passed, *H. chilensis* ingested more voluminous prey ($F = 7.15$, $P = 0.008$) than *H. cunninghami*. In numerical terms, both species ingested similar prey quantities before the arrival of coastal storms ($U = 2377$, $P = 0.45$), but *H. chilensis* ingested more prey than *H. cunninghami* after the storms (t -test, $t = 2.68$, $P = 0.008$). Therefore, the coastal storms negatively affected the prey ingestion

Fig. 5 Comparison of the main prey size (volume, mm^3) found in the guts of triplefins: **a** *Helcogrammoides chilensis*, **b** *Helcogrammoides cunninghami*; (1) harpacticoid copepods, (2) amphipods, (3) chironomid larvae, (4) megalopae, (5) polychaetes. Different letters indicate significant differences ($P < 0.05$). Photos by Javier Polanco



of *H. cunninghami*, while *H. chilensis* were able to ingest bigger prey.

Simplified Morisita overlap indices were high (> 0.7), indicating large trophic overlap between the triplefin species (Table 3). Nevertheless, there was a significant decrease in the trophic overlap after the coastal storms (Wilcoxon test, $z = 2.24$, $P = 0.025$).

Discussion

Several biological and trophic features varied in the intertidal cryptobenthic fish with the passing of summer coastal storms: (1) heavier-at-length specimens were collected after the coastal storms passed, compared to those specimens collected 3–6 days prior the storms; (2) changes in size structure of the prey, but not in prey composition, before and

after the coastal storms; (3) changes in the feeding success with the passing of the coastal storms; (4) a decrease in the trophic overlap between the triplefin species after the coastal storms passed.

Increase in weight-at-length after the coastal storms

In coastal rocky reef habitats, rapid changes in current, waves and turbulence can alter the feeding process of benthic organisms, playing a key role in the predator–prey interactions (Robinson et al. 2007, 2013). As waves move along the coast, the rough structure of the seafloor disrupts flow, forming a range of hydrodynamic microhabitats. Currents, tides, waves and wind, generate turbulent eddies of different sizes which can stir the water throughout the water column. The rocky reefs are used by many zooplanktivorous fishes (Muñoz and Ojeda 1997; Pérez-Matus et al. 2012), which

Table 2 Results of the nested PERMANOVA for testing diet composition variability (using prey volume and prey number) between locations and coastal storm events (nested into location) for (A) *Helcogrammoides chilensis* and (B) *Helcogrammoides cunninghami*

	Source	SS	Df	MS	Pseudo-F	P
(A)	<i>Prey volume</i>					
	Location	65,779	2	32,889	26.13	0.023
	Coastal storm (location)	3776.5	3	1258.8	0.893	0.575
	Residual	2.35×10^5	167	1410.1		
	Total	3.05×10^5	172			
	<i>Prey number</i>					
	Location	57,853	2	28,927	28.76	0.022
	Coastal storm (location)	3016.5	3	1005.5	0.882	0.578
	Residual	1.91×10^5	167	1140.1		
	Total	2.51×10^5	172			
(B)	<i>Prey volumen</i>					
	Location	38,397	2	19,198	13.03	0.068
	Coastal storm (location)	4475	3	1491.7	1.108	0.347
	Residual	1.57×10^5	117	1346.5		
	Total	2.00×10^5	122			
	<i>Prey number</i>					
	Location	36,067	2	18,034	11.77	0.067
	Coastal storm (location)	4815.9	3	1605.3	1.57	0.067
	Residual	1.19×10^5	117	1019.1		
	Total	1.60×10^5	122			

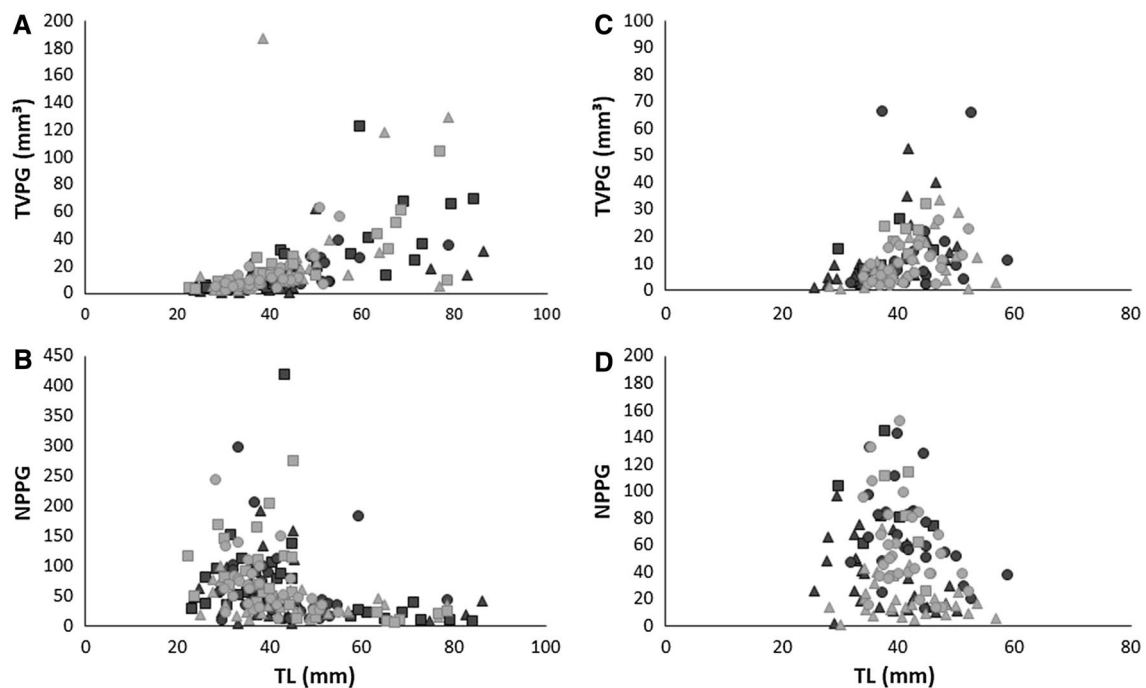


Fig. 6 Feeding success of triplefin before (black symbols) and after (grey symbols) the arrival of coastal storms. **a** TVPG vs. TL for *H. chilensis*, **b** NPPG vs. TL for *H. chilensis*, **c** TVPG vs. TL for *H.*

cunninghami and **d** NPPG vs. TL for *H. cunninghami*. Triangles, squares, and circles represent fish collected at Maitencillo, Concón and Reñaca, respectively

Table 3 Simplified Morisita index of trophic overlap between triplefin *Helcogrammoides chilensis* and *H. cunninghami* before (B) and after (A) the arrival of coastal storms

Location	First coastal storm		Second coastal storm		Third coastal storm	
	B	A	B	A	B	A
Maitencillo	0.969	0.939	0.996	0.716	0.945	0.948
Reñaca	0.901	0.880	0.934	0.980	0.944	0.913

reside on the sea bottom permanently and are exposed to the associated turbulent wave flow (Robinson et al. 2013).

High turbulence intensity may reduce fish swimming performance (i.e., body posture and swimming trajectories, Enders et al. 2003) and feeding behavior. For example, Clarke et al. (2005) showed that feeding behavior can be affected by waves and turbulence in two tube blenny species which inhabit burrows within coral heads (*Acanthemblemaria aspera* and *A. spinosa*), and which have a “sit and wait” feeding strategy, darting out rapidly from their position into the water column to capture their prey. When both species were exposed to higher turbulence, as the triplefins were exposed during coastal storms, they had greater capture rate (number of prey captured from a known amount). Thus, the capture efficiency improved with increased turbulence generated by stronger waves, due to the prey’s (copepods) decreased reaction distance (Robinson et al. 2007). Although the foraging frequency was less, blennies, and potentially triplefins, were more successful at capturing prey (Robinson et al. 2013). Therefore, a rise in turbulence and waves interfered with both the predator’s foraging behavior and prey’s escape behavior. The net result was an increase in the feeding success of the predator (Robinson et al. 2013), in this specific case, represented by an increase in the weight of both triplefin species and an increase in the prey size.

Triplefins may have reduced the locomotion cost, using the turbulent flows for displacement, decreasing the effort, time and energy expended in the foraging process, and using it for somatic growth during the 3–6 days between the collections. In addition, in these conditions, there is an increment in predator–prey encounter rates, and therefore, the foraging efficiency (the proportion of prey approached that were eaten) is improved (Robinson et al. 2013). Finally, the mechanical stress of the coastal storms may have selected heavier-at-length specimens, which were more capable of maintaining their position in the intertidal, rather than being transported to deeper and calmer waters. Small-size fish may drift and be dragged, while large fish, which have a higher swimming capacity than the smaller ones, are able to re-establish their orientation (Silva et al. 2012).

Diet composition of triplefin

The study verified the microcarnivory of the triplefins, with preference for harpacticoid copepods, gammarid amphipods, chironomid larvae and megalopa larvae. Muñoz and

Ojeda (1997) registered that amphipods, polychaetes and gastropods were the main prey for *H. chilensis* in the central coast of Chile. While in the north of Chile, Berrios and Vargas (2004) identified amphipods, isopods and decapod crustaceans as the preferred prey. On the other hand, for *H. cunninghami* in the central coast, Muñoz and Ojeda (1997) found amphipods, copepods and polychaetes as main prey source, while Winkler et al. (2017) registered coumaceans, amphipods, bivalves, gastropods and decapods.

Intraspecific diet composition differed among locations. Similar variation has also been reported by Pérez-Matus et al. (2012) and Winkler et al. (2017), where microhabitats were analyzed according to substrate type, algae cover, among others, indicating that the available resources (associated food supply) are directly related to diet composition. Although no different microhabitats were surveyed in our study, differences among locations may be due to variations of prey availability.

Intraspecific and interspecific variations in feeding success related to coastal storms

The coastal storms caused unexpected, and different, consequences in the feeding success of both species. Although the prey composition did not vary significantly, prey size did. Triplefin *H. chilensis*, which is more common in the intertidal zones of central Chile than *H. cunninghami* (Pérez-Matus et al. 2016; Palacios-Fuentes et al. 2020), ingested larger prey (i.e., chironomid larvae, gammarid amphipods), causing an increase of volume ingested after the coastal storms. Meanwhile, in *H. cunninghami*, there was a decrease in the number of prey ingested. As Pires and Gibran (2011) mention, the low dispersion, or the restriction in the bathymetric distribution, would favor the specialization of *H. chilensis* for inhabiting shallow (< 5 m depth), more turbulent coastal rocky reefs. Similarly, in two sympatric species of the genus *Bellapiscis* (Tripterygiidae) from New Zealand, there is a difference in the vertical distribution of the habitat associated with different physiological tolerance ranges, with *B. medius* living higher on the shore than *B. lesleyae*, and are largely restricted to the intertidal. This will naturally result in the former generally occurring in shallow pools (Hilton et al. 2008). Therefore, the small-scale bathymetric distribution and preferences in two sympatric triplefin species may partially explain different trophic responses in shallow subtidal under stressful conditions.

Variations in the trophic overlap after coastal storms

There was large trophic overlap between species, because both triplefin fed on the same prey items in similar proportions. The decrease of the trophic overlap after the impact of the summer coastal storms may have been caused by the reduced number of *H. cunninghami* collected after the storms (which was most noticeable in Concón). However, it may also have been produced by subtle changes in prey proportion (other than harpacticoid copepods), as observed in the triplefins from Reñaca.

Ward et al. (2006) found that the nature and intensity of competition can vary according to the characteristics of temporal and spatial resources, as well as the physical characteristics affecting prey availability, finally altering its behavior (Clarke et al. 2005; Robinson et al. 2007, 2013; Gabel et al. 2011; Higham et al. 2015). It is probable that coastal storm events change the prey field at short scales, causing *H. chilensis* and *H. cunninghami* to reduce their consumption of similar prey or to change their preferences.

Finally, the recent trends in the increment of extreme coastal storm events along Chile (around 20 per year, Martínez et al. 2018) will directly impact the rocky reef trophic web dynamics. Using both species as models representing cryptobenthic fishes, the gradual increase in the frequency and intensity of coastal storms will generate temporal as well as spatial restrictions in the species which are able to prosper in this intertidal environment. It is plausible that the increment of the water column turbulence of nearshore areas may have greater impact on small-size cryptobenthic fish (gobies, blennies, clingfishes) rather than on medium and larger ones (labrisomids, labrids). In addition, the shift from pelagic (i.e., copepods) to benthic prey (i.e., crabs, polychaetes) may change the relative contribution and the subsidy production in nearshore habitats via pelagic-benthic coupling (Docmac et al. 2017). In this way, the species which undergo the majority of their life cycle—feeding, growing, reproducing and hiding—in this habitat will be favored compared to those who do not, causing them to move to spaces better suited for them.

Acknowledgements We appreciate the field work done by Daniela Plaza, Christina D'Áz and Yanara Figueroa, who helped in the collection of triplefin. We deeply thank Mauricio Molina and Sebastian Correa for their aid in generating the wave data from the database Sistemas de Alerta de Marejadas (<https://marejadas.uv.cl>) and to ANID's Grant ID20I10404 "Desarrollo de una escala de impacto de marejadas para la comunicación efectiva y disminución del riesgo de desastre".

Author contributions JPP and MFL organized the field experimental design, and JPP carried out the collection, the gut content analysis and the data analyses; FVS and PW carried out the data analysis of the wave model; the whole team wrote the manuscript.

Funding This research was partially funded by Comisión Nacional de Investigación Científica y Tecnológica (CONICYT Chile, now Agencia Nacional de Investigación y Desarrollo, ANID) grant FONDECYT 1150296 to MFL, grant FONDAP 15110017 to PWG, and funded by Universidad de Valparaíso's project CIDI 12, Centro de Observación Marino para Estudios de Riesgos del Ambiente Costero (COSTA-R).

Data availability Data will be available upon reasonable request.

Compliance with ethical standards

Conflict of interest No conflict of interest is declared by the authors.

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