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NOTE

A plankton trap for exposed rocky intertidal shores

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ABSTRACT: This paper describes a passive Rocky Intertidal Plankton Trap (RIPT) that can be used in exposed rocky shores. The RIPT is light, simple to build, easy to install and inexpensive. It endures water velocities up to 7.7 m s^{-1} and provides an integration over time of the mero- and holoplankton arriving at the rocky shore. Two sets of 4 traps were tested, over a period of 3 d, in 2 exposed rocky shores in central Chile. The RIPTs collected a total of 21 major plankton taxa ranging in size from 100 µm (bivalve larvae) to 2700 µm (Isopoda). The cumulative number of planktonic organisms collected per trap ranged between 123 and 215. Cylinders of dentist chalk attached inside and outside the RIPTs and specially designed RIPT-flowmeters permitted an evaluation of water flux and an approximation of the rate of water filtering through the RIPTs. Maximum water velocities on the intertidal platforms were determined with the use of an intertidal dynamometer.

KEY WORDS: Plankton · Trap · Rocky intertidal

The arrival, settlement and recruitment of planktonic larvae at intertidal rocky shores vary both on temporal and spatial scales (Crisp & Southward 1953, Hawkins & Hartnoll 1982, Underwood & Denley 1984, Crisp 1985, Gaines & Roughgarden 1985, Gaines et al. 1985, Gaines & Bertness 1993). Devices to sample the water column for plankton, such as nets or pumps, have been used for decades in offshore and nearshore waters, but in general they are only useful for semi-instantaneous estimates. Effective sampling devices that integrate over time to pool the plankton arriving directly at the rocky shore are insufficient. For intertidal organisms which disperse over short and/or long distances, the lack of such samplers results in a critical lack of data that would allow a better understanding of spatial patterns of dispersal. Nevertheless, some passive cylindrical plankton traps (tube traps), based on the principle of sediment traps, have been proposed (see Yund et al. 1991) and they work well in subtidal areas with low turbulence. Otaiza (1989) designed an intertidal filter-cup plankton trap to sample larvae of barnacles in New South Wales, Australia. We modified Otaiza's (1989) design and produced a device that can be used in sheltered as well as exposed intertidal rocky shores. This paper describes the trap and the results obtained in pilot tests on the rocky shore of Las Cruces in central Chile.

Material and methods. The Rocky Intertidal Plankton Trap (RIPT) is a passive sampling device to be used in sheltered as well as in exposed intertidal shores. The trap is based on a single filter-cup and a plastic funnel which are mounted on 2 steel plates (Fig. 1). The filtering portion of the trap is a cup made from a section of 5 mm PVC water pipe, 10 cm in diameter and 12 cm long, with a volume of 450 cm^3 (discounting the funnel space, Fig. 1A, no. 1). The bottom of the cup is permanently sealed with glue to an end piece of PVC, while a removable piece of PVC with a central hole (6 cm in diameter) fits on top of the trap (Fig. 1A, no. 8). Four circular holes of 3.2 cm in diameter are cut through the sides of the pipe section, midway between the top and the bottom, and covered with a 120 µm plankton net glued to the inside wall of the pipe. The holes, spaced 5.5 cm apart, are located on the side of the pipe facing inshore (holes with plankton net facing the ocean are often ripped out by waves). A plastic funnel 9.5 cm in diameter (Fig. 1A, no. 1) is mounted vertically inside the filter cup and aligned with the hole in the top end piece. The funnel is held in place by sections of PVC glued to the inside wall of the pipe (Fig. 1B, no. 12). The small end of the funnel, with a 1-way valve system (Fig. 1A, no. 2), is cut to fit into the cup (4.5 cm above the bottom). The valve system consists of an 'o'-ring placed at the top of the narrow section of the funnel and a floating wooden ball 7 mm in diameter. This allows for drainage of the funnel at low tide but pre-

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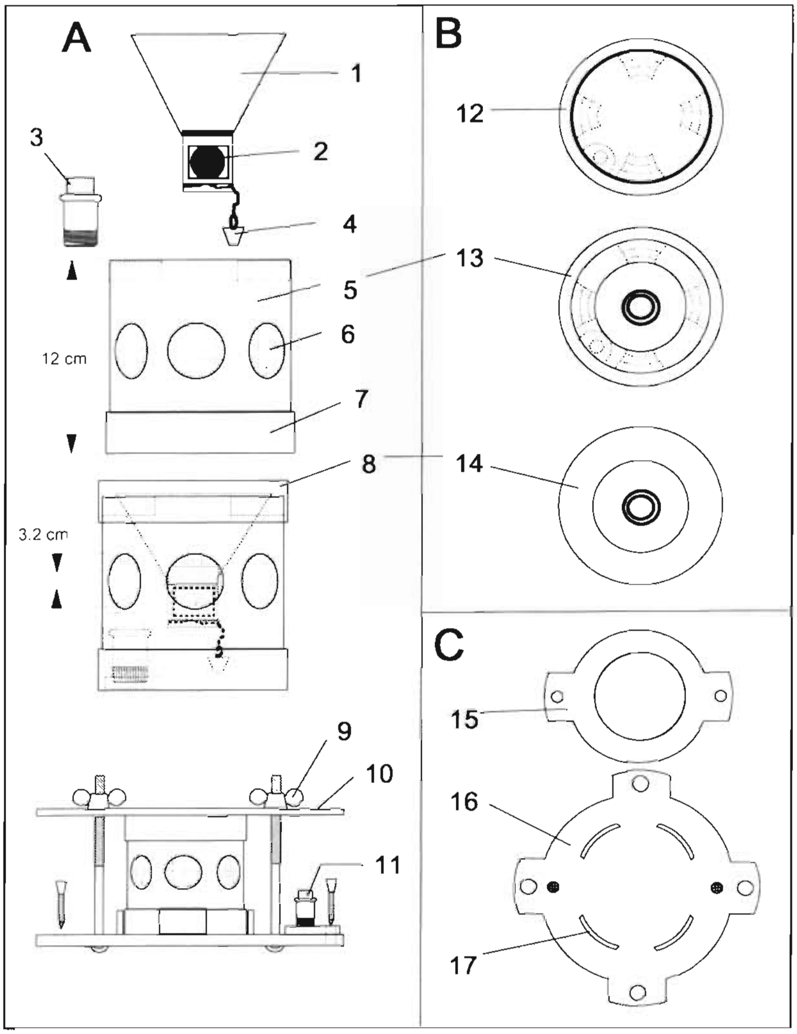
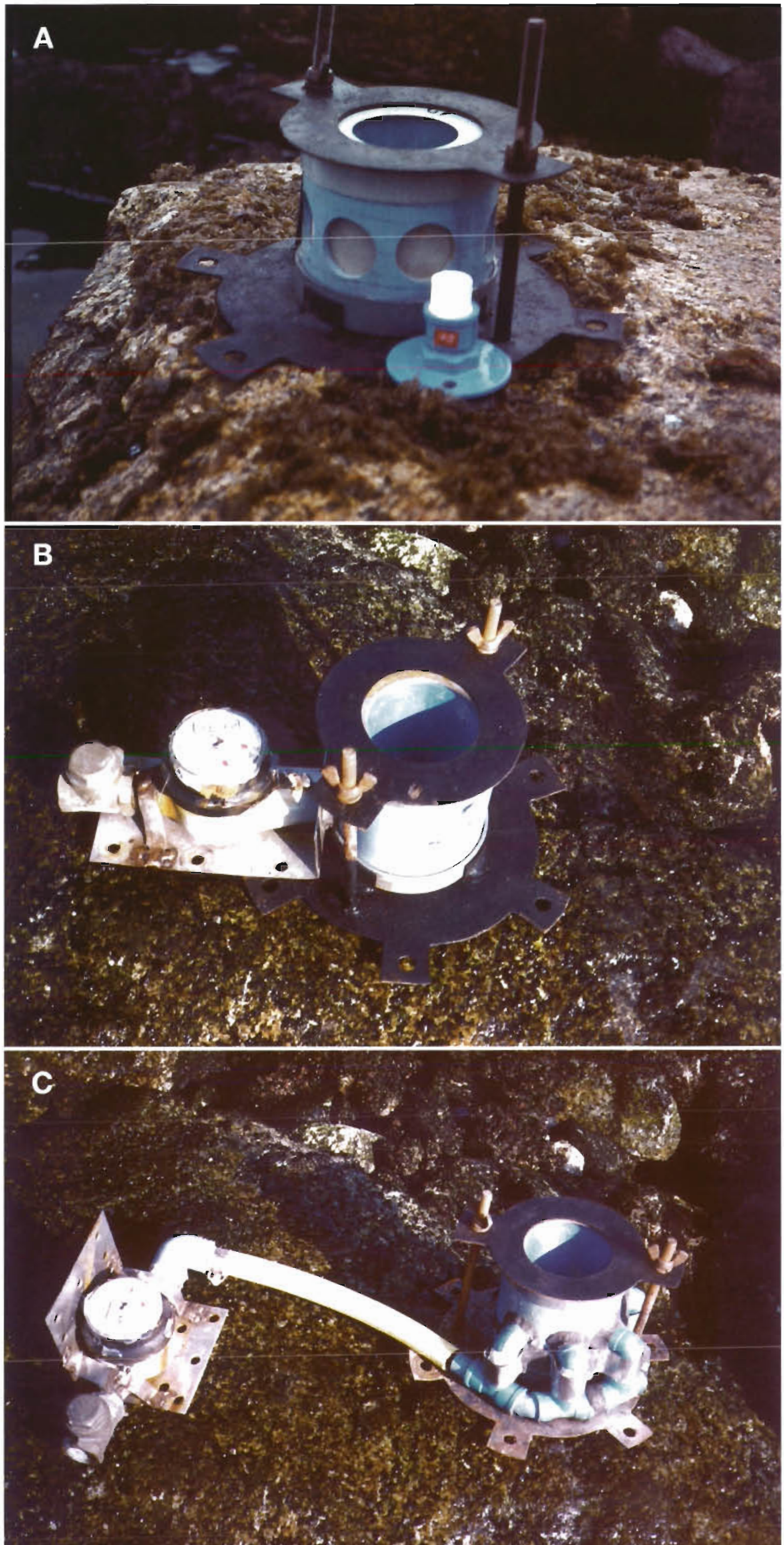


Fig. 1. Diagram of the Rocky Intertidal Plankton Trap (RIPT) and anchoring elements. (A) Lateral view. (B) Top view. (C) Steel anchoring plates. 1: plastic funnel; 2: 1-way valve; 3: internal dentist chalk cylinder; 4: formaldehyde cube; 5: PVC filter cup; 6: plankton mesh, 120 µm; 7: PVC bottom piece; 8: PVC top piece; 9: wing-nuts; 10: lateral view of complete RIPT with internal and external dentist chalk cylinders installed; 11: external dentist chalk cylinder; 12: RIPT top view before funnel installation; 13: RIPT top view after funnel installation; 14: RIPT top view with top PVC piece installed; 15: top steel plate; 16: bottom anchoring steel plate; 17: vertical pieces

vents water from leaving the cup when the cup is filled with water (Fig. 1A). An anchoring and mounting system for the trap is built out of 2 steel plates (Fig. 1C). The bottom plate (Fig. 1C, no. 16) is circular with 4 bolt holes for attachment to the rock. Four vertical pieces (Fig. 1C, no. 17), to hold the filter cup, are welded in a 12 cm diameter circle, around the center of the plate. In addition, two 0.8 cm diameter and 12 cm long bolts, with the screws facing upwards, are permanently fastened to the plate. These are set on opposite sides of the bottom plate outside the cup holder. The top plate (Fig. 1C, no. 15) is set on top of the filter cup. It is circular, with a large hole of 8 cm diameter in the center, such that the plate does not block the entrance to the filter cup. Two bolt holes on opposite sides of this plate allow it to be attached to the bolts of the bottom plate. Wing-nuts (Fig. 1A, no. 9) with pressure washers are used to hold the top plate and to keep the filter cup secure on the mounting plate.

The relative water flow through the RIPT was evaluated by 2 methods. First, we measured the mass lost by dentist chalk cylinders (Yund et al. 1991). Each trap was set with 2 cylinders (2 cm in diameter, 1.8 cm long and glued into plastic pipe fittings) of known dry weights, ranging from 25 to 35 g. One was screwed internally to the bottom of the filter cup fitting and the other externally to the bottom steel plate (Fig. 1A, nos. 3 & 11). The sides and bottom of the chalk surface were painted with polyurethane, so that only the top surface was exposed to dissolution by the water flow. Second, we directly measured water flow through a 2.5 cm freshwater domestic flowmeter (Maipo-TM-Schlumberger, with 0.1 l precision): (a) connected to a 2.5 cm diameter hole installed 3 cm above the bottom of a RIPT cup, without side holes (RIPT-flowmeter-a) facing the waves, and (b) connected directly to the 4 side holes of the cup (2.5 cm diameter each) with plankton mesh 3 cm above the bottom of the RIPT, facing the waves. Water was collected through a single 2.5 cm plastic pipe connected to 4 plastic elbows fitting each of the holes (RIPT-flowmeter-b). Fig. 2 provides photographs of the RIPT and each type (a and b) of the RIPT-flowmeters to clarify these design descriptions. In both cases the outlet was equipped with a 1-way valve. One RIPT-flowmeter-a was bolted on to a rock next to each set of 4 collecting RIPTs. Water filtration measurements through RIPT-flowmeter-a and b were compared in the field to allow for corrections. Measurements (l h^{-1}) were taken at low

Fig. 2. (A) RIPT installed on an intertidal rock. (B) RIPT-flowmeter-a. (C) RIPT-flowmeter-b


A
B
C

tide every 24 h, and it was assumed that water flowing through the RIPT-flowmeters corresponded approximately to the water flowing through the nearby collecting RIPTs. Wave force was determined through the use of the Bell & Denny (1994) dynamometer (Castilla et al. 1997). A dynamometer was bolted to the rock 25 to 35 cm apart from each RIPT. The resetting of the dynamometer, simultaneously with the removal of plankton from the filter cups, was done every 24 h. Collecting RIPTs, RIPT-flowmeters and dynamometers were bolted to the granitic rock with screws using a Ryobi gas-operated drill.

To reduce the possibility that larvae may settle inside the trap, all internal parts of the RIPTs were painted with antifouling paint. Furthermore, to reduce the possibility that trapped organisms might be consumed by other organisms, one 10 mm dentist chalk cube (molded in ice cube holders), prepared with formaldehyde, was hooked at the end of the funnel in each RIPT. The cubes were permanently covered by 4.5 cm of water (Fig. 1A). Adults of the amphipods *Hyale media* and *H. hirtipalma* collected from intertidal algal mats were used as test invertebrates in a series of RIPT laboratory experiments to determine the killing effectiveness of the formaldehyde cubes. Four replicates were tested for each condition: cubes prepared with formaldehyde at 37%, 10%, fresh water and no plaster cubes (the last 2 as controls). Each RIPT contained 10 *Hyale* spp., under a constant water flow of 200 l h^{-1}. Amphipod observations lasting 15 s were done inside the RIPT at 0 (start), 1, 5, 15, 30, 45 and 60 min. The criterion for considering an amphipod dead was its total lack of movement over the period of observation. At the end of the experiment, alive and dead amphipods were checked under a binocular microscope.

Collecting RIPTs were tested in 2 exposed rocky intertidal platforms, inside and outside the Marine Preserve of the Estación Costera de Investigaciones Marinas (ECIM) at Las Cruces (33° 29' S, 71° 38' W) in central Chile, between 16 and 18 September 1997. The platforms, approximately 400 m apart and less than 45° of slope, were directly exposed to the incoming waves. The semi-diurnal low tides ranged between 0.01 and 0.04 m. The study area has been described by Castilla & Durán (1985), Castilla (1988), Durán & Castilla (1989) and Alvarado & Castilla (1996). One set of 4 RIPT and a RIPT-flowmeter-a were placed on the Las Cruces Marine Preserve platform (human exclusion) and the second set was placed outside (human exposed, see Botsford et al. 1997). They were bolted at approximately 80 to 100 cm above the *Lessonia nigrescens* belt (Santelices et al. 1980, Castilla 1981) on the mid-intertidal fringe of each platform. This level coincides with the lower border of the barnacle *Jehlius cirratus* in the case of the Preserve, and with the lower border of the mussel *Perumytilus purpuratus* outside the Preserve (Durán & Castilla 1989). The RIPTs were exposed to incoming waves for 3 d. Every 24 h, at low tide, the filter cups were thoroughly washed with a squeeze bottle before detaching them from the anchoring device and the contents were transferred to 500 ml plastic bottles. The cups were then reinstalled in the RIPT anchoring device. The samples were fixed with 3% formaldehyde and analyzed later in the laboratory under a binocular microscope. Mero- and holoplankton were identified using taxonomic keys or descriptions (i.e. Newell & Newell 1966, Boltovskoy 1981, Ramorino & Campos 1983, Palma & Kaiser 1993). The primary substrate, the cover (%) of sessile organisms, and the presence of motile invertebrates were recorded within a circle of 3 m in diameter around the RIPTs, using 9 randomly placed replicates of 50 × 50 cm quadrants (100 regular intersection points, Marquet et al. 1990).

The data were analyzed using a *t*-test and Analysis of Variance (factorial). Residual analysis for normality (Anderson-Darling test) and homoscedasticity (Bartlett test) were performed using MINITAB 10Xtra (Minitab Inc. 1995)

Results. The laboratory RIPT test showed that within 30 min the 37% and 10% formaldehyde plaster cubes were 100% effective as amphipod killing agents, while control cubes enabled over 95% amphipod survival. Accordingly, the RIPTs were installed in the platforms with 10% formaldehyde plaster cubes to reduce predation. The antifouling paint treatment proved effective in preventing larval settlement onto the interior surface of the trap. Observations with a hand magnifying glass at the end of every exposure demonstrated a total lack of larval settlement. Over the 3 d of sampling (24 samples) the RIPTs trapped 1290 individuals (649 in the Preserve and 641 outside) of mero- and holoplankton corresponding to 21 taxonomic types, belonging to 4 Phyla and 9 Classes (Table 1). The total cumulative number of individuals captured by a trap over the 3 d ranged between 123 and 215 in the Preserve and between 145 and 186 outside (Fig. 3A). The number of individuals collected per trap, per 24 h, ranged between 14 and 118 inside the Preserve, and between 21 and 90 outside. Overall the *Crustacea nauplii* larvae were the most common item (32.1%), representing between 24.1 to 28.5% of each trap collection inside the Preserve, and between 28.5 and 49% outside. They were followed by Oncaeidae, Harpacticoida and Calanoida holoplankton. Foraminiferida, Amphipoda and Gastropoda veliger larvae were also abundant (Table 1). The maximum length of the different mero- and holoplankton trapped ranged between 100 µm (bivalve larvae) and 2700 µm (Isopoda). We did not find evidence of trapping gelatinous plankton.

Table 1. Mero- and holoplankton trapped by 8 RIPTs anchored on 2 central Chile intertidal platforms (16 to 18 September 1997), with removal of the filter cup every 24 h. Each number identifies 1 trap and the vertical columns represent cumulative numbers

Phylum	Class-Order-Family-Species	ECIM Preserve platform				Sub total	ECIM outside platform				Sub total	Grand total
		1	2	3	4		5	6	7	8		
Rhizopoda	Class Granuloreticulosea Order Foraminiferida	2	7	9	2	20	3	9	3	3	18	38
Mollusca	Class Gastropoda (eggs)	2	1	1	1	5	1	0	0	0	1	6
	Class Gastropoda (veliger larvae)	4	6	0	1	11	2	4	2	2	10	21
	Class Bivalvia											
	Semimytilus algosus											
	Larvae	0	0	1	0	1	0	0	0	1	1	2
	Post-larvae	1	1	4	2	8	1	0	0	1	2	10
	Perumytilus purpuratus											
	Larvae	0	1	0	2	3	1	2	3	1	7	10
	Post-larvae	0	1	0	0	1	0	0	0	0	0	1
Annelida	Class Polychaeta	0	0	1	1	2	8	2	2	1	13	15
Arthropoda	Subphylum Crustacea											
	Nauplii larvae	54	37	35	44	170	53	62	54	75	244	414
	Class Copepoda											
	Order Calanoida	30	17	8	13	68	26	27	23	18	94	162
	Order Cyclopoida											
	Family Oncaeidae	82	59	48	58	247	47	20	38	26	131	378
	Family Sapphirinidae	3	1	1	4	9	2	0	0	0	2	11
	Family Corycaeidae	0	0	0	0	0	0	1	0	0	1	1
	Order Harpacticoida	30	14	11	15	70	33	27	18	21	99	169
	Class Malacostraca											
	Order Isopoda	0	1	0	0	1	0	0	0	0	0	1
	Order Amphipoda	4	1	2	12	19	6	3	2	1	12	31
	Order Decapoda											
	Infraorder Brachyura											
	Zoea larvae	0	0	0	1	1	1	0	0	2	3	4
	Family Porcellanidae											
	Zoea larvae	0	1	0	0	1	0	0	0	0	0	1
	Order Euphausiacea	2	3	0	0	5	0	0	0	0	0	5
	Class Ostracoda	0	0	0	0	0	1	0	0	0	1	1
	Class Cirripedia											
	Cypris larvae	1	2	2	2	7	1	0	0	1	2	9
Total		215	153	123	158	649	186	157	145	153	641	1290

Water flowing through the RIPT-flowmeter-a ranged between 622 and 811 l (24 h)$^{-1}$, showing no significant differences (t = 1.86, p = 0.16) between the Preserve ($\bar{x}$ = 741 [24 h]$^{-1}$, SD = 61.8) and the outside platforms ($\bar{x}$ = 663.3 [24 h]$^{-1}$, SD = 38.10). Additional field measurements of volumetric flows made side by side between the RIPT-flowmeters design a and b gave estimates 10 to 14% lower for RIPT-flowmeter-b ($\bar{x}$ = 716.9 l [24 h]$^{-1}$, SD = 110.0) than for RIPT-flowmeter-a ($\bar{x}$ = 858.8 l [24 h]$^{-1}$, SD = 74.1), a non-significant difference (t = 2.14, p = 0.76). Water movement in and around the collecting RIPTs (Fig. 3B), determined by the loss of weight of the dentist chalks, showed that there were no significant differences between sites among the chalk placed outside and inside the RIPTs (ANOVA, F = 1.71, p = 0.20, F = 0.10, p= 0.75). Nevertheless, the mean loss was greater and significantly different (both sites) in the external chalks when compared with the internal ones (ANOVA, F = 0.38, p = 0.0001). Water velocity (Fig. 3C) on the platform in the Preserve ranged between 3.7 and 7.7 m s^{-1}, and on the outside between 4.3 and 7.7 m s^{-1}. No significant differences were found between the 2 platforms (ANOVA, F = 0.38, p = 0.71).

The main sessile organisms on the platforms were the barnacles *Jehlius cirratus* and *Notochthamalus scabrosus*, with a cover ranging from 39 to 41%. Macroalgae (*Mazzaella laminarioides*, *Ceramium* spp., *Polysiphonia* spp., *Ralfsia* spp., *Centroceras* spp., *Ulva* spp., *Corallina* spp., *Gelidium* spp. and crustose coralline) accounted for cover between 21 and 24%. Other sessile invertebrates present were the mussels *Perumytilus purpuratus* and *Semimytilus algosus*, the barnacle *Balanus flosculus* and the sea anemone *Phymactis clematis*. Free substrate (bare rock) ranged between 27 and 34%. Motile macroinvertebrates were abundant, including: Gastropoda (*Concholepas concholepas*, *Fissurella crassa*, *F. limbata*, *Scurria arau-*

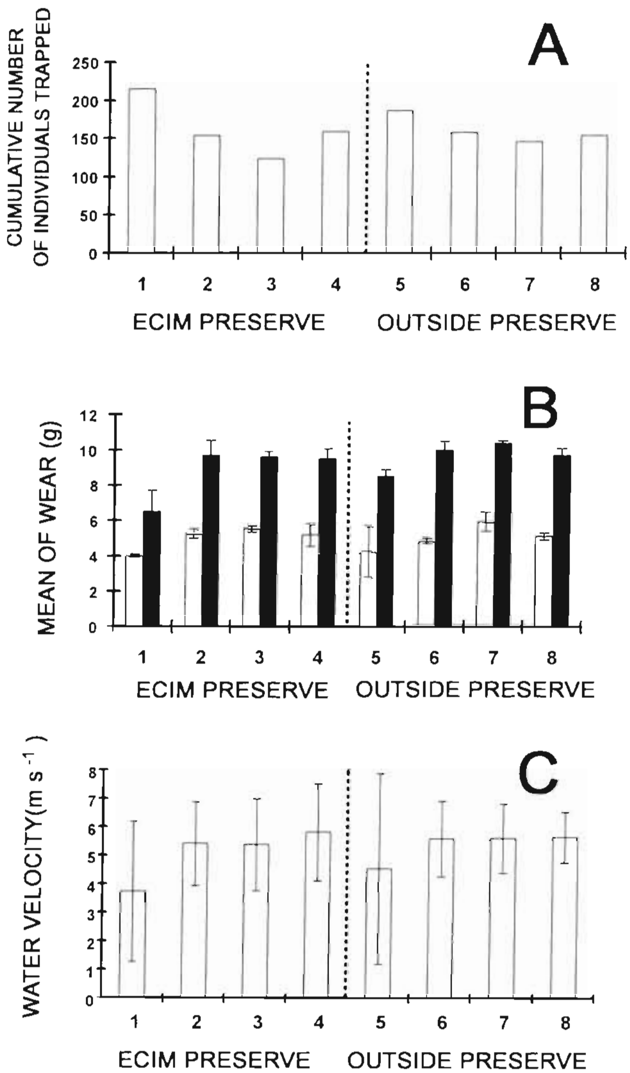


Fig. 3. (A) Cumulative number of individual mero- and holoplankton trapped per RIPT over the 3 d of exposure. (B) Mean weight loss (g) per day in the external (black) and internal (white) dentist chalk cylinders. (C) Mean of maximum water velocity per day (m s^{-1}) measured next to each RIPT over the time of exposure. Bars indicate standard errors

cana, *S. ceciliana*, *S. boehmita*, *Tegula atra*, *Prisogaster niger*, *Littorina araucana*); Amphineura (*Chiton granosus*, *Acanthopleura echinata*); Crustacea (*Acanthocyclus* spp., *Allopetrolisthes* spp., *Hyale* spp., Isopoda); Echinodermata (*Heliaster helianthus*); and Polychaeta (*Nereis* spp).

Discussion. The strong construction of our passive Rocky Intertidal Plankton Trap, bolted on horizontal platforms, permits its use in zones receiving strong wave impact (Bell & Denny 1994, Alvarado & Castilla 1996, Castilla et al. 1997), with water velocities of at least 7.7 m s^{-1} (Fig. 3C). Our RIPT seems to be more resistant than that invented by Otaiza (1989), which is bulkier and had the trap mouth facing the waves in a horizontal position. Our design is lighter, simpler and inexpensive to build (approximately US$ 10 each), and easier to install in wave-exposed habitats (10 to 15 min) with the filtering cup more readily detachable (5 to 10 min during low tides) than other intertidal or subtidal plankton trap devices (i.e. the 'map-tube' plankton trap invented by Yund et al. 1991). Both Otaiza's (1989) RIPT and ours include a 1-way valve, allowing for the drainage of water but preventing it from leaving the filtering cup when full. Furthermore, our RIPT reduces predation and larval settlement inside the trap while the water retained at the bottom prevents desiccation (Fig. 1). These improvements help to get a better approximation for the integration of the plankton trapped by the RIPT over time. Moreover, the RIPTs could be used to test if larval availability is limited, for instance in the case of an overexploited area, confronted with a Marine Reserve acting as a larvae source, and to determine if larval abundances decline with distance over some spatial scale.

According to the results in some cases the meroplankton trapped by the RIPTs was related to the dominant or present sessile macroinvertebrates on the monitored platforms, namely: unidentified Cirripedia cyprid larvae, more abundant inside the Preserve; larvae and post-larvae of the mussels *Perumytilus purpuratus*, more abundant outside the Preserve; and larvae and post-larvae of *Semimytilus algosus*, more abundant in the Preserve (Table 1). According to Durán & Castilla (1989) the intertidal population of barnacles are significantly more abundant inside the Preserve than outside whereas the opposite is true for *P. purpuratus* (Botsford et al. 1997).

Otherwise, the meroplankton trapped corresponded to groups related to benthic mobile macroinvertebrates commonly found on the platforms, namely, Gastropoda (unidentified eggs and larvae), and unidentified *Crustacea nauplii* (although Crustacea are also part of the holoplankton). Among the holoplanktonic Crustacea the most abundant groups were Cyclopoida, Harpacticoida and Calanoida, accounting for 55.9% of the total trapped organisms (Table 1).

Although the Las Cruces RIPT tests were aimed to trap the plankton every 24 h, our field experience indicates that the plankton removal from the collecting cup can be extended to 48 h before the 120 µm plankton nets are clogged. This will depend on the plankton concentration, the sediment in the area and the size of the net used. Hence, our passive RIPT facilitates the integration over time of the diversity and abundance of mero- and holoplankton arriving onto exposed rocky intertidal shores and has the potential to allow comparative studies among and between exposed rocky intertidal sites.

The RIPTs field results using plaster cylinders (Fig. 3B), RIPT-flowmeters and dynamometers (Fig. 3C) demonstrated that water dissolution, filtering rates and maximum water velocities experienced by intertidal platforms in different sites can be compared and used in future studies as covariates. Furthermore, the results of the RIPT-flowmeters suggest that the total amount of water passing through the collecting RIPTs over 24 h is less than 1 m^3 (maximum of 811 l [24 h]$^{-1}$ in RIPT-flowmeter-a). It should be considered that when the collecting cup is completely immersed in water filtration stops. Furthermore, the flowmeter used is designed for domestic water consumption under a continuous flow, and in the outlet pipe we added a 1-way valve to prevent bidirectional water flow. Hence, the water filtering rates reported must be considered as a preliminary estimation. Water flowing in the intertidal does not meet continuous flow conditions. In the future, there is a need to perform laboratory experiments in flume tanks to understand the hydrodynamics of the filtration and water flow processes through the RIPT, particularly those related to the horizontal advection at the mouth of the trap and its efficiency under different flow regimes (Yund et al. 1991).

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LITERATURE CITED

Alvarado JL, Castilla JC (1996) Tridimensional matrices of mussels *Perumytilus purpuratus* on intertidal platforms with varying wave forces in central Chile. Mar Ecol Prog Ser 133:135–141

Bell EC, Denny MW (1994) Quantifying 'wave exposure': a simple device for recording maximum velocity and results of its use at several field sites. J Exp Mar Biol Ecol 181: 9–29

Boltovskoy D (1981) Atlas del zooplancton del Atlántico sudoccidental y métodos de trabajo con el zooplancton marino. Publicación especial del INIDEP, Mar del Plata, p 1–936

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277: 509–515

Castilla JC (1981) Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile Central. II Depredadores de alto nivel trófico. Medio Ambiente 5:190–215

Castilla JC (1988) Earthquake-caused coastal uplift and its effects on rocky intertidal kelp communities. Science 242:440–443

Castilla JC, Durán LR (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). Oikos 45:391–399

Castilla JC, Steinmiller DK, Pacheco CJ (1997) Quantifying wave exposure daily and hourly on the intertidal rocky shore of central Chile. Rev Chil Hist Nat 71:23–29

Crisp DJ (1985) Recruitment of barnacle larvae from the plankton. Bull Mar Sci 37:478–486

Crisp DJ, Southward AJ (1953) Isolation of intertidal animals by sea barriers. Nature 172:208–209

Durán LR, Castilla JC (1989) Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. Mar Biol 103:555–562

Gaines SD, Bertness MD (1993) Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360: 579–580

Gaines SD, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67:267–272

Gaines SD, Roughgarden J (1985) Fish in offshore kelp forest affect recruitment to intertidal barnacle populations. Science 235:479–481

Hawkins SJ, Hartnoll RG (1982) Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). J Exp Mar Biol Ecol 62:271–283

Marquet PA, Navarrete SA, Castilla JC (1990) Scaling population density to body size in rocky intertidal communities. Science 250:1125–1127

Newell GE, Newell RC (1966) Marine plankton a practical guide. Hutchinson Educational, University of London, p 1–221

Otaiza RD (1989) Arrival and recruitment of intertidal barnacles on rocky shores in central New South Wales, Australia. PhD thesis, University of Sydney, p 1–110

Palma S, Kaiser K (1993) Plancton marino de aguas chilenas. Ediciones Universitarias de Valparaíso. Universidad Católica de Valparaíso, p 1–151

Ramorino L, Campos B (1983) Larvas y postlarvas de Mytilidae de Chile (Mollusca: Bivalvia). Rev Biol Mar 19: 143–192

Santelices B, Castilla JC, Cancino J, Schmiede P (1980) Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in Central Chile. Mar Biol 59: 119–132

Underwood AJ, Denley E (1984) Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong D, Simberloff D, Abele L, Thistle A (eds) Ecological communities. Princeton University Press, Princeton, NJ

Yund PO, Gaines SD, Bertness MD (1991) Cylindrical tube traps for larval sampling. Limnol Oceanogr 36:1167–1177

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