

Effects of tidal current-induced flow on reef fish behaviour and function on a subtropical rocky reef

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ABSTRACT: Tidal currents are important features in reef environments with high tidal range. Such current-influenced areas can be attractive for fish due to transport of nutrients and food items. Biological sampling, however, is difficult in these environments and it remains poorly understood to what degree strong currents actually shape tropical and subtropical reef fish communities. We used remote underwater video to investigate effects of flow velocity on fish across the tidal cycle at a rocky reef in southern Mozambique. Fish were recorded during flow velocities ranging from 0 to 1.44 m s⁻¹. Current flow velocity had no significant effect on the benthic fish assemblage, while increasing flow velocity had a negative effect on pelagic fish abundance and influenced trophic group composition. Limits for tolerated flow velocity on the pelagic assemblage were species-specific, with the highest resistance for larger predatory fish using subcarangiform swimming. Flow velocity had significant positive effects on size of *Caranx* spp., showing that smaller individuals had lower tolerance to flow than larger conspecifics. Planktivorous pomacentrids and monodactylids were very abundant in flows up to 0.5 m s⁻¹, suggesting that the area functions as an important foraging ground for planktivorous fish up to this flow velocity, while abundance of barracudas *Sphyraena* spp. was higher in moderate currents compared to slack water. For the benthic assemblage, benthic structures seemed to provide sufficient flow refuge for fish throughout the tidal cycle, highlighting the importance of structural complexity for benthic fish in this environment. Fish assemblages on reefs subjected to strong tidal currents might therefore be sensitive to habitat modifications. The ecological importance of tidal currents should be considered in marine management.

KEY WORDS: Rocky reef · Reef fish · Tidal current · Water flow · Subtropical

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INTRODUCTION

In marine environments, hydrodynamics such as currents and wave action can have major structuring impacts on fish species distribution at a variety of spatial and temporal scales (Fulton et al. 2005, Heatwole & Fulton 2013, Schmiing et al. 2013). As marine management moves in the direction of holistic approaches such as ecosystem-based management (Pikitch et al. 2004, Arkema et al. 2006) and marine spatial planning (Douvere 2008, Foley et al. 2010, Caldow et al. 2015), the understanding of ecosystem complexity becomes increasingly important. For in-

stance, detailed ecological knowledge about the importance of specific biotopes for keystone species, and the functions that they maintain, is needed for integration of ecological data into management plans (Sale et al. 2005, Crowder & Norse 2008). Such data are in many cases lacking (Sale et al. 2005, Boström et al. 2011). The ecological functions in marine environments dominated by strong currents and the structuring role of flow velocity are particularly unexplored. It is known that water flow affects fish behaviour (Fulton & Bellwood 2004, Heatwole & Fulton 2013, Noble et al. 2014, Longo et al. 2015) but biological field data from current-swept areas are

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underrepresented because of sampling difficulties in these environments (Liao 2007, Pearson et al. 2010, Shields et al. 2011).

High flow velocities ($>1 \text{ m s}^{-1}$) typically develop in areas with high tidal amplitude and where the coastal morphology restrains the tidal waves (Kowalik 2004). Such strong currents provide an environment that may affect ecological functions and shape fish assemblages. Beneficial effects of flow usually include an increase in local food abundance due to transport of plankton, organic material and nutrients (Lewis & Pedley 2001), and also enhancement of respiration and nutrient uptake by photosynthesizing organisms through diminishing of the boundary layer (Dennison & Barnes 1988, Carpenter et al. 1993). In addition, tidal currents function as migration routes for predatory fish, which take advantage of the currents to minimise energy loss to reach their foraging grounds down the flow (Gibson 2003, Krumme 2009).

The main advantage for predatory fish residing in this type of environment is the increased possibility of predator–prey encounters (Chapman & Bjornn 1969, Rothschild & Osborn 1988, Mackenzie et al. 1994). Planktivorous fish, for example, are often common in current-exposed areas (Hamner et al. 1988, Schmiing et al. 2013). Efficient predators (i.e. those that often succeed in capturing their prey) probably also benefit from a certain level of turbulence, which causes their prey organisms to become unbalanced (Lewis & Pedley 2001). In freshwater high-flow habitats, fish such as salmonids rely on a current-dependent foraging strategy as they position themselves near fast-flowing currents to catch prey (Fausch & White 1981). These advantages of foraging in high-flow habitats are balanced against the difficulties of capturing prey in fast-flowing waters (Rothschild & Osborn 1988, Lewis & Pedley 2001), with a trade-off between energy gain from food and energy loss from swimming, positioning and balancing in this environment (Fausch 1984, Flore & Keckeis 1998). In this way, current-swept areas might constitute attractive habitats for fish that have the ability to negotiate strong water flows.

Traits such as body shape, fin aspect ratio, swimming mode, flow-refuging behaviour, buoyancy and size determine the ability of fish to exploit currents (Fulton et al. 2001, Fulton & Bellwood 2005, Liao 2007). For example, among different body shapes, compressiform fish tend to become unbalanced sooner than fusiform fish, and thus require more energy to correct their positions in the water column (Webb 2004). Further, larger fish can tolerate a higher level of turbulence and hold station better

than smaller specimens (Lupandin 2005). Through these mechanisms, turbulence and flow velocity act size-selectively and species-specific on fish (Aadland 1993, Fulton & Bellwood 2004, Lupandin 2005). Similarly, wave-induced flow velocity has been found to shape coral reef fish assemblages in terms of swimming mode, refuging behaviour and fin morphology (Fulton et al. 2001, 2005, 2013).

To minimize energy loss when swimming in currents, fish can position themselves behind structures, or use the energy of vortices generated either by objects or other swimming fish (Johansen et al. 2007, 2008, Liao 2007). These flow-refuging strategies allow fish to exploit high-flow areas at relatively low energy costs (Liao et al. 2003, Johansen et al. 2008). While the importance of structures that provide flow refuges for benthic fish communities have been demonstrated in several studies (e.g. Gerstner 1998, Johansen et al. 2008), pelagic fish depend more on other strategies such as exploiting vortices to negotiate currents (Liao 2007).

In the marine environment, members of the Sphyrnidae family (barracudas) are some of the few species known to be particularly associated with strong currents (Barreiros & Santos 2002). In general, marine fish assemblages subject to strong tidal currents are poorly described and assessed, with a few exceptions from temperate waters (Gerstner 1998, Viehman 2012). In tropical and subtropical waters, it is virtually unknown how strong tidal currents affect fish assemblages (but see Hammar et al. 2013, 2015). With the aim of increasing the understanding of fish behaviour and functions in current-swept marine habitats, this study targeted how varying flow velocity in a subtropical tidal channel influenced fish of different swimming modes and trophic groups. We hypothesized (1) that fish assemblages would be structured by flow velocity, and (2) that total abundance of fish would decrease with increased flow velocity.

MATERIALS AND METHODS

Study site

Field data were collected at the subtropical Inhaca Island ($26^{\circ} 0' \text{ S}$, $32^{\circ} 3' \text{ E}$) in southern Mozambique in March and April 2012. Inhaca Island is situated between the shallow Maputo Bay and the open Indian Ocean (Fig. 1). The island is separated from the Machangulo peninsula by the narrow Ponta Torres strait, where tide- and wave-induced currents reach $\sim 1.5 \text{ m s}^{-1}$ (Mavume 2000). Sampling was con-

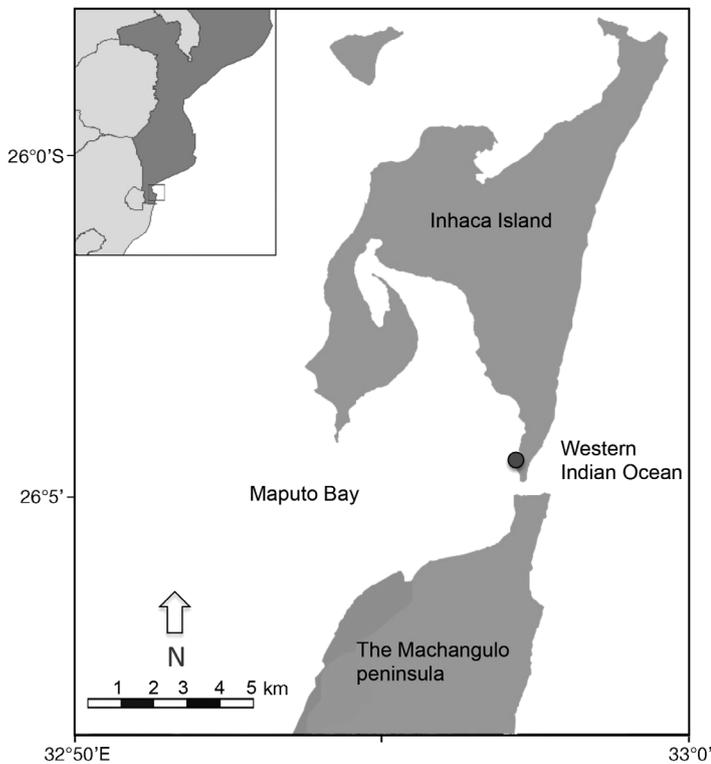


Fig. 1. Study site (●) off Inhaca Island, Mozambique

ducted at the main tidal channel of Ponta Torres, within the boundaries of the Ponta do Ouro partial Marine Reserve, where fishing is prohibited. The area consists of a rocky reef with sparse coral cover, gradually shifting into sand interspersed with a few larger rocks towards the middle of the tidal channel, with a maximum mean sea level depth of 18 m. Tides

are semi-diurnal with a mean spring tide amplitude of 3 m (de Boer et al. 2000). The area supports a high diversity of reef-associated tropical and subtropical fish (Hammar et al. 2013). Surrounding shallow-water areas embrace a wide variety of marine habitats such as mudflats, sandbanks, tidal channels, sea-grass beds, small-patch coral reefs and mangroves. While the sampling location is protected from wave exposure by the coastline configuration, the distance to open sea is only about 1 km.

Sampling design

Fish data were sampled during daylight hours (07:00 to 17:00 h) using 4 identical stereo-video underwater camera systems. Pelagic and benthic fish assemblages were studied separately, using slightly different procedures. This is because the data presented here is partly based on the same video material as was used in previous tidal turbine-related studies (although no turbine was deployed during the recordings in this study) (Hammar et al. 2013, 2015).

The pelagic fish assemblage was investigated from 3 different positions where the cameras could be safely fixed to mooring lines or rock outcrops at 8 to 12 m depth, as in Hammar et al. (2015). At each position, the cameras were directed toward the water column, viewing both bottom and surface at optimal visibility conditions. The benthic fish assemblage was studied from a fourth position where cameras were installed on the rocky bottom at 9 m depth, recording bottom-dwelling fish from a horizontal direction, as in Hammar et al. (2013).

All camera positions were within 500 m of each other and within 50 m of the rocky shore. Sampling was carried out randomly over time, over the tidal cycle and with different camera positions. Fig. 2 illustrates how sampling was distributed over the tidal cycle and in relation to tidal-induced flow velocities based on a locally validated tidal model (Hammar et al. 2012). Surveys were conducted in flow velocities between 0.15 and 1.44 m s⁻¹ (Table S1 in the Supplement at www.int-res.com/articles/suppl/m559p175_supp.pdf). For the pelagic fish assemblage, 30 separate video recordings of 45 min each generated a total of 1350 min of video for analysis. For the benthic fish assemblage, 40 time-separated video

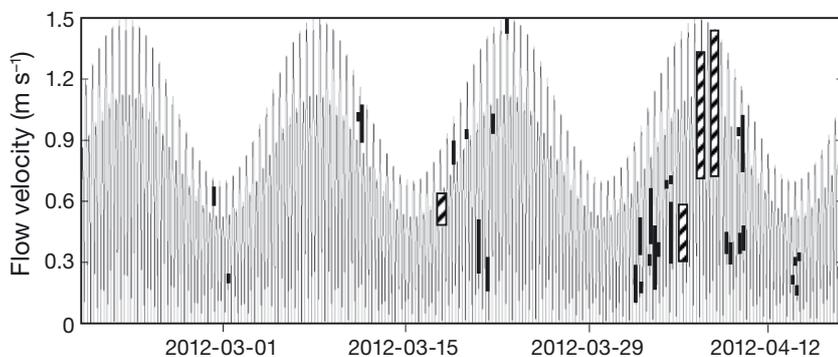


Fig. 2. Data collection in relation to tidal cycle and flow velocity. Grey line: tidal flow velocity in the sampling area during the data collection period (based on tidal model). Sampling date and span of flow velocity are indicated. The higher peaks represent spring tides and the lower peaks neap tides. Flow velocity of ebbing tides was always higher than flooding tides. Black bars: pelagic fish samples (each 45 min video); dashed bars: benthic fish sampling occasions (each 50 min video from 10 samples). All data collection took place during ebb, with the exception of 4 pelagic fish samples that were collected during flood. Date: yy/mm/dd

sections of 5 min each were extracted from each of 4 different sampling occasions, generating 200 min of video for analysis. The difference in the duration of recordings targeting pelagic (45 min) and benthic (5 min) fish assemblages was due to the much higher abundance of benthic fish.

Video analysis

Stereo-video systems, as was used in this study, generate 3-dimensional coordinates of recorded objects and allow for accurate measurements of distances and lengths (Harvey et al. 2002). The camera systems were designed as in Hammar et al. (2013) and were calibrated using the software CAL (SeaGIS) before deployment. Videos were analysed through the SeaGIS EventMeasure software.

Fish were classified into pelagic- and benthic-associated taxa according to Froese & Pauly (2013) and identified to the lowest taxonomic level possible. All taxa were categorised by trophic groups (invertivores, omnivores, roving herbivores, piscivores and planktivores) based on Froese & Pauly (2013), and by swimming mode (labriform, subcarangiform, carangiform, thunniform, balistiform, chaetodontiform, ostraciiform, and tetraodontiform) following Sfakiotakis et al. (1999) and Fulton (2007). For pelagic fish we investigated relative abundance, body length, swimming speed and swimming direction. For benthic fish we measured relative abundance and body length. Body length could only be measured for fish that passed through the stereo-field (the overlap between the 2 synchronised cameras in each system). Following the recommendations in the SeaGIS software, all measurements with error (rms values) >20 mm were removed. Swimming direction was measured in relation to the direction of the current and was later categorised as 'along-current', 'counter-current' or 'cross-current'.

Fish relative abundance was assessed as the frequency of by-passing fish over time in order to investigate the relationship between fish abundance and flow velocity. Relative abundance was defined as the number of fish specimens entering the field of view per 45 min, while correcting for variations in visibility conditions by dividing the number of entering fish with the total entry-area given by the cone-shaped field of view as in Hammar et al. (2015). This means that, in water with low visibility, the number of recorded fish was divided by a lower entrance-area than in waters with high visibility (units: fish m⁻² 45 min⁻¹). We used 45 min for standardisation due to

the duration of pelagic recordings that contained zero-values (benthic recordings could be time-adjusted because every data point was above zero). This method implies that fish specimens that left and re-entered the monitored water column were registered multiple times, and passage frequency is therefore not a strict measure of fish abundance. N_{max} , which is commonly used in studies using baited stereo-video systems (e.g. Goetze et al. 2015) was not used in the present study because there were too few fish in the pelagic samples.

Water visibility was estimated every 15 min using the stereo-function of the cameras (Hammar et al. 2013, 2015). The visibility differed among samples, typically with lower visibility at high flow velocity (Hammar et al. 2013). Differences in visibility during fish counts were corrected for as described above, and samples with low visibility (<3 m) were disregarded from the analyses. Flow velocity was measured with a Doppler current meter (ALEC infinity-EM) and by speed measurements of drifting pieces of small debris to increase the temporal resolution of flow velocity, as in Hammar et al. (2015).

Statistical analyses

The measured fish variables were analysed separately for benthic and pelagic video samples, but without consideration of sampling position. This was justified by the geographical proximity and environmental similarity among camera positions. The power density of water (kW m⁻²) was used as the predictor variable for fish activity in addition to flow velocity, since power density is what fish are actually subjected to when swimming in a flow. The relationship between power density (P) and flow velocity (V) is:

$$P = 0.5\rho AV^3 \quad (1)$$

where ρ (1025 kg m⁻³) is the density of water and A is cross-section of flowing water (1 m²) (Fraenkel 2002). This cubic relationship (Eq. 1) means that power density, i.e. the force that the fish experiences, increases very rapidly at high flow velocities, and is not linear as is flow velocity.

Linear regression was used to investigate relationships between fish activity and flow velocity as well as between fish activity and power density. Data not fulfilling parametric test requirements despite square-root transformation were analysed through the Spearman rank-order correlation test. For regressions with non-significant results, the statistical power was calculated using refined Fisher Z power,

with α set to 0.05. Logistic regressions were applied to examine how flow velocity may predict swimming direction among fish. The prediction models were tested separately for each family of fish in the pelagic recordings, but only where at least 30 specimens were registered, whereof at least 10 specimens were in each level of the response variable: along-current versus counter-current (cross-current not included). The predicted critical flow velocity when fish started to swim along-current instead of counter-current was then combined with oceanographic data on flow velocities during the tidal cycles (neap and spring tides) (Hammar et al. 2012) to predict the extent of habitat use by fish during the tidal cycles. Critical flow velocity for each species was determined as the upper limit for habitat use. All tests were computed using STATISTICA version 13 (StatSoft).

RESULTS

Fish assemblage composition

A total of 62 taxa were recorded during the study. Of these, 1811 fish were recorded in the pelagic samples, comprising 30 taxa from 20 families. The benthic samples showed a more species-diverse assemblage, consisting of 1326 individuals of 49 taxa belonging to 23 families (Table 1). Twenty of the recorded taxa occurred in both the pelagic and benthic samples.

The pelagic and benthic fish assemblages differed in terms of composition of taxa and trophic groups (Table 1, Fig. 3). The pomacentrids (*Abudefduf* spp.; mainly *A. vaigiensis* but also *A. sexfasciatus*) were by far the most common species in the pelagic ($n = 947$), followed by *Monodactylus* spp. (*M. argenteus* and *M. falciformis*, Monodactylidae) ($n = 208$) and species of the *Caranx* genus ($n = 237$). In the benthic samples, *Ctenochaetus binotatus* (Acanthuridae) ($n = 131$), *Thalassoma lunare* (Labridae) ($n = 113$) and *Rhabdosargus sarba* (Sparidae) ($n = 109$) were the most common species.

Omnivorous taxa were common in both types of assemblages, but the benthic fish assemblage also comprised a high proportion of invertivorous and roving herbivore taxa, while planktivorous and piscivorous taxa were more common in the pelagic (Fig. 3).

At all flow velocities, the benthic assemblage was strongly dominated by specimens of the invertivore and roving herbivore trophic groups. For the pelagic assemblage, however, the proportion of piscivorous fish increased with increasing flow velocity while planktivore abundance decreased (Fig. 3).

Relative fish abundance in relation to water flow

Spearman rank correlation tests showed that pelagic fish relative abundance was negatively correlated with flow velocity and power density of water (Spearman rank correlation test: $\rho = -0.586$, $p < 0.05$). As shown in Fig. 4, pelagic fish relative abundance decreased already at flow velocities between 0.3 and 0.5 m s^{-1} and very few pelagic fish were present at flow velocities above 0.5 m s^{-1} (corresponding to 0.2 kW m^{-1}). No significant correlation was found between flow velocity and benthic fish relative abundance (linear regression, $F_{1,18} = 0.510$, $p = 0.484$).

Swimming mode

Labriform fin use was the most common swimming mode within the benthic fish assemblage at all flow velocities (43.0% at 25–49 m s^{-1} , 48.2% at 55–74 m s^{-1} , 45.9% at 75–99 m s^{-1} , 54.6% at 100–124 m s^{-1} and 48.5% at $>125 \text{ m s}^{-1}$) (Fig. 5), largely composed of representatives of the families Labridae and Acanthuridae. Chaetodontiform (10.0, 24.4, 8.5, 19.4 and 22.2% respectively) and subcarangiform swimming (33.5, 21.8, 35.0, 25.9 and 23.2% respectively) were also common and rather constant at all flow velocities, while balistiform swimmers were rare in flow above 1 m s^{-1} (10.0, 3.9, 8.0, 0 and 1.0%). In the pelagic assemblage, labriform swimming mode was most common in flow velocities below 0.5 m s^{-1} (66.1 and 60% respectively), mainly due to the high relative abundance of *Abudefduf* spp. At moderate velocities (0.50 to 0.74 m s^{-1}), the subcarangiform swimming mode dominated (61.3%), largely due to occurrences of barracudas *Sphyaena* spp. At high flow velocities ($\geq 0.75 \text{ m s}^{-1}$), carangiform swimmers were most common (93.3%).

Fish size

Total length was measured for pelagic fish at a range of flow velocities, with mostly large individuals being observed in flow velocities above 0.5 m s^{-1} (Figs. 6 & 7). Most taxa were not recorded or measured consistently over a wide span of flow velocities, thus not allowing for correlative analysis. However, non-parametric analyses of the relationship between size and flow were conducted on 3 fish groups. The total length of *Caranx* spp. was found to be positively correlated with flow velocity and power density (Spearman rank correlation test: $\rho = 0.507$, $p < 0.01$). A

Table 1. Fish species occurrences in all flow velocity categories in the benthic and pelagic video samples. Swimming mode (defined according to Sfakiotakis et al. 1999 and Fulton 2007) and trophic group (defined according to Froese & Pauly 2013) are shown for each taxa. Trophic group—INV: invertivore; OMN: omnivore; ROVH: roving herbivore; PISC: piscivore; PLANK: planktivore. Swimming mode—Lab: Labriform; Sub: Subcarangiform; Bal: Balistiform; Car: Carangiform; Cha: Chaetodontiform; Ost: Ostraciiform; Thu: Thunniform; Tet: Tetraodontiform; Unid.: unidentified, taxa only identified to family level

Family/Genus	Species	Trophic group	Swimming mode	No. of observed fish at different current speed (cm s ⁻¹) intervals								
				Benthic stereo-video sampling					Pelagic stereo-video sampling			
				25–49	55–74	75–99	100–124	125+	<25	25–49	50–74	75+
Acanthuridae												
<i>Acanthurus</i>	<i>auranticavus</i>	ROVH	Lab	1	2	19	8	7	1	12		
<i>Acanthurus</i>	<i>dussumieri</i>	ROVH	Lab	7	32	5	2	10				
<i>Acanthurus</i>	<i>nigrofuscus</i>	ROVH	Lab			6	7	2	1			
<i>Acanthurus</i>	sp.	ROVH	Lab	24	33	17	5	3		1		
<i>Ctenochaetus</i>	<i>binotatus</i>	ROVH	Lab	23	38	49	15	6		2		
<i>Naso</i>	<i>brevirostris</i>	PLANK	Sub		1							
<i>Naso</i>	sp.	PLANK	Sub			1			1	2		
Unid.		OMN	Lab	3	6	1			3			
Balistidae												
<i>Balistoides</i>	<i>viridescens</i>	INV	Bal	5		14					1	
<i>Sufflamen</i>	<i>chrysopterum</i>	INV	Bal		2	13					1	
<i>Sufflamen</i>	sp.	INV	Bal	1				1			0	
Unid.		INV	Bal	19	10	5						
Caesionidae												
<i>Aprion</i>	<i>virescens</i>	PISC/INV	Sub		4							
<i>Aprion</i>	sp.	PISC/INV	Sub						5			
Carangidae												
<i>Carangoides</i>	<i>coeruleopinnatus</i>	PISC	Car	1								
<i>Caranx</i>	sp.	PISC/INV	Car						69	43	2	20
<i>Caranx</i>	<i>ignobilis</i>	PISC/INV	Car							4	6	
<i>Caranx</i>	<i>melampygus</i>	PISC	Car						3	2		
<i>Caranx</i>	<i>papuensis</i>	PISC	Car						26	26	8	
Unid.		PISC/INV	Car						8	11	1	8
Chaetodontidae												
<i>Chaetodon</i>	<i>auriga</i>	OMN	Cha	9	19	22	1	1				
<i>Chaetodon</i>	<i>blackburnii</i>		Cha						1			
<i>Chaetodon</i>	<i>kleinii</i>	OMN	Cha		4	12		1				
<i>Chaetodon</i>	<i>lunula</i>	INV	Cha	1	3	1						
<i>Chaetodon</i>	<i>madagaskariensis</i>	INV	Cha	5	7	2	19	19				
<i>Chaetodon</i>	sp.	OMN	Cha	1	7			1				
<i>Chaetodon</i>	<i>vagabundus</i>	INV	Cha		7							
<i>Heniochus</i>	<i>acuminatus</i>	PLANK	Cha		3							
Ephippidae												
<i>Platax</i>	<i>orbicularis</i>	OMN	Sub			1						
<i>Platax</i>	sp.	OMN	Sub	3					17	10		
<i>Tripteron</i>	<i>orbis</i>	INV	Sub	3								
<i>Platax</i>	<i>teira</i>	PISC/INV	Sub							5	15	2
Haemulidae												
<i>Plectorhinchus</i>	<i>flavomaculatus</i>	PISC/INV	Sub	1	2	15		2				
<i>Plectorhinchus</i>	sp.	PISC/INV	Sub	2	2		1		1			
Holocentridae												
<i>Sargocentron</i>	<i>praslin</i>	PISC/INV	Sub	2	7							
Kyphosidae												
<i>Kyphosus</i>	sp.	OMN	Sub	13						8	11	
<i>Kyphosus</i>	<i>vaigiensis</i>	OMN	Sub	17	1							
Labridae												
<i>Bodianus</i>	<i>diana</i>	INV	Lab	1	2	8	1	2				
<i>Coris</i>	sp.	INV	Lab		2							
<i>Halichoeres</i>	<i>hortulanus</i>	INV	Lab	1		4						
<i>Thalassoma</i>	<i>lunare</i>	INV	Lab	16	12	56	12	17				
<i>Thalassoma</i>	sp.	INV	Lab									
Unid.		INV	Lab	1	5	1						
Lethrinidae												
<i>Lethrinus</i>	<i>crocineus</i>	INV	Sub	2								
<i>Lethrinus</i>	<i>harak</i>	PISC/INV	Sub	1	1	5		2				
<i>Lethrinus</i>	<i>nebulosus</i>	INV	Sub	2	7	3		1				
<i>Monotaxis</i>	<i>grandoculis</i>	INV	Sub	5	3				1	1		
<i>Monotaxis</i>	sp.	INV	Sub			1		1				

Table 1 (continued)

Family/Genus	Species	Trophic group	Swimming mode	No. of observed fish at different current speed (cm s^{-1}) intervals								
				Benthic stereo-video sampling					Pelagic stereo-video sampling			
				25–49	55–74	75–99	100–124	125+	<25	25–49	50–74	75+
Lutjanidae												
<i>Lutjanus</i>	<i>fulviflamma</i>	PISC/INV	Sub			1						
<i>Lutjanus</i>	<i>gibbus</i>	PISC/INV	Sub			7	4					
<i>Lutjanus</i>	sp.	PISC/INV	Sub	1	1	2				1		
Monacanthidae												
<i>Cantherhines</i>	<i>pardalis</i>	INV	Bal			5						
Mullidae												
<i>Parupeneus</i>	<i>indicus</i>	INV	Sub	1	4	1		3				
<i>Parupeneus</i>	<i>macronemus</i>	INV	Sub		1	3						
Monodactylidae												
<i>Monodactylus</i>	sp.	OMN	Sub						195	13		
Nemipteridae												
<i>Scolopsis</i>	<i>vosmeri</i>	INV	Cha	3	1	2						
Ostraciidae												
<i>Ostracion</i>	<i>cubicus</i>	OMN	Ost	3								
<i>Ostracion</i>	<i>meleagris</i>	OMN	Ost			4						
<i>Ostracion</i>	sp.	OMN	Ost		2							
Mugilidae												
<i>Mugil</i>	<i>cephalus</i>	OMN	Sub							15	19	
Unid.		OMN	Sub						3			
Pomacanthidae												
<i>Centropyge</i>	<i>multispinis</i>	OMN	Cha	6	25		1			1		
<i>Pomacanthus</i>	<i>rhomboides</i>	OMN	Lab	8	2				1			
<i>Pomacanthus</i>	<i>semicirculatus</i>	OMN	Lab	2	2							
<i>Pomacanthus</i>	sp.	OMN	Lab			4						
<i>Abudefduf</i>	sp.	PLANK	Lab	4					539	198	38	
<i>Abudefduf</i>	<i>vaigiensis</i>	PLANK	Lab						113	53	6	
<i>Chromis</i>	sp.	PLANK	Lab		4							
Unid.			Lab		1				68			
Scaridae												
<i>Scarus</i>	<i>ghobban</i>	ROVH	Lab	4		24	3		1			
<i>Scarus</i>	<i>rubroviolaceus</i>	ROVH	Lab			1						
<i>Scarus</i>	sp.	ROVH	Lab	16	20	18	6	1				
Serranidae												
<i>Epinephelus</i>	<i>flavocaeruleus</i>	PISC/INV	Sub			1						
<i>Epinephelus</i>	sp.	PISC/INV	Sub								1	
Siganidae												
<i>Siganus</i>	sp.	ROVH	Sub		1	3		1				
<i>Siganus</i>	<i>stellatus</i>	ROVH	Sub				1					
<i>Siganus</i>	<i>sutor</i>	ROVH	Sub	15	22	27	18	6				
Scombridae												
<i>Scomberoides</i>	sp.	PISC/INV	Thu							2	1	
<i>Scomberoides</i>	<i>lysan</i>	PISC/INV	Thu							1		
<i>Scomberomorus</i>	<i>plurilineatus</i>	PISC	Thu						10			
Scorpididae												
<i>Neoscorpis</i>	<i>lithophilus</i>	OMN	Sub									1
Sparidae												
<i>Diplodus</i>	<i>cervinus cervinus</i>	OMN	Sub	2								
<i>Rhabdosargus</i>	<i>sarba</i>	OMN	Sub	7	10	83	4	5	4	2		
<i>Rhabdosargus</i>	sp.	OMN	Sub	6	1	7		2	8	3	11	
<i>Sarpa</i>	<i>salpa</i>	ROVH	Sub						1			
Unid.		OMN	Sub	1								10
Sphyaenidae												
<i>Sphyaena</i>	<i>jello</i>	PISC	Sub						2	15	25	
<i>Sphyaena</i>	sp.	PISC	Sub						16	11	5	
Tetraodontidae												
<i>Canthigaster</i>	<i>amboinensis</i>	OMN	Tet	1		3		1				
<i>Canthigaster</i>	<i>valentini</i>	OMN	Tet	1		1		4				
<i>Canthigaster</i>	sp.	OMN	Tet	3	3	4						

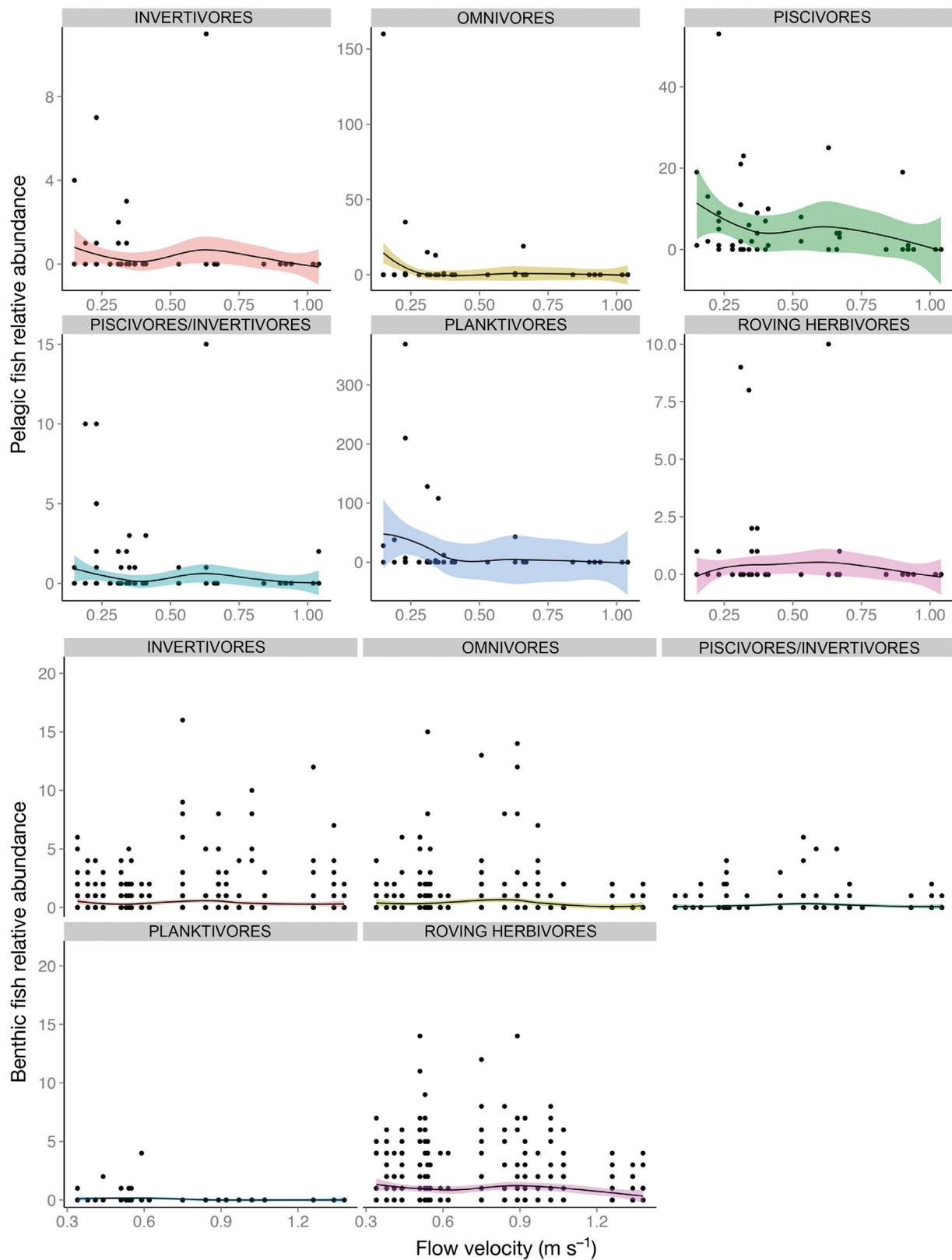


Fig. 3. Relative abundance of different trophic groups of pelagic and benthic fish in relation to flow velocity. Each dot represents the number of individuals of a species in 1 sample. Fitted line: least squared distance to sample points; coloured space: SE. No strict piscivores were recorded in the benthic assemblage

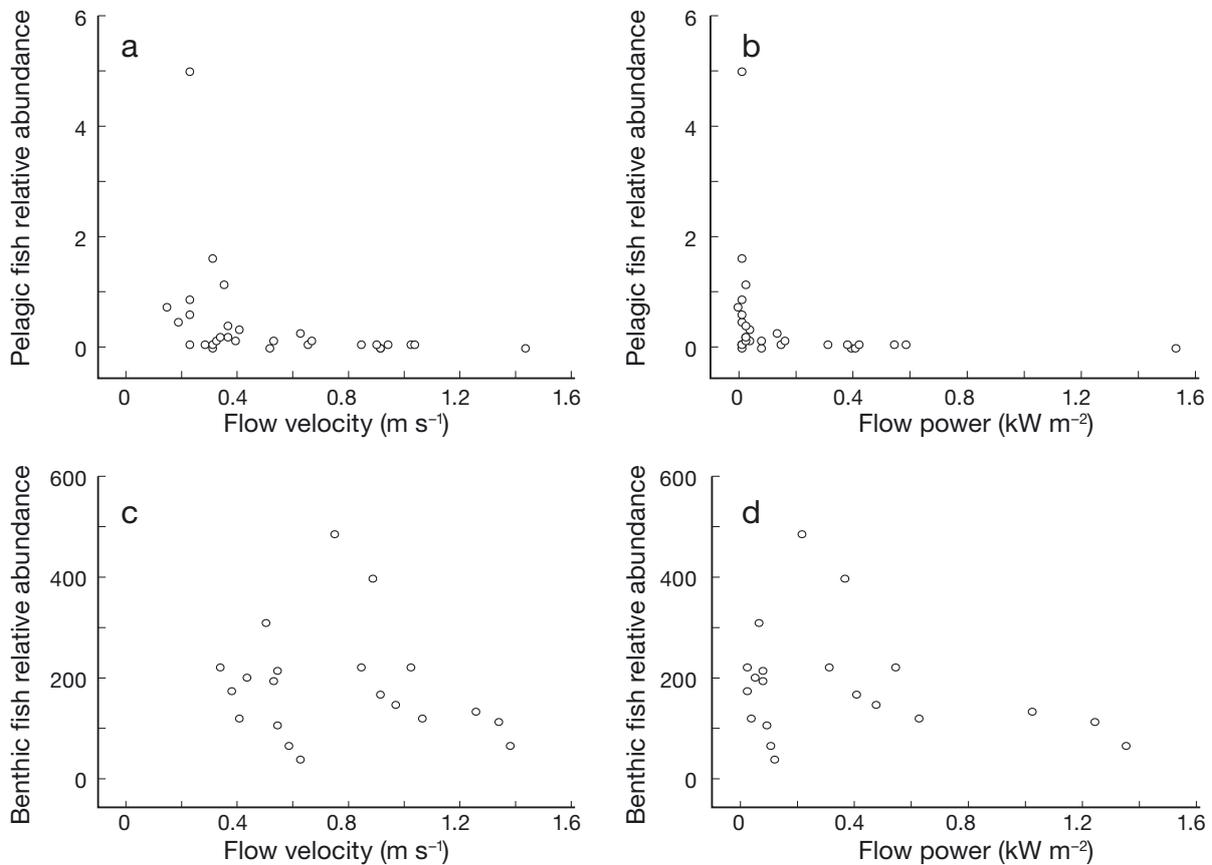


Fig. 4. Relationships between relative fish abundance and flow velocity and energy in flow shown as flow power density for pelagic and benthic fish. Fish relative abundance represents the average number of fish specimens entering each m^2 of the recorded water body during 45 min (units: $\text{fish m}^{-2} 45 \text{ min}^{-1}$)

substantially weaker positive relationship was found for benthic fish as a group ($\rho = 0.201$, $p < 0.05$). No correlation was detected for *Abudefduf* spp. (Fig. 6).

Swimming direction and temporal habitat use

Fish swimming direction was only investigated and compared among pelagic fish. Very few fish swam transverse to the current (i.e. cross-current direction) and less than 1% of the recorded fish were found to move backwards with the current (i.e. swimming against the current at lower speed than the flow). The critical flow velocity where it became more probable for fish to swim along- rather than counter-current differed among taxa. Using logistic regression, the critical velocities were predicted to be 0.46 m s^{-1} for *Platax teira* (logit: $n = 32$, $\chi^2 = 4.932$, $df = 1$, $p = 0.026$), 0.65 m s^{-1} for *Abudefduf* spp. (logit: $n = 60$, $\chi^2 = 19.327$, $df = 1$, $p < 0.001$), and 0.76 m s^{-1} for *Caranx* spp. (logit: $n = 142$, $\chi^2 = 78.845$, $df = 1$, $p < 0.001$) (Fig. 8). For *Sphyr-*

ena spp., flow velocity was not found to be a significant predictor of swimming direction ($p > 0.05$). The Mugilidae family was the only other taxa that showed a similar swimming pattern to *Sphyrana* spp., with an increase in activity as flow speed increased, followed by a sudden drop in relative abundance (observations) at flows faster than 75 m s^{-1} . However, the data distribution of the 41 Mugilidae observations did not allow for statistical analysis.

The predicted critical flow velocity for *Abudefduf* spp. occurred at 0.65 m s^{-1} . Using the oceanographic data on flow velocities, we determined that this allowed fish to use the tidal channel for 65% of the tidal cycle during neap tides, but only 28% during spring tides (Fig. 9). *Caranx* spp. were predicted to be able to use the area during the whole tidal cycle in neap tides, but only 45% of the time during spring tides (Fig. 9). The benthic fish assemblage, which did not show any statistical decline with increased flow velocity, was predicted to be able to utilise the area during all times and all tides.

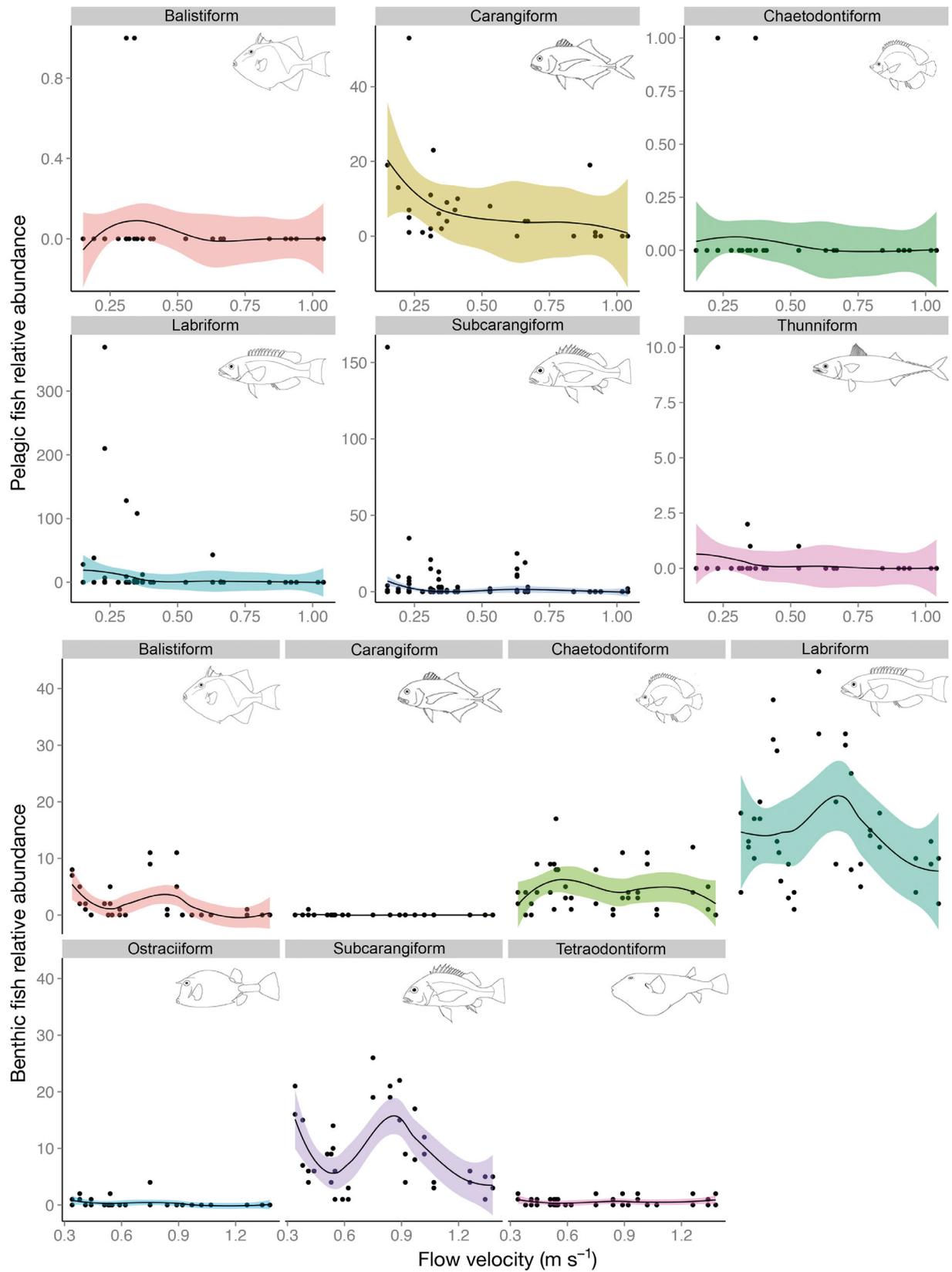


Fig. 5. Fish relative abundance in relation to flow velocity for pelagic and benthic fish categorised by swimming mode. Each dot represents the number of individuals in 1 sample. Fitted line: least squared distance to sample points; coloured space: SE

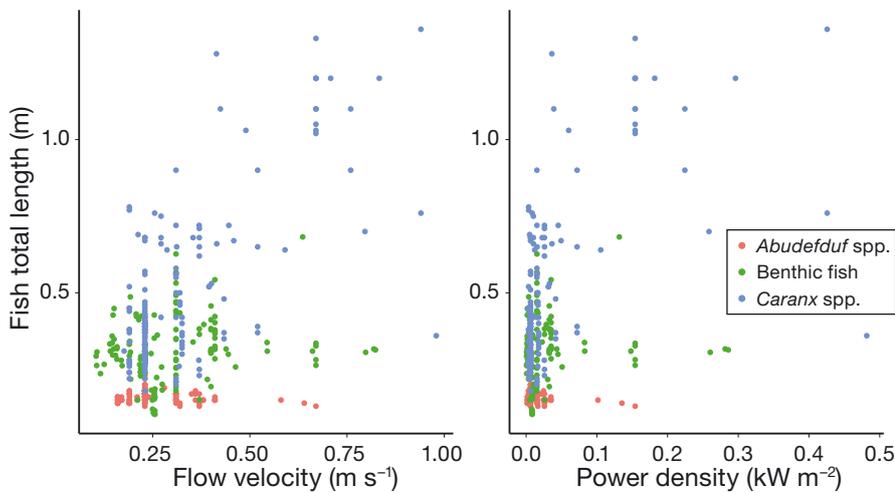


Fig. 6. Relationships between fish total length and flow velocity and power density for *Caranx* spp., *Abudefduf* spp. and the benthic fish assemblage

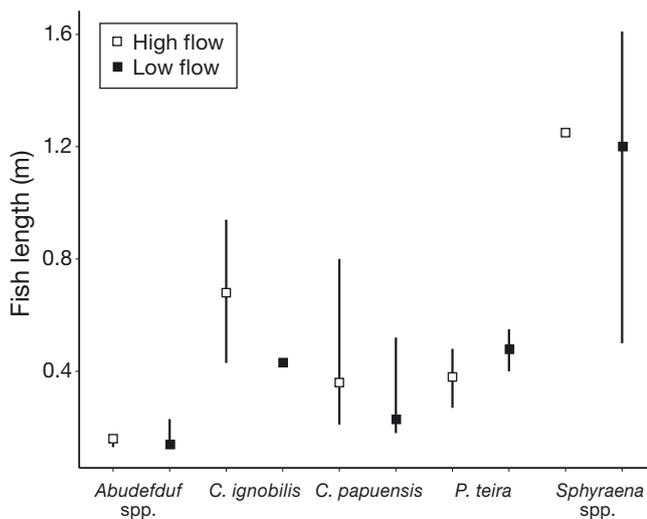


Fig. 7. Total body length for different fish taxa in the pelagic for 2 different flow velocity categories: low flow ($\leq 0.5 \text{ m s}^{-1}$) and high flow ($> 0.5 \text{ m s}^{-1}$). Spreads indicate mean, min. and max. values of measured body length. Numbers of measured fish in each flow category (low, high) were: *Abudefduf* spp. (143, 3), *Caranx ignobilis* (1, 15), *Caranx papuensis* (50, 16), *Platax teira* (28, 7) and *Sphyaena* (35, 1)

Observed behaviour

Sphyaena spp. and *Caranx* spp. were observed patrolling the pelagic in groups and swimming in formations. No ambitious attack of prey was observed during the study, although specimens from both taxa showed some vague attempts to follow prey. *Abudefduf* spp. was observed feeding on plankton in the water column while solitary or in small groups. In the benthic community, roving herbivores and omni-

vores such as acanthurids and sparids were found frequently grazing on the epilithic algal matrix.

DISCUSSION

Fish relative abundance in relation to water flow

Flow velocity has previously been shown to modify fish behaviour (Gerstner 1998, Johansen et al. 2007, Heatwole & Fulton 2013). In this study, the relative abundance of the pelagic fish assemblage in the tidal channel significantly decreased with increased flow. The relative abundance of the benthic

fish assemblage was less influenced during the tidal cycle, probably because benthic structures (in this case rocks and boulders) that could be used as flow refuges were present. It is, however, possible that increased flow induced behavioural effects not examined in the present study, such as altered swimming behaviour (Heatwole & Fulton 2013) or flow refuging.

Flow-refuging behaviour in reef fish greatly reduces energy expenses for swimming fish, allowing fish with a range of swimming abilities to occupy and exploit current-swept locations (Gerstner 1998, Johansen et al. 2007). The absent or weak effect of flow velocity on the benthic fish assemblage as shown in this study probably reflects flow-refuging behaviour, where fish chose to utilize flow-protected micro-habitats when water velocity increased. The increase in abundance of labriform and subcarangiform swimmers at flow velocities around 0.9 m s^{-1} might be related to a lesser risk of predation at those flow velocities (Fig. 5). Since statistical power was low (< 0.6) regarding the influence of flow on benthic fish activity, the possibility of weaker relationships between flow velocity and benthic fish activity cannot be ruled out. According to the results, benthic fish relative abundance appeared to decrease at high flows, but to a much lesser degree than for pelagic fish. In a parallel study at the same location, Hammar et al. (2013) found a negative correlation between benthic fish abundance and flow velocity only when a hazardous object (a tidal power turbine) was introduced at the site, thus preventing fish from swimming their preferred route. The repelling effect was strongest on compressiform fish such as *Chaetodon*

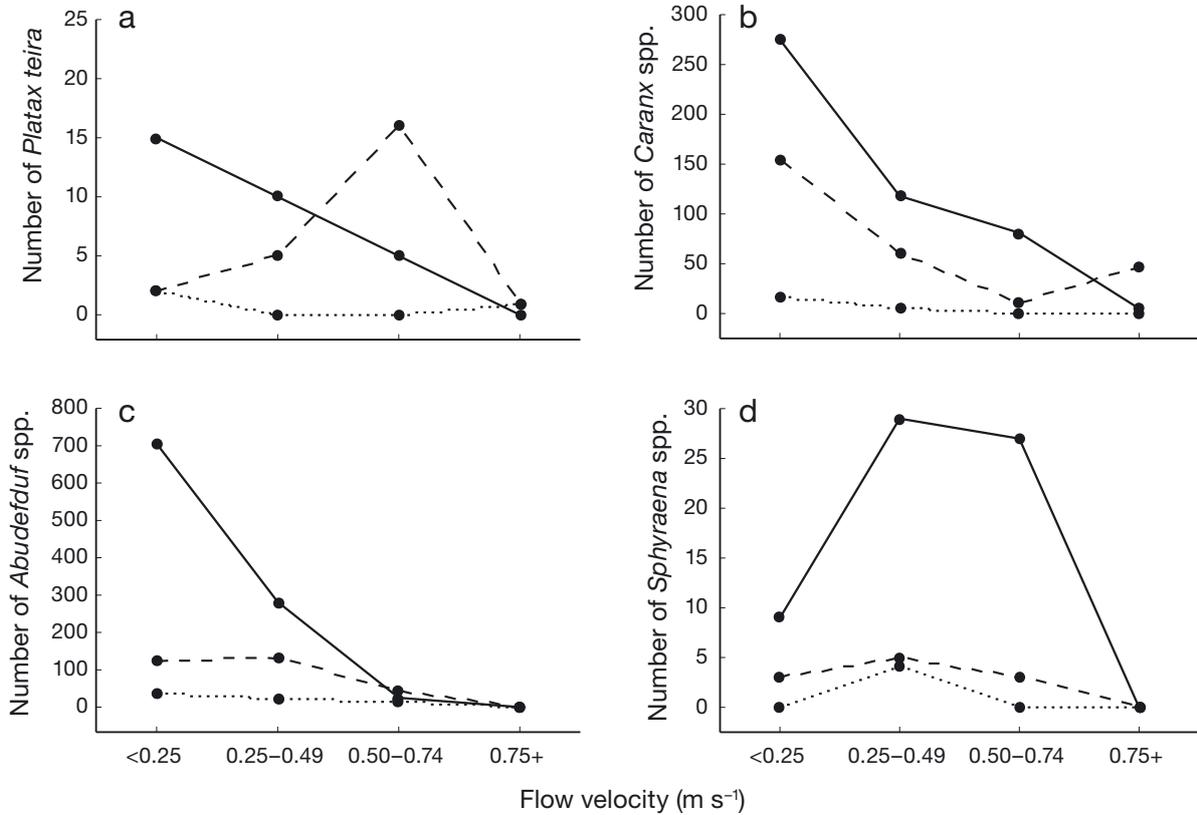


Fig. 8. Swimming directions over flow velocity categories for (a) *Platax teira*, (b) *Caranx* spp., (c) *Abudefduf* spp., and (d) *Sphyraena* spp. (*S. barracuda* and *S. jello*). Black lines: counter-current swimming; dashed lines: cross-current swimming; dotted lines: along-current swimming

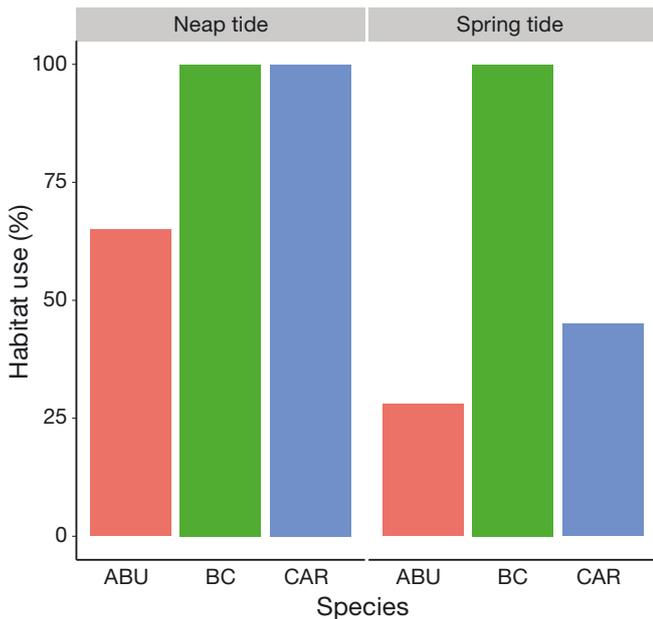


Fig. 9. Habitat utilisation, in proportion of time of the tidal cycle, by the benthic fish community (BC), *Abudefduf* spp. (ABU) and *Caranx* spp. (CAR) during neap and spring tide periods

spp., *Acanthurus* spp. and *Siganus* spp. More fusiform-shaped fish such as *Thalassoma* spp., *Lethrinus* spp. and *Rhabdosargus* spp. were less affected, suggesting that body shape also influences fish response to flow velocity. It is also possible that the fish had adapted phenotypically to a high-flow environment, allowing them to exploit the area at all flows. Fulton et al. (2013) found that fin aspect ratio of a damselfish was higher and that they swam faster on wave-exposed reefs compared to on sheltered reefs. The tidal flow could also have acted as an environmental filter, filtering away smaller, more vulnerable species. For example, only adults of *T. lunare* was observed, while juveniles were common on a shallow, sheltered part of the reef nearby (authors' pers. obs). Juveniles of the genus *Thalassoma* go through an ontogenetic shift in fin aspect ratio from low to high, which indicates that species of this genus possess lesser swimming abilities as juveniles (Fulton & Bellwood 2002).

In the pelagic, where no solid flow refuges exist, fish relative abundance diminished as expected with flow velocity. The relationship between fish

relative abundance and flow velocity most likely represents the different species' ability to maximize energy gain with regard to energy losses in water flow and the success of catching prey items, a mechanism observed in salmonids foraging in fast-flow streams (Fausch 1984). Fish that were recorded at higher flow speeds (*Caranx* spp. and *Sphyraena* spp.) were almost always seen swimming in formation against the current, a strategy utilised to minimize energy costs by taking advantage of vortices generated by the other swimming fish (Liao 2007). Abundance of pomacentrids (*Abudefduf* spp.), which do not use such behaviour, declined sharply at flow velocities above 0.5 m s^{-1} . This probably reflects the lesser swimming ability of these species compared to the larger and more fusiform *Caranx* spp. and *Sphyraena* spp.

Flow power density might be a better predictor than flow velocity for fish behaviour in unidirectional flows, because it reflects the energetic costs of swimming in a flow. Exponential changes in energy consumption using flow velocity as a predictor variable has been recorded in other studies (e.g. Korsmeyer et al. 2002). While this apparent observation is trivial from a physical point of view it can be a noteworthy remark for biologists. Ecological studies might benefit from using power density when statistically testing the influence of currents on aquatic fauna. However, flow velocity and power density are not the only factors impacting fish; other characteristics of the flow such as turbulence can have major impacts on fish behaviour (e.g. decreased fish swim speed) (Lupandin 2005). Comparing the findings from this study with other locations and especially wave-induced flows thus requires caution, since wave-induced flow is likely much more turbulent than unidirectional tidal-induced flow. A highly structural complex reef would probably also create more turbulence compared to the present study, where bottom substrate was mainly composed of large rocks and boulders.

Fish assemblage composition and function in relation to water flow

The difference in trophic group composition between the pelagic and benthic assemblages clearly reflects the resources of the 2 distinct habitats. Flow velocity had no clear structural influence on the benthic assemblage, allowing functions such as herbivory to be maintained during the whole tidal cycle (Figs. 5 & 9), and fish were frequently observed grazing on the epilithic algal matrix during all flow

velocities. This suggests that benthic structures creating flow refuges for fish are important features in the seascape.

Current-swept locations can be attractive for planktivorous species due to transport of large amounts of zooplankton (Hamner et al. 1988). The planktivorous *A. vaigiensis* and *A. sexfasciatus* were very abundant in the pelagic, while on a nearby shallow reef, which is not subjected to the same type of tidal current, *A. vaigiensis* was found to be distinctively less abundant (250 vs. 2 ind. 250 m^{-2} respectively) (Pereira 2000). The omnivores *Monodactylus argenteus* and *M. falciformis* that also feed on plankton were also very abundant in lower flows but not recorded at nearby sheltered reefs (Pereira 2000, authors' pers. obs.).

The change to dominance of piscivores at higher velocities in the pelagic (e.g. *Caranx* spp. and *Sphyraena* spp.) is likely due to a combination of morphological traits (e.g. the ecosiform body shape of sphyraenids) and the efficiency of carangiform and subcarangiform swimming modes in these conditions, allowing for catching prey in high-flow environments. This can be compared to the planktivorous fish (mainly *Abudefduf* spp.) that diminished at intermediate flow velocities. For example, microhabitat utilisation of freshwater fish in fast flows is strongly influenced by prey capture success (Hill & Grossman 1993). The increase in abundance of the piscivore *Sphyraena* spp. at moderate to high current velocities compared to low velocities suggests a preference for fast flows compared to slack water. This behaviour probably reflects a current-dependent predation strategy. *Sphyraena* uses ram feeding (i.e. a fast lunging attack towards its prey) at extremely fast velocities (1.44 m s^{-1} ; Porter & Motta 2004). The ecosiform body shape of sphyraenids, with posteriorly placed fins and small body depth, facilitates acceleration (Webb 1988), and makes them excellent exploiters of fast currents in search of prey. In this study, *Sphyraena* seemed to prefer flow velocities between 0.25 and 0.75 m s^{-1} . In one of the few studies of the genus *Sphyraena*, Barreiros & Santos (2002) also recorded that occurrences were always associated with strong currents (although the magnitude of these 'strong currents' was not defined). Despite being an important food fish in many tropical and subtropical regions, as well as an important top predator, little is known about the biology of the *Sphyraena* taxon and their behaviour in relation to strong currents (O'Toole et al. 2010). The results presented in this study are the first data on measured flow velocities related to abundance of sphyraenids.

Swimming direction and habitat use in relation to flow velocity

Counter-current swimming (rheoreaction) is the most common behaviour of fish swimming in a current (Lupandin 2005). In this study, rheoreaction was the most common swimming direction up to certain flow velocities; thereafter fish turned and their presence rapidly decreased. Since the flow velocity at which fish start to swim with the current instead of against it (i.e. critical flow velocity) appears to be species-specific (Fulton & Bellwood 2004, Fulton et al. 2005), it seems that the velocity level most likely reflects the swimming ability and energetic cost of swimming in the studied species. Species-specific limits have also been recorded in laboratory studies where species with distinct morphological traits and of different swimming techniques (median pectoral swimming versus body-caudal propulsion) differ in energetic costs and swimming performance over flow velocities (Korsmeyer et al. 2002, Walker et al. 2013). Flow might also initiate distinct behavioural responses in species with different morphological traits and swimming abilities (Heatwole & Fulton 2013). In this study, *Platax teira* started to swim transverse current when flow increased, while Sphyraenids did not use that strategy. The critical flow velocity was high for some predatory species, and it seems as though the study site was used as a foraging area until the flow increased above this point. For *Caranx* spp. and *Sphyraena* spp., who displayed the highest critical flow velocities, it would thus be possible to take advantage of food resources in the current channel during most of the tidal cycle, while *Abudefduf* spp. and *P. teira* have shorter 'time windows' and need to seek shelter in suitable flow refuge microhabitats during a longer period of time (Fig. 9). Since flow reaches higher velocities in spring tide, the lunar cycle (i.e. the spring and neap tidal regime dynamic) is an important factor in shaping the pelagic fish assemblage and influenced patterns of habitat use in the tidal channel. It should, however, be noted that the spring tide flow velocities recorded in the present study are rather extreme.

Interestingly, the benthic fish assemblage did not show any significant decrease in relative abundance with flow velocity. The large (~1 m height) benthic structures in the present study thus seem important for maintaining of ecological functions during the tidal cycle. But even small coral heads (7.4 × 7.4 × 7.5 cm) have been found to reduce flow velocities up to 66% in laboratory experiments (Johansen et al. 2008). Low-relief structures like sand ripples (Gerst-

ner 1998) or even the bottom boundary layer (Lough et al. 1989) can be utilised as flow refuges for fish but are probably not enough to permit activities such as foraging.

Swimming mode

Similar to studies of wave-induced flow-exposed fish assemblages (Fulton et al. 2001, Fulton & Bellwood 2004, 2005), labriform swimming (mainly represented by the genus *Thalassoma*) was the most common swimming mode for the benthic community in all flow velocities tested in this study. *Thalassoma* has been proposed as a good exploiter of flow-exposed sites due to morphological traits such as a high fin aspect ratio and the use of lift-based thrust for swimming propulsion (Wainwright et al. 2002, Fulton & Bellwood 2004). The increase in abundance of labriform swimmers in moderately strong currents might be due to difficulties of predators to capture agile prey in this flow, thereby making it possible for fish with good swimming abilities to exploit the area. It seems that tidal-induced flow shapes fish assemblages differently with regard to swimming mode compared to wave-induced flow (e.g. Fulton & Bellwood 2005). The abundance of subcarangiform swimmers, who possess lesser manoeuvrability than labriform swimmers, has been shown to be lower in locations with high wave exposure (Fulton & Bellwood 2005). In this study, the proportions of different swimming modes among benthic fish were largely maintained at all velocities. This is most likely because in this setting (a unidirectional flow) the large rocks provided sufficient flow refuges, allowing for species of differing swimming capacities to exploit the area due to flow-refuging behaviour. The unidirectional flow in this study is probably also much less turbulent than wave-induced flow in general, allowing access to fish of lesser manoeuvrability (e.g. subcarangiform swimmers). Subcarangiform swimmers such as *Rhabdosargus* spp. were recorded feeding on the turf algae covering the rocks while the main current reached flow velocities exceeding 1 m s⁻¹.

The effects of flow velocity on the pelagic assemblage showed that carangiform swimming was the most efficient swimming mode in high flow velocities, followed by subcarangiform swimming, indicating that these are the swimming modes that allow for energetic gain in unidirectional high-flow velocity conditions where flow refuges are absent. The sharp decrease in abundance of the smaller labriform swimmer *Abudefduf* spp. at flow velocities above

0.5 m s⁻¹ implies a lower swimming capacity, less prey capture success and a higher energetic cost of swimming compared to carangids and sphyraenids. Thus, species of the *Abudefduf* genus are more restricted by the physical conditions in this environment. It should, however, be noted that the spring tide flow velocities recorded in the present study are rather extreme. The critical flow velocity of *Abudefduf* spp. at 0.65 m s⁻¹ represents a strong current that most humans would find it difficult to hold station in.

Labriform swimming might be the dominating swimming mode in high-flow benthic habitats due to a need for speed and manoeuvrability (Fulton & Bellwood 2005), while subcarangiform and carangiform swimming seem more useful in strong currents where fine-scale manoeuvrability is of less importance and flow refuges are absent.

As studies on temperate reef fish assemblage and in freshwater have suggested, flow velocity can act size-selectively, excluding small specimens at high velocities (Fulton & Bellwood 2004, Lupandin 2005). On coral reefs however, fish distribution seems to be more strongly related to morphological traits such as fin aspect ratio than size (Wainwright et al. 2002, Fulton & Bellwood 2004). For the benthic assemblage in the present study, a weak effect positive effect on size with increasing flow was detected. Also, fish smaller than 5 cm were not common during any tidal phase, suggesting that species of that size avoided the area. For example, *Chromis dimidiata* that otherwise is common on the Inhaca reefs (Pereira 2000) was not observed. However, this might also be related to the low coral cover at the study site.

In the pelagic, Carangidae was the only family with a sufficient number of individuals recorded over a range of sizes and flow velocities to allow for size-selectivity comparisons. In accordance with earlier studies (e.g. Fulton & Bellwood 2004), we found that the number of small individuals significantly decreased with increasing flow velocity. This suggests that predator pressure changes with flow velocity. No small (juvenile) *Sphyraena* spp. were recorded, probably due to ontogenetic habitat shifts, since juveniles prefer shallow seagrass beds and mangroves (Faunce & Serafy 2008). Both *Caranx papuensis* and *C. ignobilis* were represented by larger individuals in high flow, and for *Sphyraena*, only large individuals were recorded. The absence of *Abudefduf* spp. at higher flows might be a combination of swimming mode and its smaller size. No distinct effect on size by flow could be seen for *P. teira*, but all recorded individuals were adults, suggesting that the area is not a suit-

able habitat for smaller individuals. Size might thus be more important than swimming mode when negotiating flows.

Implications for ecosystem functioning

This study is one of few assessing the strength of unidirectional flows in structuring fish assemblages, while also providing information of effects on trophic groups and ecological functional groups during the whole tidal cycle. This study provides information that distinct assemblages (benthic and pelagic) differ in response to flow velocity, and also that these assemblages are structured differently. Despite extreme flow velocities, a number of pelagic specimens utilised the water column, indicating that energetic gain exceeds the cost of holding station and swimming. Flow also seems to explicitly attract certain species, such as sphyraenids and planktivorous pomacentrids—however the pomacentrids were largely restricted to flows less than 0.5 m s⁻¹.

While flow velocity shaped trophic group composition in the pelagic, effects on the benthic fish assemblage were weak, demonstrating that the presence of structures allows fish to utilise certain habitat functions during the whole tidal cycle. Due to flow-refuging behaviour and utilization of microhabitats, fish of a range of swimming capacities can exploit resources in high-flow habitats; this has also been demonstrated in studies of wave-induced flow impacts on fish assemblages (e.g. Fulton & Bellwood 2005, Johansen et al. 2008). Since habitat utilisation by fish in fast flows are suggested to be largely based on net energy gain (Hill & Grossman 1993), these results suggest that the advantages exceed the disadvantages of residing in the area for a number of species, despite very high flow velocities. One of the advantages could be abundant food resources due to current-induced transport (Lewis & Pedley 2001), as indicated by the large number of *Abudefduf* spp. and *Monodactylus* spp., and that primary production of algae and corals augment with flow velocity (Carpenter et al. 1993). Actually measuring primary production of coral and algae would provide valuable information on productivity and indications of resource availability within high-flow areas. Another advantage could be less predation pressure in high flow velocities (>0.8 m s⁻¹), explaining the increase in activity for some of the benthic species, especially for labriform swimmers.

Limitations of the study

Our study provides information from one high-flow location concerning effects of a tidal current on the present fish assemblage in general. However, to be able to detect fine-scale flow effects at the species level, further information is needed related to morphology of fish species as well as information of higher spatial resolution on flow velocity for determination of flow refuges. Some rare species were not included in the analyses due to very low abundances, and diel variation of the fish assemblage was not considered. Also, size of fish was not measured for all species across all flow velocities, limiting the possibility to further explore size effects on the benthic assemblage. It is further important to remember that turbulence also influences fish swimming speed and ability to negotiate currents (Lupandin 2005), a variable that was not measured in the present study.

CONCLUSIONS

Flow velocity did structure the fish assemblage in the pelagic, but not in the benthic samples, during the surveyed tidal cycles. The same was true for fish relative abundance. Hence, ecological functions such as herbivory in the benthic fish community were largely maintained during the whole tidal cycle, with presence of most feeding guilds and phenotypes of fish, because of the presence of flow refuges at the bottom. For pelagic fish, utilization of the habitat changed over the tidal cycle, with small-sized fish and plankton-feeding fish utilizing only low and intermediate flows while large predators were also present at faster flows, when they are likely to have an advantage during foraging due to their stronger physical ability. The combination of high tidal flow velocity and presence of flow refuges is thus likely to enhance the ecological value of an area as it consists of a productive area that both sustains the ordinary reef assemblage and generates different 'time windows' of particularly beneficial conditions for plankton feeders and large predatory fish. According to these results, areas with complex bathymetry (such as reefs), subjected to strong tidal currents should be regarded as exclusive entities of the seascape, and their potential ecological value should be increasingly considered in marine management. Care should also be taken to maintain benthic structures intact in this environment.

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