water

MDPI

Article

Habitat Shift for Plankton: The Living Side of Benthic-Pelagic Coupling in the Mar Piccolo of Taranto (Southern Italy, Ionian Sea)

Fernando Rubino [1] and Genuario Belmonte [2,*]

[1] National Research Council of Italy Water Research Institute CNR-IRSA, Unit of Taranto, 72100 Taranto, Italy; rubino@irsa.cnr.it
[2] Laboratory of Zoogeography and Fauna, Dipartimento di Scienze e Tecnologie Biologiche e Ambientali, University of the Salento, 73100 Lecce, Italy
* Correspondence: genuario.belmonte@unisalento.it

Abstract: Resting stages represent the answer for species to the variability of environmental conditions. In confined marine habitats, variability of conditions is high, and bottoms host plankton resting stages in the so-called "marine cyst banks". The Mar Piccolo of Taranto was chosen as a pilot site in which to investigate how marine cyst banks and plankton affect each other in the living part of the benthic–pelagic coupling. The attempt was based on the use of multiple devices for integrated sampling of benthic and pelagic stages and allowed us to identify 207 *taxa*/categories in the whole system (127 as active forms, 91 as resting stages). The sediments added 80 *taxa* to the plankton list obtained only from the water column, thus confirming the importance of this kind of approach in perceiving the actual diversity of the studied site. The sediment cyst bank involved 0.15–1.00% of its content in daily benthic-pelagic exchanges, in terms of cyst germination and import, respectively. In addition, the cyst production, which was higher than the cyst germination, is responsible for the existence of a permanent biological reservoir in the sediments. The benthic-pelagic coupling, however, was completely depicted in the present investigation only for seven *taxa*. This result is due to the still scant knowledge of the life cycles and life histories of single species. Apart from the identification difficulties that still have to be clarified (which cysts belong to which species), the cycle presence/absence is also characterized by the diversification of strategies adopted by each species. The observation of plankton dynamics from the benthos point of view was useful and informative, unveiling a huge assemblage of resting forms in the sediments only minimally affected by cyst import/export, because it is more devoted to a storing role over long periods. Consequently, the continuation of life cycle studies appears necessary to understand the diversity of strategies adopted by the majority of plankton species.

Keywords: plankton; life cycles; resting stages; cysts; benthic-pelagic coupling; resurrection ecology

Citation: Rubino, F.; Belmonte, G. Habitat Shift for Plankton: The Living Side of Benthic-Pelagic Coupling in the Mar Piccolo of Taranto (Southern Italy, Ionian Sea). *Water* **2021**, *13*, 3619. https://doi.org/10.3390/w13243619

Academic Editor: Arantza Iriarte

Received: 4 October 2021
Accepted: 10 December 2021
Published: 16 December 2021

1. Introduction

Resting stage production represents a life cycle adaptation of planktonic organisms to survive problematic fluctuations of the environment, even on a multiannual scale [1–3]. Once produced by plankton, resting stages (commonly indicated as "cysts") generally sink to the bottom where they form a reservoir of potential biodiversity (cyst banks), particularly conspicuous in confined coastal areas [4,5]. This storage of plankton biodiversity in the sediments is largely responsible for the reactivation of planktonic populations at the onset of suitable conditions in the water column [6] and it needs to be carefully considered in ecological studies [7,8]. The existence of separated methodological approaches for the study of plankton and benthos does not help in understanding the importance of benthic-pelagic exchanges of living material. This is the reason why the proposal of an integrated sampling approach adding data coming from benthos to those usually collected from pelagos will provide more information and reliability to studies of the composition of plankton communities and their functioning [9,10].

In small confined habitats, where the dominance of a few species drives simple dynamics, many rare species also rely upon resting stages to remain in the environment, avoiding competition in the water column. This behavior represents a powerful way to ensure resilience for the whole community. Different solutions are adopted by different species to solve the same environmental problems and continue to exist in extremely variable systems. The most obvious of such solutions is the timing of rest, which helps the alternation of species in the same environment. In many cases, the species exhibit short life cycles to combine with the brief duration of suitable conditions [2]. For each species, in these cases, the resulting periods of absence from the water column can often be longer than the ones where they are present, and are thus perceivable only with multiannual investigations [11]. Moreover, resting stages may have different dormancy periods, which are not only species-specific, but also vary in the same clutch [12], thus avoiding the synchronous hatching from the sediment bank of co-generated descendants.

Resting stages have been proven to maintain their viability over long periods of time [13,14] and to be insensitive to both harsh abiotic conditions [15], and chemicals [16,17] as well as and microbial attacks [18]. Nevertheless, losses of cysts not due to germinations occur in the sediment banks. They can derive from: (1) the burial of cysts in deeper layers of sediment, induced by remixing and/or deposit feeders [19,20]; (2) the different sensitivity of cyst walls (mainly in dinoflagellates) to chemicals present in the sediments [21]; and (3) the possible predation by meiofauna [22], besides natural mortality, which is still to be ascertained.

This complex frame of continuous replenishment/impoverishment of the cyst bank in coastal sediments needs to be precisely quantified to allow us a better understanding of its consequences for plankton community dynamics (the so-called "Resurrection Ecology" of Kerfoot and Weider, [8]) (Figure 1).

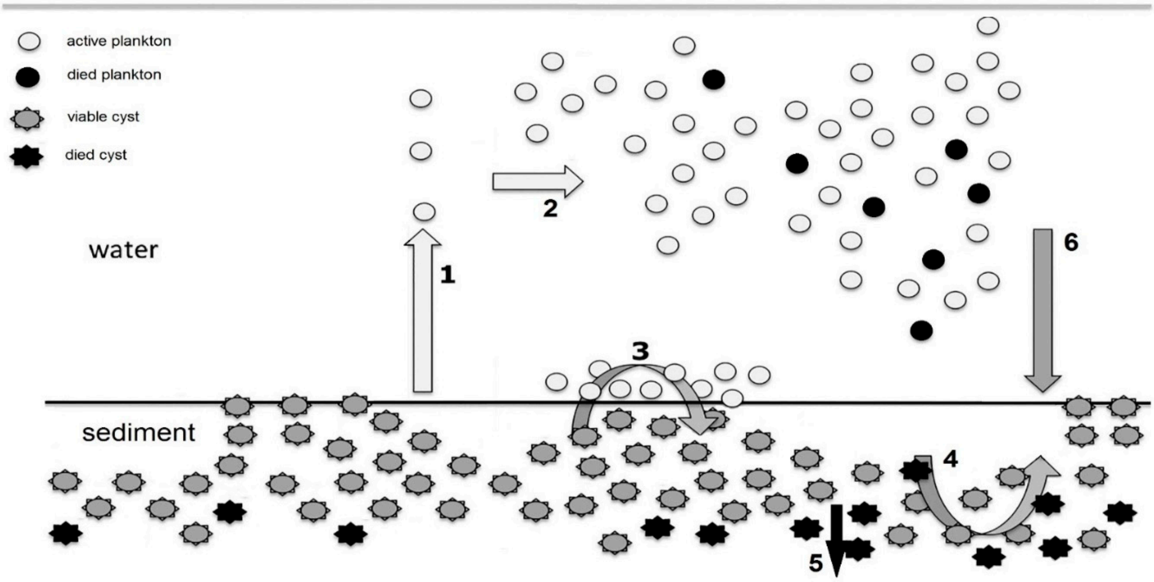


Figure 1. A schematic diagram of the dynamic interactions of plankton between active life in the water column and rest in sediment cyst bank. (**1**) Subtraction in favor of water column (germination); (**2**) multiplication of active stages; (**3**) tight and fast supply-removal (encystment–germination) from/to hyperbenthos; (**4**) mixing within the bottom cyst bank as a consequence of sediment re-working; (**5**) subtraction due to death; and (**6**) cysts supply from plankton (encystment).

The first studies on the marine cyst bank of the Mar Piccolo [4,23] represented the starting attempts to evaluate the role of cyst banks in the plankton dynamics of that site.

To fully understand the functioning of species alternation and succession in the plankton of the Mar Piccolo, the quantification of the fluxes of cysts sinking to the bottom, and active stages germinating from the sediments, appear to be more revealing than the simple collection of plankton and benthos, even if repeated at different time intervals.

The aim of the present study, in fact, is not only the analysis of the cyst bank composition, but also its dynamics in bottom sediments, and its role in the benthic-pelagic coupling in the Mar Piccolo, with a first description of community dynamics considering the marine cyst bank point of view. The composition and richness of the sediment cyst bank are the first elements to be ascertained. The quantification of arrivals and departures of elements (in term of cysts sunk and germination) to and from the cyst bank is also necessary to understand the role of this reservoir for the plankton dynamics. The adoption of an integrated sampling and a common measure unit is the still lacking methodological approach, which the study will aim to propose.

2. Materials and Methods

2.1. Study Area

The Mar Piccolo of Taranto is a coastal semi enclosed sea located north of the town of Taranto in southern Italy (Figure 2). It has a total surface of 21 km^2 and is partitioned by a promontory into two sub-basins. The western sub-basin, namely, First Inlet, has a maximum depth of 13 m and is more affected by the sea than the eastern sub-basin, namely, Second Inlet (maximum depth, 9 m), where dystrophic events may occur in late summer [11,23,24]. The two sub-basins of the Mar Piccolo, together with the adjacent Mar Grande and the open area of the Gulf of Taranto (Ionian Sea, central Mediterranean), are aligned along a progressive degree of confinement, which affects the structure of planktonic communities [11]. For the present study, the sampling site was located in the center of the First Inlet (lat. 40°29′00″ N, long. 17°15′00″ E, depth 12 m).

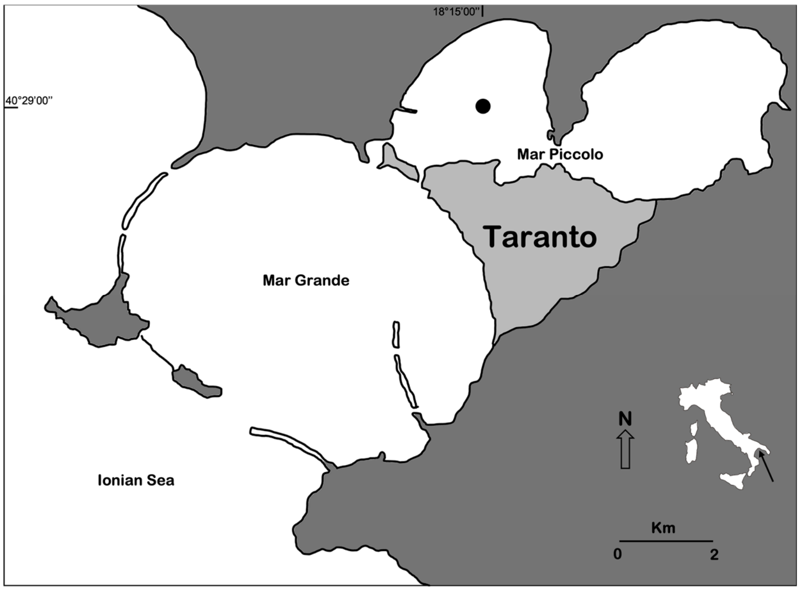


Figure 2. Map of the Taranto sea system with the location of the study site in the center of the First Inlet of the Mar Piccolo.

The sedimentation rate in the First Inlet of the Mar Piccolo is quite high with a mean value of 1 mm/year [25], but the first 2 cm of bottom sediments are fluid and host vagile fauna that impede a perfect layering of the sunk sediment. The presence of submarine springs, in the north of the two inlets, determines the presence of a thin surface layer

(<10 cm) of brackish water at the level of the sampling site considered. The remaining water column is generally homogeneous and not stratified.

2.2. *Investigation Design*

Different tools and devices were used to collect the different life stages of phyto- and zoo-plankton in the water column and in the bottom sediments. We considered (in brackets the sampling device): (1) active stages in the water column (Niskin bottle for phytoplankton, plankton net for zooplankton); (2) cyst production and sink to the sediments (sediment traps); (3) injection of newly germinated active stages from cysts (inverted sediment traps); and (4) cyst presence in the sediment (sediment cores).

The whole study was carried out in 2010–2011 and was structured in two periods (T = times) (Table 1). One in autumn (T1), and one in the following spring–summer (T2), focused on the individuation of possible rest periods (overwinter/oversummer), and their consequence on the pelagic community. T1 ran from 16 September to 15 December 2010, and T2 ran from 19 May to 7 September 2011.

Table 1. Timetable of the sampling activities. T1 (2010) and T2 (2011). x: punctuated sampling; grey color: duration of collection activity of the sediment traps (direct and inverse).

	2010												**2011**														
	Sep			**Oct**		**Nov**				**Dec**			**May**			**Jun**		**Jul**					**Aug**			**Sep**	
	16	**21**	**27**	**1**	**14**	**4**	**12**	**17**	**23**	**1**	**7**	**15**	**19**	**25**	**30**	**6**	**21**	**4**	**7**	**13**	**18**	**27**	**10**	**23**	**29**	**2**	**7**
multiprobe	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
phytoplankton	X			X	X	X			X			X	X		X	X	X	X		X		X	X	X		X	
zooplankton	X				X			X				X		X			X			X			X				X
Sediment cores	X					X						X	X			X				X			X				X
Sediment traps	▨	▨	▨	▨ X	▨ X	▨ X	▨	▨ X	▨	▨ X	▨	▨ X	▨	▨	▨	▨ X	▨ X	▨ X	▨	▨	▨ X	▨ X	▨ X	▨ X	▨	▨	▨ X
Inverted traps		▨	▨ X	▨ X			▨	▨ X	▨ X	▨	▨ X		▨	▨ X	▨ X	▨ X		▨	▨ X	▨ X	▨ X			▨	▨ X	▨ X	▨ X
code	Sep1	Sep2	Sep3	Oct1	Oct2	Nov1	Nov2	Nov3	Nov4	Dec1	Dec2	Dec3	May1	May2	May3	Jun1	Jun2	Jul1	Jul2	Jul3	Jul4	Jul5	Aug1	Aug2	Aug3	Sep1	Sep2

2.3. *Sampling Procedures*

The field activity employed the research boat "A. Cerruti" (IRSA-CNR of Taranto) as a support.

At each sampling date, the main physical-chemical variables of the water (temperature, salinity, dissolved oxygen, pH, and photosynthetically active radiation—PAR) were measured along the water column by means of a multiparametric probe (Idromar IP050D, Genoa, Italy). Moreover, the temperature of surface sediments was measured from a sample quickly transported aboard by using a digital thermometer (Hanna Instr. HI98510, Smithfield, RI, USA).

The phytoplankton was collected every two weeks with a Niskin bottle (volume, 2 L) at three levels of the water column: sub-surface (less than 1 m below the sea surface), −6 m, and close to the bottom (−12 m). For this latter depth, the Niskin bottle was maneuvered by a SCUBA diver, horizontally at about 20–30 cm over the bottom. This technique was adopted to ensure the collection of hypoplankton/hyperbenthos organisms, possibly involved in a benthic-pelagic exchange a short distance from the bottom. Each sample was immediately fixed with Lugol's iodine solution (final dilution 1%).

The zooplankton was collected every month by means of a plankton net (mesh size = 80 μm), equipped with a flowmeter (Hydro-Bios 438115, Qingdao, China) at the mouth, to calculate the volume (m^3) of filtered water of each collection. Three replicates were executed for each sampling date. To obtain an adequate volume of filtered water, the net was vertically towed (along a water column of about 11 m) three times × replicate, due to the shallowness of the water column. Each sample obtained from the net was reduced by filtration on adequate mesh size sieves to 50 mL of an 85% ethanol solution.

The cyst production rates were estimated considering cysts as inert particles of sediment that, once produced, sink to the bottom. Cysts were collected from a set of five sediment traps replaced every 15 days. The sediment traps (vol = 50 mL; aspect ratio = 4.4; mouth = 6.2 cm^2) were placed with the mouth upward at about 1 m above the bottom to avoid the collection of resuspended particles from the sediments. The traps were positioned being previously filled up with filtered sea water (0.2 µm) to avoid contaminations during their positioning. The samples obtained were not fixed to allow germination experiments in the laboratory. All the available cysts were used in germination experiments to perfect their attribution to species involved in the benthic pelagic shift in the Mar Piccolo.

The cyst germination in situ was evaluated using transparent inverted traps (Vol. = 500 mL; bottom area entrapped = 9.6 cm^2) to allow for the penetration of sunlight on the enclosed bottom area and to catch organisms swimming out of the sediment. The inverted traps (filled up with 0.2 µm filtered sea water before the positioning on the sea bottom) were fixed to a support previously inserted into the sediment, taking care to avoid resuspension. Three collections were executed for each "time" (T1 and T2). Each collection comprised three steps, except for the third collection of T1 (December 2010) when, due to bad weather conditions, only a single step was carried out. Each step lasted for 4–6 days and employed four inverted traps at about a 1 m distance from each other (total bottom surface interested in the collections, 38.4 cm^2). At each step, the positioning of the traps was changed to interesting new sediment surfaces. The obtained samples were immediately fixed onboard with Lugol's iodine solution (final dilution 1%).

The consistency and dynamics of the cyst bank were evaluated by a monthly collection of sediments using small corers (diameter = 2.5 cm, length = 10.0 cm; three replicates). The top 2 cm of the collected sediments (vol ≈ 8 mL) were sliced off from each core and put into little vials. Cysts also obtained with this sampling activity were not fixed and specimens of each morphotype were used in germination experiments in the laboratory.

According to studies from different parts of the world [4,13,20,26], for the sedimentation rate at the sampling site and the sediment reworking, the surface layer of 2 cm (roughly corresponding to a sedimentation history of 20 years) has been considered to be the most sensitive to the encystment/germination dynamics.

All the sampling procedures concerning sediment traps, inverted traps, and sediments were always carried out by two SCUBA divers, paying attention to avoid sediment resuspension [27,28].

2.4. Laboratory Procedures and Analyses

The phytoplankton was analyzed under an inverted microscope Zeiss Axiovert S-200 at 400 magnification, according to the classical Utermöhl procedure [24]. Only Dinophyta have been considered for detailed studies on benthic-pelagic exchanges due to their representativeness of the phytoplankton resting stage producers in the Mar Piccolo [4,23]. Data are reported as cells L^{-1}.

The zooplankton samples were filtered and re-hydrated (to eliminate the ethanol) in 200–300 mL of filtered (0.45 µm) seawater; then, after gentle homogenization, 2–3 aliquots, 7–10 mL each, were taken from each sample to be analyzed under an inverted microscope Zeiss Axiovert S-100 (Carl Zeiss, Oberkochen, Germany) at 30–125 magnifications. Further aliquots were used to estimate the presence of rare *taxa*. Data are expressed as ind. m^{-3}.

The samples obtained from the sediment traps were ultrasonicated (Branson-Emerson CP102, Danbury, CT, USA) at low frequency for 1 min, and then filtered through a 20 µm mesh sieve (Endecott's Ltd., ISO3310-1 London, UK). The material retained on the sieve was stored at 4 °C in the dark until analysis was performed under an inverted Zeiss Axiovert S-100 equipped with a digital camera Coolpix 990 (Nikon, Tokyo, Japan) at 320–400 magnification. Each sample was completely analyzed, and the data were reported as cysts m^{-2} d^{-1}.

The samples from the inverted traps were filtered through a 20 µm mesh sieve and collected into 50 mL jars with Lugol (final dilution 1%). Each sample was completely observed under an inverted microscope Axiovert S-200 (Carl Zeiss, Oberkochen, Germany) equipped with a digital camera Coolpix 990 (Nikon, Tokyo, Japan) at 400 magnifications. Data from the four inverted traps placed during each step of the experiments were merged to obtain maximum reliability of quantitative data as germinated ind. m^{-2} d^{-1}).

To quantify the cyst content in the sediment bank, the surface sediment samples were treated using the sieving technique described in [28,29] without chemicals to preserve the walls of calcareous cysts of Dinophyta. A fixed aliquot (2–3 mL of wet sediment) from each sample was filtered through a 20 µm mesh sieve, ultrasonicated at low frequency for 1 min, and then put through a sieve battery (mesh sizes of 200, 75, and 20 µm). This procedure gave a fine-grained fraction (20–75 µm) containing protistan cysts and a coarser fraction (>75 µm) containing larger Dinophyta cysts and zooplankton resting eggs. The material retained onto the 200 µm mesh sieve was not considered. The analysis was carried out under an inverted microscope Zeiss Axiovert S-100 equipped with a digital camera (Nikon Coolpix 990) at 320–400 magnifications. Full (i.e., with cytoplasmic content and presumably viable) and empty (i.e., already germinated) cysts were separately counted. At least 200 full cysts were counted in each sample to obtain homogeneous data on species/types abundance. Resting stages were identified at the species level, when possible, on the basis of published descriptions, and the results of germinations obtained during the present study. As a rule, the modern biological names were used, but the paleontological ones were maintained for those cyst types whose active stage is unknown.

To estimate the water content of sediment, an aliquot of sediment from each sample was weighed and dried out overnight at 70 °C. Quantitative data of cysts are expressed as cysts g^{-1} of dry sediment to allow us comparisons with the literature. The final comparison with other data of this same study, however, was performed using quantitative data expressed as cysts mL^{-1} of wet sediment.

For germination experiments, all the cyst morphotypes available from the sampling activity were considered. Cysts were isolated into Nuclon microwells (Nalge Nunc International, Roskilde, Denmark) each containing ≈1 mL of natural sterilized sea water with a Guillard's F/2 marine water enrichment (final dilution 1/10). Cysts were incubated in a rearing chamber (Sanyo MLR 350-H) at: (1) 17 °C–18 °C, 12:12 h L:D cycle, and 80 µmol photons m^{-2} s^{-1} irradiance for samples collected in T1 (autumn 2010); (2) 25 °C, 14:10 h L:D cycle, 120 µmol photons m^{-2} s^{-1} irradiance for samples collected in T2 (spring–summer 2011).

The comparison between the temporal trends of plankton dynamics in the water column and cyst bank dynamics in the sediments was carried out by referring to a unique measurement unit (specimens m^{-2} of sea floor).

In the case of plankton, the abundance values calculated per volume units of water (1 L for phytoplankton, 1000 L for zooplankton) were quoted as items (i.e., cells and/or specimens) contained in a water column with 1 m^2 of base and a height of 11 m (the water column above the sediment traps, corresponding to 11,000 L of water). The concentration of phytoplankton was obtained averaging the values coming from the three depths of water collection considered (below the surface, −6 m, and close to the bottom). In the case of the sediments, the values of cyst concentration (cysts cm^{-3}) were quoted as the number of cysts contained in 1 m^2 of sea floor having a thickness of 1 cm (i.e., considering 10,000 cm^3).

3. Results

3.1. Hydrographic Conditions

Physical data registered at the surface and over the bottom in all the sampling days, followed the seasonal trend typical of the Mar Piccolo of Taranto (Table 2). Interestingly, the temperature during the T1, autumn–winter, showed values always higher at the bottom, while in T2, spring–autumn, this situation was inverted. The temperature registered at the upper layer of the bottom sediments showed great fluctuations, according to the sampling period, ranging from a minimum of 13.5 °C in December 2010 to 27.7 °C in September 2011.

Table 2. Physical data measured at the surface (s) and close to the bottom (b) in the Mar Piccolo of Taranto in the dates of T1 and T2; PAR %, percentage of irradiance (photosynthetic active radiation) measured at the bottom vs. surface.

	Temp (°C)		**Sal (psu)**		**O_2 (%)**		**PAR (μmol phot m^{-2} s^{-1})**		**PAR %**	**Water Transp (m)**	**Temp Sedim (°C)**
	s	**b**	**s**	**b**	**s**	**b**	**s**	**b**			
T1											
sep1	24.1	24.2	36.4	38.2	98.3	78.3	3014	178	5.9	3.0	24.4
sep2	23.9	24.2	36.7	38.5	99.5	77.1	2770	164	5.9	3.0	24.2
sep3	22.7	23.5	36.2	38.3	98.5	75.3	467	22	4.7	4.0	23.3
oct1	22.6	22.9	36.3	38.4	101.0	98.9	450	54	12.0	4.0	22.7
oct2	21.0	21.8	36.1	37.7	100.5	91.1	1150	44	3.8	7.0	21.5
nov1	18.5	18.6	35.8	38.2	100.1	98.5	522	22	4.2	5.5	18.4
nov2	17.3	18.2	35.8	38.0	99.9	85.9	2170	185	8.5	9.5	17.8
nov3	17.5	18.1	35.6	38.1	99.5	92.3	2280	175	7.7	8.0	17.8
nov4	16.9	17.4	36.4	38.0	100.3	93.9	1560	165	10.6	5.0	17.2
dec1	15.6	16.1	36.3	38.1	98.5	88.4	1590	59	3.7	7.0	15.7
dec2	14.4	15.6	36.2	38.2	100.5	98.1	1620	158	9.7	7.0	15.6
dec3	12.5	14.1	36.8	38.6	97.3	91.9	2120	161	7.6	10.0	13.5
T2											
may1	18.6	17.1	36.5	38.4	100.6	100.7	3870	381	9.8	6.0	18.1
may2	22.1	18.5	36.2	38.7	100.5	99.7	2930	264	9.0	6.0	19.7
may3	21.8	19.3	36.4	38.5	97.7	88.9	2990	240	8.0	8.0	20.0
jun1	23.0	20.3	35.6	38.3	102.8	98.8	1800	204	11.3	7.0	21.1
jun2	24.7	21.7	36.2	38.2	97.4	98.7	3050	261	8.6	7.0	23.9
jul1	24.9	21.8	36.4	38.4	102.1	101.0	2750	189	6.9	6.0	23.0
jul2	26.2	23.1	36.4	38.1	99.9	90.3	3460	226	6.5	6.0	24.1
jul3	27.9	23.8	36.3	38.2	100.0	96.1	3030	222	7.3	5.5	24.6
jul4	26.7	24.5	36.2	38.3	100.4	98.9	2490	185	7.4	5.5	26.0
jul5	26.1	22.7	36.8	38.7	101.4	98.9	1640	162	9.8	6.0	24.1
aug1	26.8	25.4	37.3	38.4	90.8	87.3	2540	222	8.7	6.0	26.0
aug2	26.5	25.7	36.4	38.7	91.5	87.4	2960	196	6.6	6.0	26.1
aug3	27.1	26.0	36.9	38.6	100.5	80.81	2220	163	7.3	6.0	26.5
sep1	27.5	26.8	37.1	38.5	104.8	96.2	3150	166	5.3	5.0	27.1
sep2	26.9	26.9	37.2	38.7	87.3	78.4	2700	160	5.9	6.0	27.0

3.2. Taxonomic Composition of Samples

During the present study, a total of 261 samples were collected: 177 from the water column (107 of phyto- and zoo-plankton, 70 of sinking cysts in sediment traps), and 84 from the sediment (60 of germinated organisms from inverted traps, 24 of cysts from sediment cores).

A total of 207 *taxa*/categories were recognized, 141 were active (coming from collection in the water column, from sediments, and from germinations obtained in laboratory), and 91 were resting (81 morphotypes captured by sediment traps, 68 collected from sediments) (Table 3). Only 43 of the 141 *taxa* of active stages found in the study are known from the literature [5] as resting stage producers. Hence, the first result is an evident disproportion between planktonic *taxa* producing cysts (43) and cyst morphotypes found (91). The puzzle is even more complex if we note that for only 15 of the 43 species known as cyst producers, the corresponding resting stage was recognized in the sediment collections (directly from the bottom or captured by sediment traps). Finally, germination experiments allowed us to identify an additional 14 species not found as active stages in other samples.

Table 3. List of the *taxa* recognized in the different sampling devices utilized in the study. The *taxa* registered with different life stages (e.g., nauplii and copepodites) were considered only once. **as w**: active stages in water column; **as it**: active stages in inverted traps; **rs s**: resting stages in the surface sediments; **rs st**: resting stages in the sediment traps; **ger**: germination achieved. * paleontological taxon.

		as w	**as it**	**rs st**	**rs s**	**ger**
Dinophyta	*Akashiwo sanguinea* (K. Hirasaka) G. Hansen & Ø. Moestrup	X	X			
	Alexandrium minutum Halim			X	X	X
	Alexandrium cf. *minutum* Halim	X	X			
	Alexandrium pseudogonyaulax (Biecheler) Horiguchi ex Kita & Fukuyo			X		
	Alexandrium tamarense (Lebour) Balech			X	X	X
	Alexandrium sp.1			X	X	
	Alexandrium sp.2			X	X	
	Alexandrium sp.4			X	X	
	Alexandrium sp.7			X	X	
	Alexandrium sp.8				X	
	Alexandrium sp.10			X		
	Alexandrium sp.	X	X			
	cf. *Calciodinellum albatrosianum* (Kamptner) Janofske & Karwath			X	X	
	Calciodinellum operosum (Deflandre) Montresor			X	X	
	**Calciperidinium asymmetricum* Versteegh			X	X	X
	Ceratium candelabrum (Ehrenberg) Stein	X				
	Ceratium furca (Ehrenberg) Claparède & Lachmann		X			
	Ceratium fusus (Ehrenberg) Dujardin	X				
	Ceratium horridum (Cleve) Gran	X				
	Ceratium cf. *longipes* (J.W. Bailey) Gran		X			
	Ceratium sp.	X				
	Cochlodinium polykrikoides Margalef (2 cyst types)			X	X	X
	Dinophysis caudata Saville-Kent	X				
	Dinophysis cf. *sacculus* Stein	X	X			
	Dinophysis rotundata Claparède & Lachmann	X				
	Dinophysis sp.	X	X			
	Diplopelta parva (Abé) Matsuoka			X		
	Diplopsalis lenticula Bergh	X	X	X	X	
	cf. *Dissodinium pseudocalani* (Gonnert) Drebes ex Elbrachter			X	X	
	**Follisdinellum splendidum* Versteegh			X	X	
	Goniodoma polyedricum (Pouchet) Jørgensen	X				
	Goniodoma sp.		X			
	Gonyaulax cf. *polygramma* Stein	X	X			
	Gonyaulax cf. *scrippsae* Kofoid		X			
	Gonyaulax spinifera (Claparède & Lachmann) Diesing	X	X			X
	Gonyaulax sp.	X	X			
	Gonyaulax group			X	X	
	Gymnodinium impudicum (Fraga & Bravo) G. Hansen & Moestrup cyst type argyr			X	X	X
	Gymnodinium cf. *impudicum* (Fraga & Bravo) G. Hansen & Moestrup	X				
	Gymnodinium cf. *litoralis* A. Reñé (2 cyst types)			X	X	X
	Gymnodinium nolleri Ellegaard & Moestrup			X		X
	Gymnodinium uncatenatum (Hulburt) Hallegraeff			X		X
	Gymnodinium sp.1			X	X	
	Gymnodinium sp.3			X		
	Gymnodinium sp.4			X		
	Gymnodinium sp.7				X	
	Gymnodinium sp.8			X		
	Gymnodinium sp.	X	X			
	Lingulodinium polyedrum (Stein) Dodge	X		X	X	X
	**Melodomuncula berlinensis* Versteegh			X	X	
	Nematodinium armatum (Dogiel) Kofoid & Schwezy			X	X	
	Nematodinium sp.	X				
	Neoceratium furca (Ehrenberg) Gomez, Moreira & Lopez-Garcia	X				
	Oblea rotunda (Lebour) Balech ex Sournia	X	X	X	X	X
	Ornithocercus sp.	X				
	Oxyphysis sp.		X			
	Oxytoxum sp.	X				
	Pentapharsodinium dalei Indelicato & Loeblich			X	X	X
	Pentapharsodinium cf. *dalei* Indelicato & Loeblich		X			
	Pentapharsodinium tyrrhenicum Montresor, Zingone & Marino (2 types)			X	X	X
	Polykrikos hartmannii Zimmermann			X	X	
	Polykrikos kofoidii Chatton			X		
	Polykrikos schwartzii Bütschli	X			X	
	Posoniella tricarinelloides (Versteegh) Streng et al.			X	X	
	Prorocentrum compressum (Bailey) Abè ex Dodge	X				
	Prorocentrum micans Ehrenberg	X	X			
	Prorocentrum cf. *rhathymum* A.R.Loeblich III, Sherley & Schmidt		X			
	Prorocentrum cf. *triestinum* J. Schiller		X			
	Prorocentrum sp.	X				
	Protoceratium sp.	X				
	Protoperidinium abei (Paulsen) Balech	X				
	Protoperidinium claudicans (Paulsen) Balech				X	
	Protoperidinium compressum (Abé) Balech	X		X	X	X
	Protoperidinium conicum (Gran) Balech	X		X	X	
	Protoperidinium cf. *minutum* (Kofoid) Loeblich III	X				
	Protoperidinium mite (Pavillard) Balech	X	X			

Table 3. *Cont.*

		as w	as it	rs st	rs s	ger
	Protoperidinium oblongum (Aurivillius) Parke & Dodge	X	X	X	X	X
	Protoperidinium ovatum Pouchet	X				
	Protoperidinium cf. *pacificum* (Kofoid & Michener) F.J.R.Taylor & Balech ex Balech	X	X			
	Protoperidinium parthenopes Zingone & Montresor			X	X	X
	Protoperidinium cf. *pyriforme* (Paulsen) Balech		X			
	Protoperidinium quinquecorne (Abé) Balech	X		X	X	
	Protoperidinium shanghaiense Gu, Liu & Mertens				X	
	Protoperidinium cf. *steinii* (Jørgensen) Balech		X			
	Protoperidinium subinerme (Paulsen) Loeblich III			X		
	Protoperidinium cf. *subinerme* (Paulsen) Loeblich III	X	X			
	Protoperidinium thorianum (Paulsen) Balech			X	X	
	Protoperidinium sp. a	X				
	Protoperidinium sp. b	X				
	Protoperidinium sp. c		X			
	Protoperidinium sp. 1			X	X	
	Protoperidinium sp. 4				X	
	Pyrophacus horologium Stein			X	X	
	Pyrophacus steinii (Schiller) Wall & Dale	X				
	Scrippsiella acuminata (Ehrenb.) Kretschmann et al. (4 cyst types)	X	X	X	X	X
	Scrippsiella cf. *erinaceus* (Kamptner) Kretschmann, Zinssmeister & Gottschling, type bal			X	X	X
	Scrippsiella kirschiae Zinnssmeister, S. Soehner, S. Meier & Gottschling			X		
	Scrippsiella lachrymosa Lewis			X	X	X
	Scrippsiella precaria Montresor & Zingone			X	X	
	Scrippsiella ramonii Montresor			X	X	X
	Scrippsiella spinifera Honsell & Cabrini			X	X	
	Scrippsiella cf. *spinifera* Honsell & Cabrini		X			
	Scrippsiella trifida Lewis			X		
	Scrippsiella sp.1			X	X	
	Scrippsiella sp.4			X	X	
	Scrippsiella sp.5			X	X	
	Scrippsiella sp.6			X	X	
	Scrippsiella sp.8			X	X	
	Scrippsiella sp.		X			
	Thoracosphaeraceae spp.			X	X	
	Warnowia rosea (Pouchet) Kofoid & Schwezy			X		
	Dinophyta sp.2			X	X	
	Dinophyta sp. 9			X		
	Dinophyta sp.14			X		
	Dinophyta sp.33			X	X	
	Dinophyta spp.		X			
Foraminifera	*Globigerina* sp.	X				
	Miliolidacea spp.	X				
	Rotaliacea spp.	X				
	Textulariacea spp.	X				
	Foraminifera undetermined	X				
Radiolaria	undetermined	X				
Acantharia	*Diploconus* sp.	X				
	Acantharia undetermined	X				
Ciliophora	*Codonellopsis* sp.	X				
	Coxliella sp.	X				
	cf. *Cyrtostrombidium boreale* Kim, Suzuki & Taniguchi, 2002				X	
	Cyttarocilis sp.	X				
	Eutintinnus sp.	X				
	Favella sp.	X				
	Hexasterias problematica Cleve, 1900				X	
	Laboea strobila Lohman, 1908			X	X	
	Strombidium acutum Leegaard, 1915			X	X	
	Strombidium biarmatum Agatha, Struder-Kypke, Beran & Lynn, 2005			X	X	
	Strombidium conicum (Lohmann, 1908) Wulff, 1919			X	X	
	Strombidium crassulum (Leegaard, 1915) Kahl, 1932			X		
	Tintinnopsis sp.	X	X			
	Tintinnina spp.	X				
	Ciliophora sp.a	X				
	Ciliophora sp.b		X			
	Ciliophora sp.c		X			
	Ciliophora sp.d		X			
	Ciliophora sp.e		X			
	Ciliophora sp.f		X			
	Ciliophora sp.2			X		
	Ciliophora sp.4				X	
	Ciliophora sp.5			X	X	
	Ciliophora sp.6			X		
Rotifera	*Synchaeta* sp.	X				
	Synchaeta sp.1 (rest. egg smooth type)			X	X	
	Synchaeta sp.2 (rest. egg rough type)			X	X	
	Synchaeta sp.3 (rest. egg spiny type)			X		

Table 3. *Cont.*

		as w	as it	rs st	rs s	ger
Hydrozoa	Medusae undetermined	X				
Mollusca	Bivalvia veliger	X				
	Gastropoda veliger	X				
	Thecosomata spp.	X				
Polychaeta	Owenidae mitraria	X				
	Spionidae larvae	X				
	Polychaeta undetermined	X				
Crustacea	*Acartia clausi* Giesbrecht, 1889	X				
	Acartia clausi/margalefi (resting egg)				X	
	Acartia italica Steuer, 1910	X		X	X	
	Acartia sp.2			X		
	Calanidae spp.	X				
	Canuella sp.	X				
	Centropages kroyeri Giesbrecht, 1893	X				
	Centropages ponticus Karavaev, 1895	X				
	Centropages sp. (resting egg)			X	X	
	Centropagidae spp.	X				
	Cirripedia Balanomorpha (nauplius)	X				
	Cirripedia Lepadomorpha (nauplius)	X				
	Coryceidae spp.	X				
	Cyclopoida undetermined	X				
	Decapoda Anomura (zoea)	X				
	Decapoda Brachyura (zoea)	X				
	Decapoda Natantia (zoea)	X				
	Euterpina acutifrons (Dana, 1847)	X				
	Evadne sp.	X				
	Facetotecta (nauplius Y)	X				
	Harpacticoida undetermined	X	X			
	Longipedia sp.	X				
	Microsetella sp.	X				
	Oithona nana Giesbrecht, 1893	X				
	Oithonidae undetermined	X				
	Oncaeidae undetermined	X				
	Paracalanidae undetermined	X				
	Paracartia latisetosa (Kriczaguin, 1873)			X	X	
	Penilia avirostris Dana, 1849	X				
	Podon sp.	X				
	Pteriacartia josephinae (Crisafi, 1974)	X		X	X	
	Temora stylifera (Dana, 1849)	X				
	Temoridae undetermined	X				
	Amphipoda undetermined	X				
	Isopoda undetermined	X				
	Ostracoda undetermined	X				
Echinodermata	Holothuroidea auricularia	X				
	Echinoidea pluteus	X				
	Ophiuroidea pluteus	X				
Chordata	Ascidiacea tadpole larva	X				
	Branchiostoma sp.	X				
	Fritillaria sp.	X				
	Oikopleura sp.	X				
	Osteychthies undetermined	X				
Unidentified	Phytoplankton cells	X				
	Cyst type 6			X		
	Resting Egg 1			X		
	Resting Egg 9			X	X	
Total		108	38	81	69	20
Total pelagic stages			127			
Total encysted stages					91	
Additional pelagic stages germinated from cysts						14

Among the 81 *taxa* collected by sediment traps, cysts of *Calciperidinium asymmetricum*, *Follisdinellum splendidum*, and *Melodomuncula berlinensis* were collected from the water column. These are known to science as "fossils" (the active stage is unknown) and reported here with their paleontological name (Figure 3).

3.2.1. Active Stages in the Water Column (Niskin Bottle, Plankton Net)

Dinophyta were present with 43 *taxa* in the water column (Table 3). The highest concentration of Dinophyta active stages was in general registered at the sea sub-surface. This is particularly true in T2 when the sub-surface concentrations were generally far higher than those at the other depths, especially in May, June, and July 2011, while in T1, more variability was registered (Supplementary Material 1).

The Dinophyta abundance at the surface layer in T2 was nearly double than T1 and the *taxa* richness reached a mean value of 21 ± 5 in T2 against 16 ± 3 in T1 (Figure 4). The three most abundant Dinophyta species were *Akashiwo sanguinea*, *Protoperidinium* cf. *pacificum*, and *Scrippsiella* cf. *acuminata*, representing nearly 50% of the total Dinophyta abundance in the entire study.

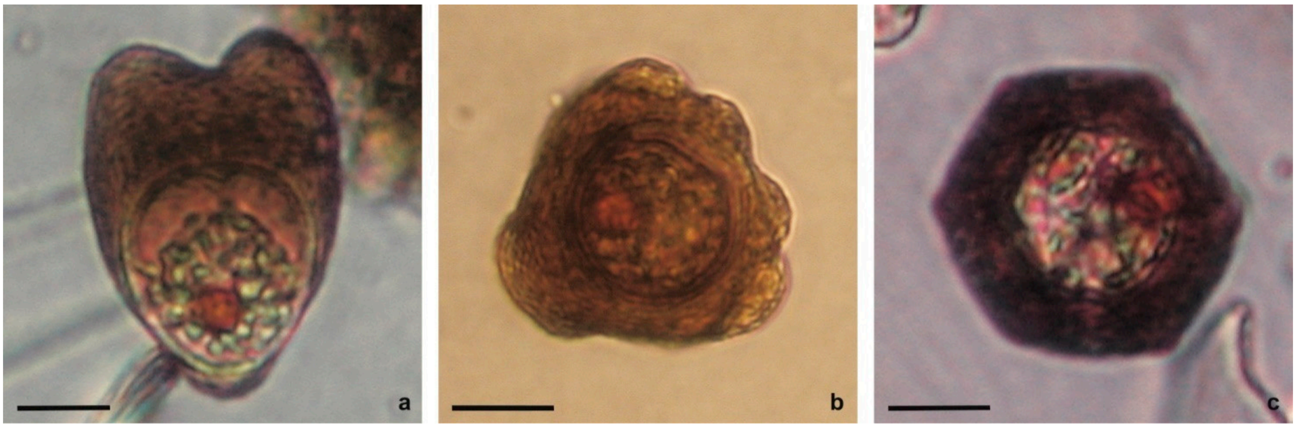
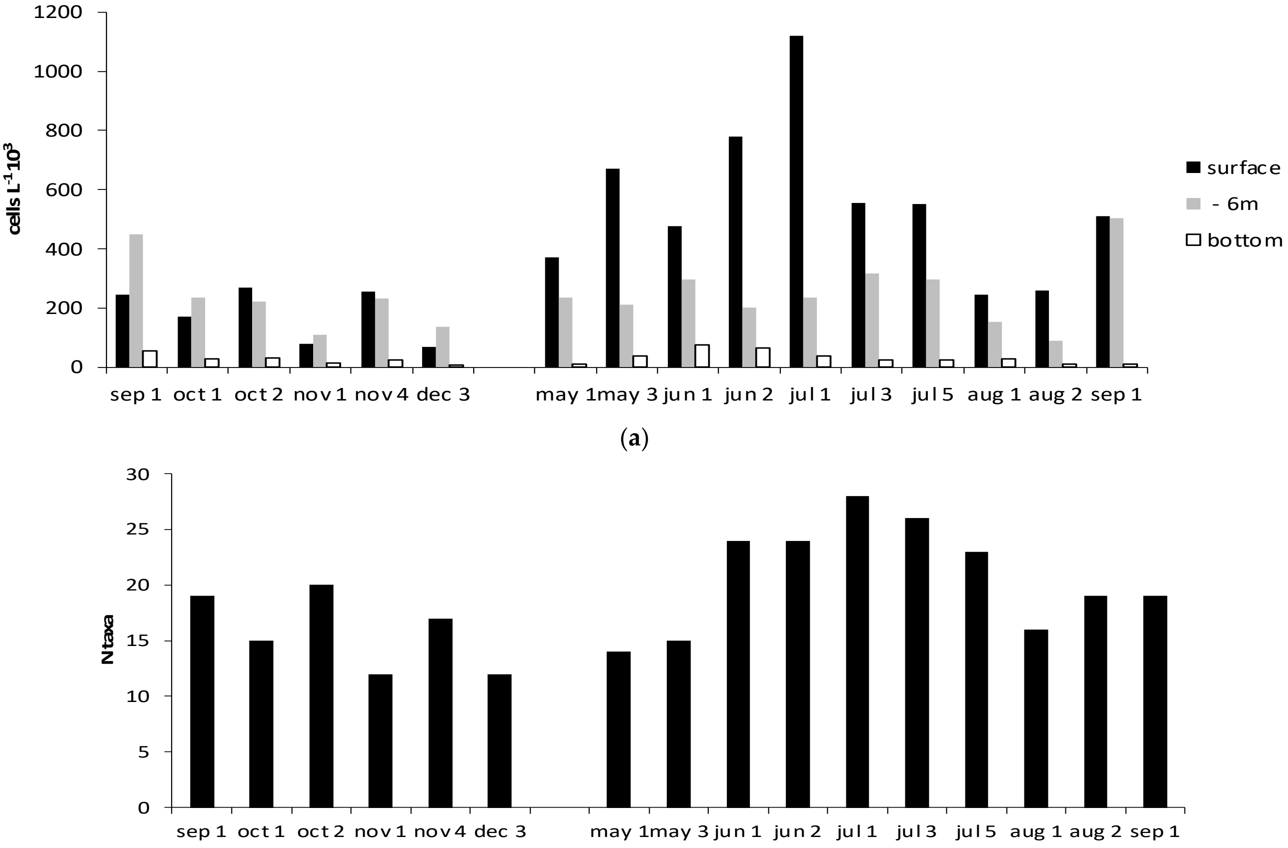


Figure 3. Cysts of *Calciperidinium asymmetricum* (**a**), *Follisdinellum splendidum* (**b**), and *Melodomuncula berlinensis* (**c**) found in sediment traps. Scale bar: 10 µm.



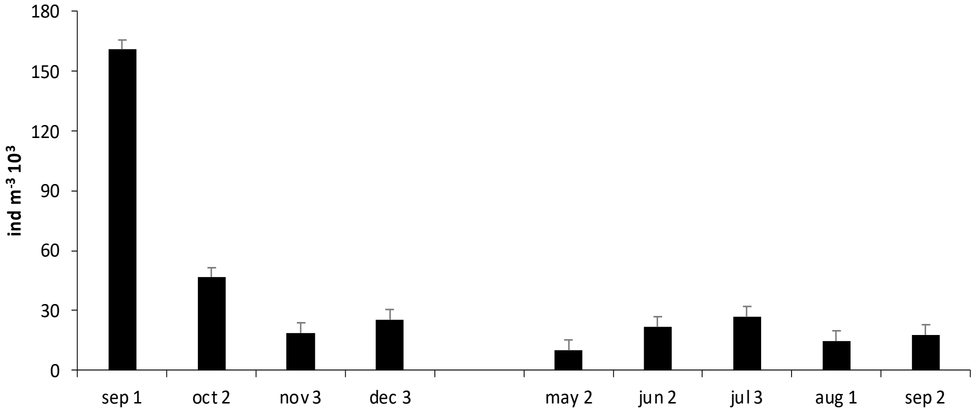
(**a**)

(**b**)

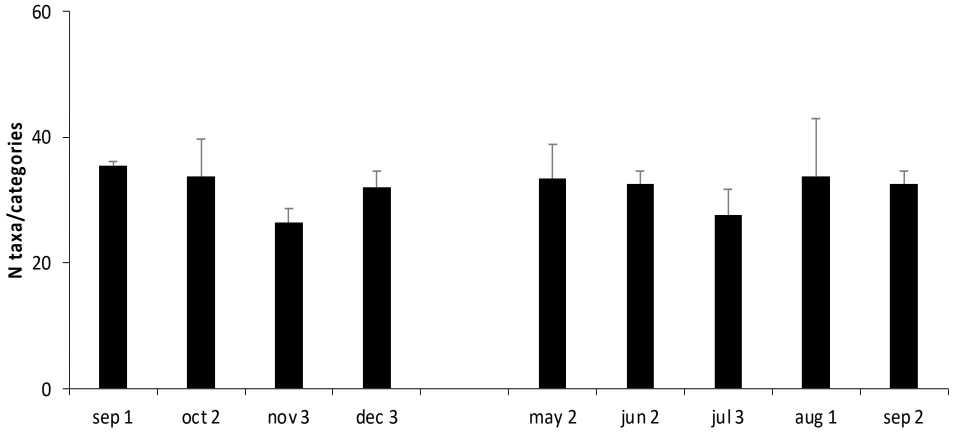
Figure 4. Temporal variation (abundance and *taxa* richness) of Dinophyta at three different depths (sub-surface, −6 m, and bottom at −11 m) in the Mar Piccolo, Taranto. (**a**) Abundance (cells 10^3 L^{-1}) for the three depths of sampling; (**b**) number of *taxa* in each sampling date (all the depths together).

The plankton collected in the water column by using a net was represented by 65 *taxa*/categories dominated by Crustacea (33 *taxa*) (Supplementary Material 2) (Table 3). Only two *taxa*, *Synchaeta* sp. (Rotifera) and *Oithona nana* (Copepoda, Cyclopoida) were present in all the sampling dates. A total of 22 *taxa* were meroplankton or benthic organisms resuspended in the water column. Of the remaining zooplankton, only 17 species are known as cyst producers.

The total abundance of net-plankton ranged from 160,812 ± 26,051 ind. m^{-3} in September 2010 (T1) to 9939 ± 6505 ind. m^{-3} in May 2011 (T2) (Figure 5a) (Table 4). The *taxa* richness ranged from 36 ± 1 in September 2010 (T1) to 27 ± 2 in November 2010 (T1) (Figure 5b).



(**a**)



(**b**)

Figure 5. Temporal variation (abundance and *taxa* richness) of zooplankton in the water column. (**a**) Total abundance (average ± SD); (**b**) *taxa* richness.

3.2.2. Cyst Fluxes (Sediment Traps)

A total of 91 cyst morphotypes produced by 79 *taxa* (62 Dinophyta, eight Ciliophora, three Rotifera, and six Copepoda, with some different morphotypes belonging to the same species) were collected by sediment traps and identified thanks to the germination experiments carried out in the laboratory (Table 3). Three morphotypes remained undetermined (Supplementary Material 3). Among the collected *taxa*, 43 were known as cyst producers. For 15 of these *taxa*, however, the cyst was recognized in the present study. Germination experiments allowed us to add another 14 *taxa* to the list. For 49 cysts, the identification was limited to high level *taxa* (e.g., Ciliophora, Dinophyta, and so on) but their identity is still unknown at level of species.

Table 4. Quantification of benthic-pelagic exchanges in terms of individuals in the Mar Piccolo of Taranto (2010–11). The unit of measurement of the plankton assemblages (indiv. 11 m^{-3} of water) has been referred to the whole water column over the mouth of the sediment traps. The fluxes of cysts toward the bottom and of germinated specimens toward the water column, are indicated as indiv. m^{-2} d^{-1}. The cyst bank content (indiv. m^{-2}) refers to a sediment layer of 1 cm. All the values in bold are averages of the period (T1 and T2), with indication of minimum and maximum values. *Scrippsiella acuminata* has been chosen as a single species case. T1, T2, periods of sample collections.

	T1	min	max	T2	min	max	Tot Average
	Sep–Dec			**May–Sep**			
indiv. 11 m^{-3}							
plankton (Niskin bottle)	**1.4 × 10^9**	0.7 × 10^9	2.5 × 10^9	**2.8 × 10^9**	1.2 × 10^9	4.6 × 10^9	**2.3 × 10^9**
plankton (net)	**0.6 × 10^6**	0.2 × 10^6	1.6106	**0.2 × 10^6**	0.1 × 10^6	0.1 × 10^6	**0.4 × 10^6**
indiv. m^{-2} d^{-1}							
cyst production (sediment traps)	**40,864**	23,655	66,489	**36,767**	13,911	77,706	**38,816**
cyst germination (inverted traps)	**9850**	521	62,500	**1300**	0	5200	**5600**
indiv. m^{-2}							
cyst bank content	**3.87 × 10^6**			**3.56 × 10^6**			**3.71 × 10^6**
Scrippsiella acuminata							
indiv. 11 m^{-3}							
plankton (Niskin bottle)	**382 × 10^6**	50 × 10^6	922 × 10^6	**583 × 10^6**	133 × 10^6	1.45 × 10^9	**482 × 10^6**
indiv. m^{-2} d^{-1}							
cyst production (sediment traps)	**17,900**	9900	28,500	**22,000**	6100	63,000	**19,900**
cyst germination (inverted traps)	**1340**	0	10,800	**87**	0	521	**714**
indiv. m^{-2}							
cyst bank content	**1.44 × 10^6**			**1.40 × 10^6**			**1.42 × 10^6**

The cyst production by the whole plankton was continuous during the two times in the present study. Highest daily sink rates of cysts toward the bottom were observed on 1 October (T1) and 3 July (T2), with 66,489 ± 6700 and 77,706 ± 35,000 cysts m^{-2} d^{-1}, respectively (Table 4) (Figure 6a). *Scrippsiella acuminata* was the most abundant *taxon* with 43% of the total flux in October 2010 and 80% in July 2011 (46% of the total abundance in T1 and 60% in T2). After *Scrippsiella acuminata*, the Dinophyta *Scrippsiella* sp.1 (6% in T1 and 4% in T2), *Gymnodinium impudicum* (5% in T1 and 0.3% in T2), and *Pentapharsodinium tyrrhenicum* (4% in T1 and 5% in T2) were also abundant.

The *taxa* richness in the sediment traps resulted constant during the entire study, with a mean of 37 ± 6 *taxa* in T1 and 38 ± 2 *taxa* in T2 (Figure 6b).

Among Metazoa, *Acartia*, and *Paracartia* species of the family Acartiidae (Copepoda Calanoida) showed cyst sink rates comparable to those of Dinophyta, contributing to 3.9% to the total in T1, and 4.6% in T2.

3.2.3. In Situ Germination (Inverted Traps)

The inverted traps revealed the presence of active stages of 38 *taxa* (Table 3 and Supplementary Material 4).

The identified *taxa* were Dinophyta (31), Ciliophora (6), and Copepoda (1).

All the *taxa* observed in the inverted traps were planktonic, with the exception of *Prorocentrum* cf. *rhathymum* and Copepoda Harpacticoida, benthic organisms.

Active stages have been always found in inverted traps during the summer–autumn (T1) (Figure 7) with an average rate of 9850±11,583 excysted forms m^{-2} d^{-1}. In particular, on 1 September and 2 November, we recorded 17 and 15 *taxa* of plankton respectively, with very high abundances of active stages in September (average of the three experimental steps, 62,500 ± 34,164 excysted forms m^{-2} d^{-1}).

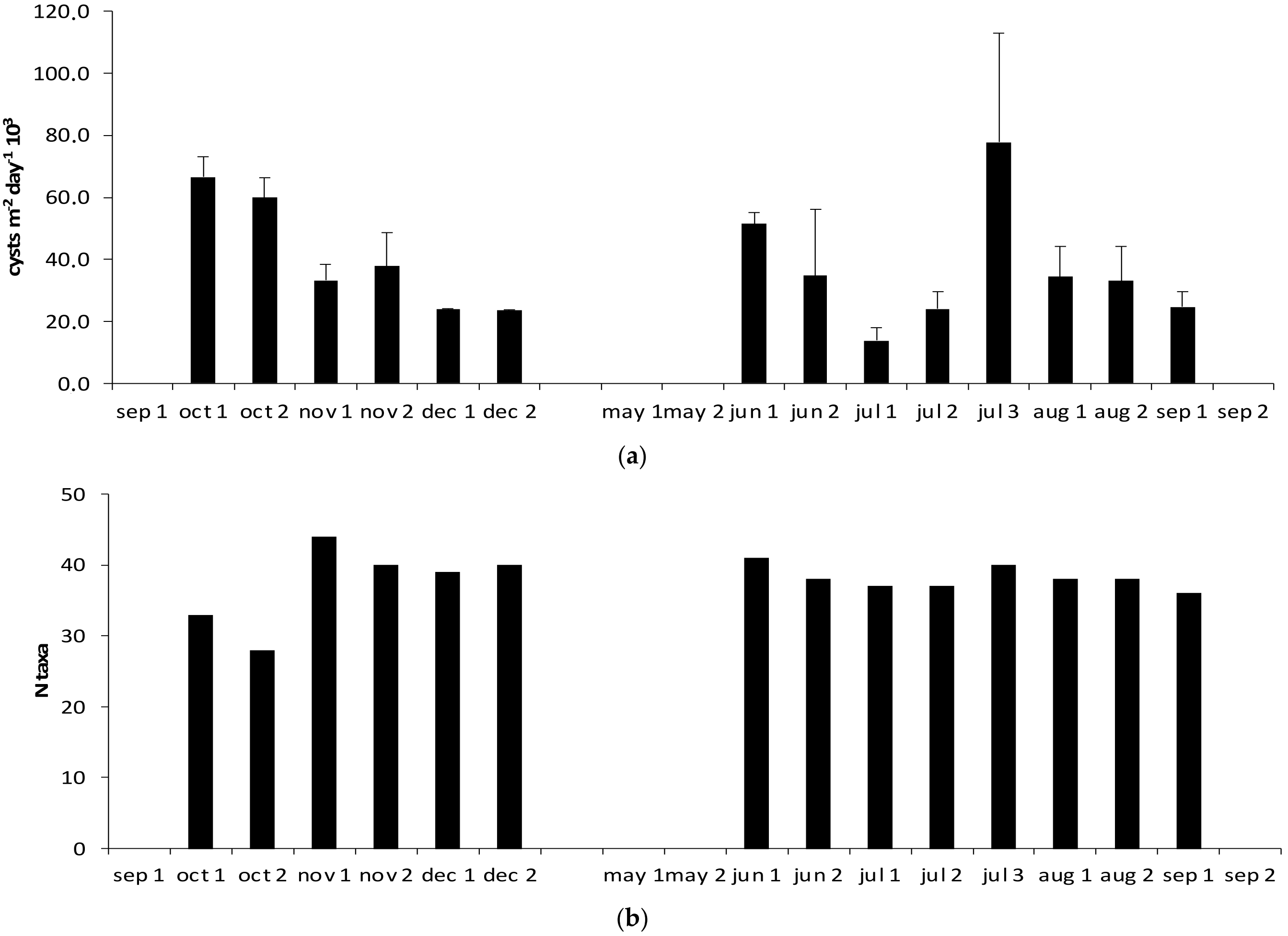


Figure 6. Cysts in the sediment traps of the Mar Piccolo of Taranto. The daily rates of cysts sunk in traps derived by an exposition of 15 days consecutively (at each sampling date). (**a**) Total daily sink rates (average ± SD); (**b**) *taxa* richness.

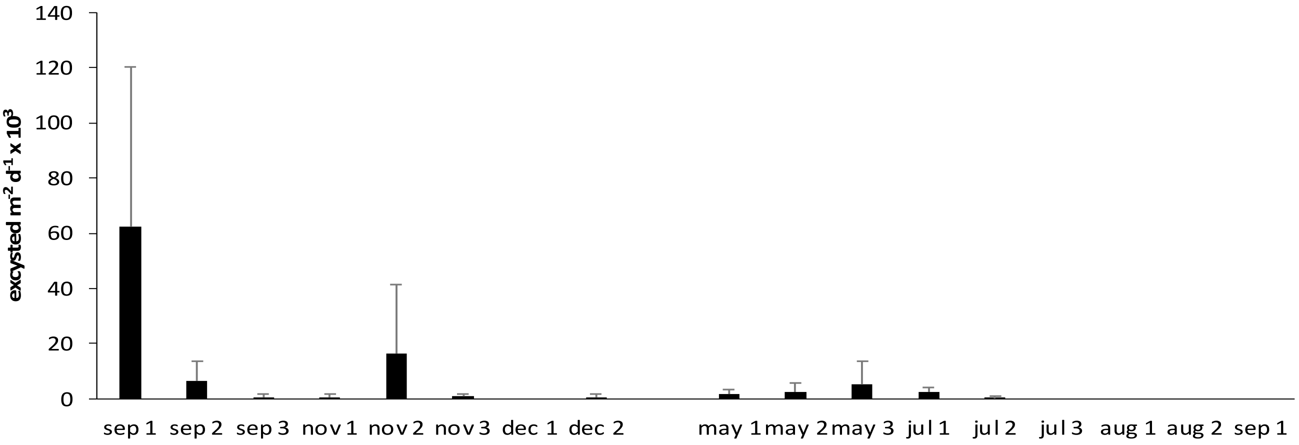
Tintinnopsis sp. (Ciliophora) was observed only on 2 November (T1), together with high numbers of the Dinophyta *Akashiwo sanguinea*, *Alexandrium* sp., and *Protoperidinium mite*. Among these, *P. mite* and the ciliate *Tintinnopsis* are not known as cyst producers, while for *A. sanguinea*, only cysts produced in laboratory cultures are reported [30].

During spring–summer (T2) the inverted traps caught active forms only from 1 May to 2 July and the abundance was sensibly low (1300 ± 1781 excysted forms m^{-2} d^{-1}). No excystment apparently occurred between 3 July and 1 September.

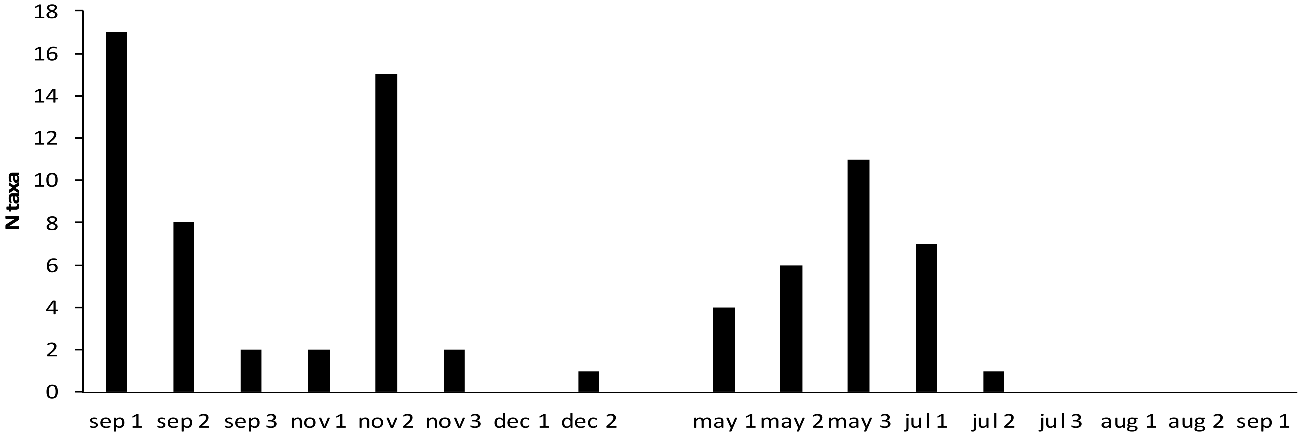
3.2.4. Sediments Cyst Bank (Sediment Cores)

Cysts recognized in sediment samples were subdivided from a total of 68 morphotypes produced by 69 *taxa* (53 Dinophyta, eight Ciliophora, two Rotitera, and six Copepoda, with some species represented by several morphotypes) (Table 3 and Supplementary Material 5). Three morphotypes were found exclusively as empty (*Cochlodimium polykrikoides*, *Gymnodinium* sp.1, *Protoperidinium* sp.1) and in very low numbers.

The whole cyst bank was quite constant in terms of cyst abundance and species richness, with the empty forms always less abundant and diverse than the full ones in the sediment layer interested by the collection of samples (Figure 8).



(**a**)



(**b**)

Figure 7. Active stages collected with inverted traps on the floor of the Mar Piccolo of Taranto. (**a**) Abundance (average ± SD); (**b**) *taxa* richness.

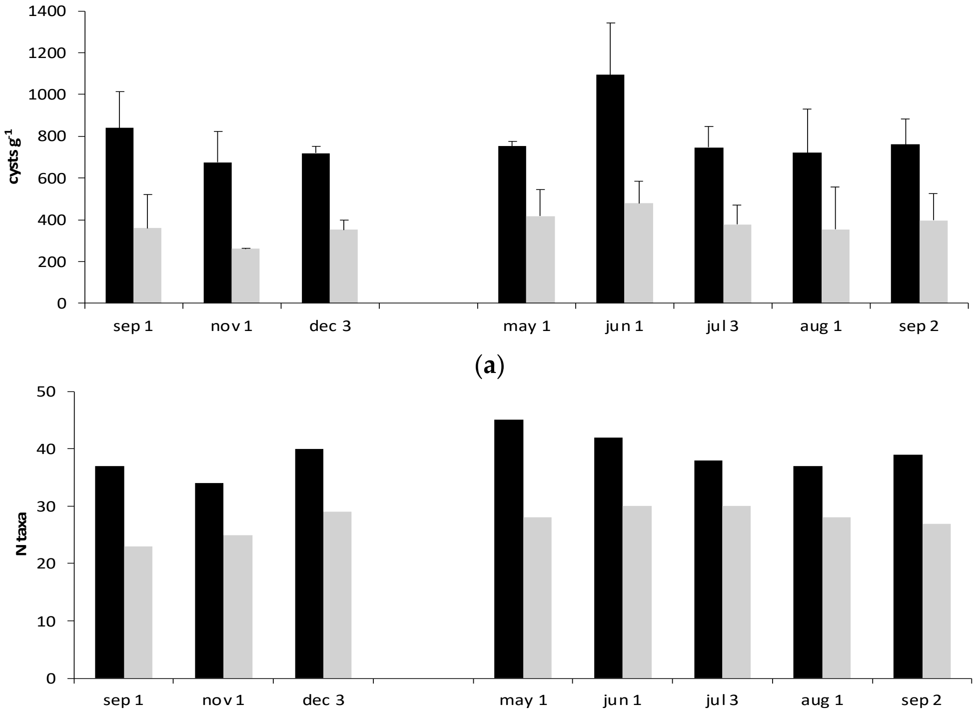
The total abundance of full cysts in sediments ranged from 1094 ± 249 cysts g^{-1} in June 1 (T2) to 674 ± 147 cysts g^{-1} in 1 November (T1).

The most abundant species (as full cysts) were Dinophyta *Scrippsiella acuminata* (39% of total abundance) and *Gymnodinium impudicum* (11%).

3.2.5. Benthic-Pelagic Coupling

The unicellular plankton exchanged more specimens between benthos and plankton than the metazoa (Table 4). The whole community showed an average of 2.3 10^9 active organisms in a water column of 1 m^2 × 11 m (the distance of the trap mouth from the surface). Such a community generated (with a different contribution of single species) an average flux of 38,816 cysts m^{-2} d^{-1} toward the bottom. The bottom just below the considered water column (1 m^2) hosted an average of 3.7 × 10^6 full cysts m^{-2}, which were injected into the water column an average of 5600 newly germinated specimens m^{-2} d^{-1} (Table 4).

Regarding germination, a difference between T1 and T2 appeared, with a rate of 9850 germinations m^{-2} d^{-1} in T1 and 1300 germinations m^{-2} d^{-1} in T2, indicating the summer (July–September) of 2011 was a less favorable period for germination.



(**a**)

(**b**)

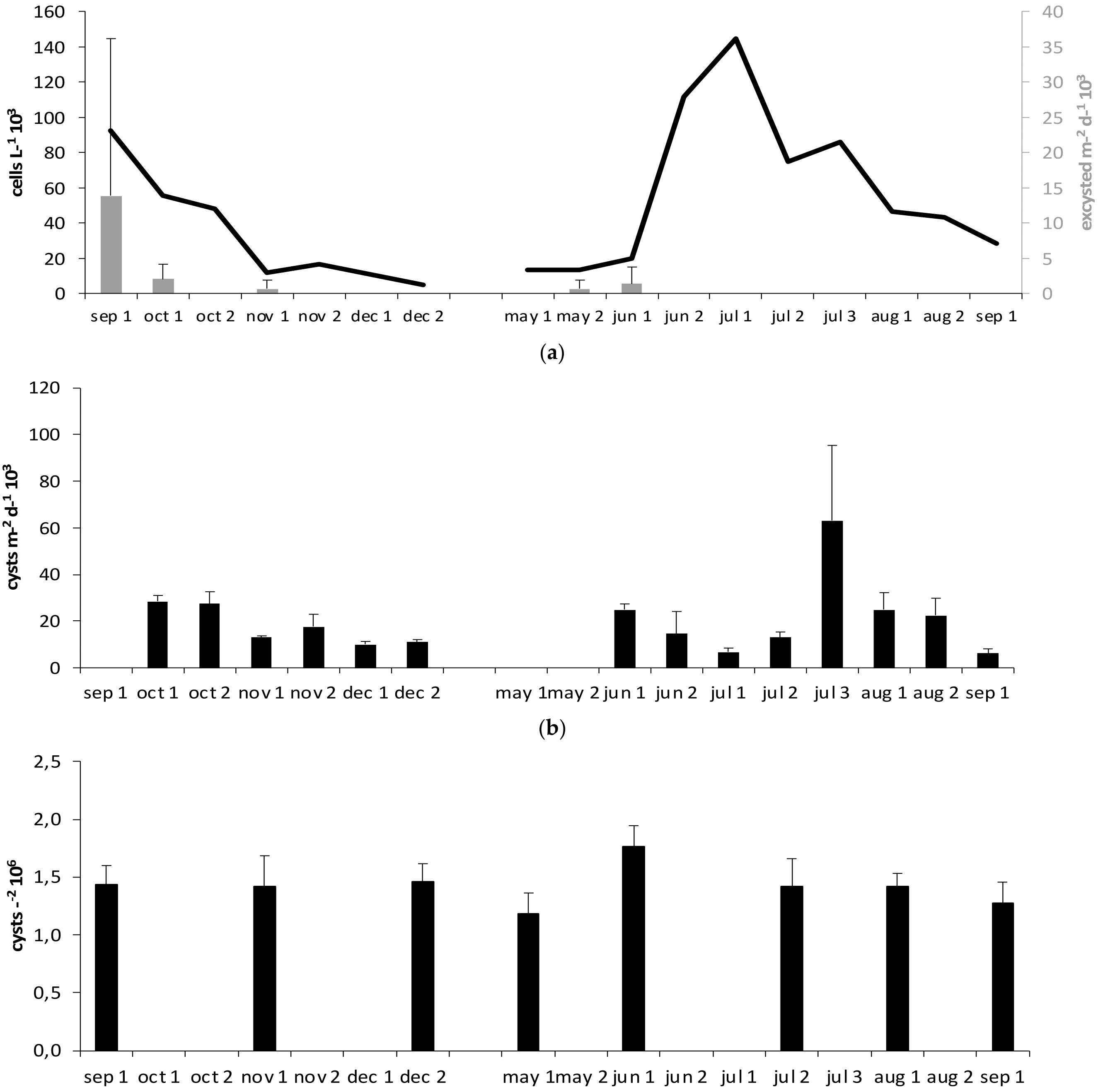
Figure 8. Temporal variation (abundance and *taxa* richness) of resting stages in surface sediments of the Mar Piccolo, Taranto. (**a**) Total abundance referred to 1 g of dry sediment (average ± SD); (**b**) *taxa* richness. Black bars, full cysts; grey bars, empty cysts.

Focusing attention on single species, we obtained information regarding the whole sampling devices in only four cases (those showing presence in water column, sediment traps, inverted traps, and sediments). Scrippsiella acuminata, one of the most abundant species both in the pelagic and benthic domain, showed wide fluctuations in the water column during the study period, according to classical seasonal dynamics.

High abundance values of *Scrippsiella acuminata* in the plankton preceded high cyst fluxes toward the sediments, and fueled a cyst bank that was found to always be present and influenced by abundance fluctuations, in accordance with those of the active cells in the water column. The highest abundance of excysted *S. acuminata* in the inverted traps was registered in September 2010 (T1), corresponding to a peak of plankton population. In June 2011 (T2), a moderate germination of benthic cysts was observed, in any case, it was recorded just before a growth in the plankton population (Figure 9).

These kinds of dynamics were also observed in other dinoflagellate species such as *Alexandrium minutum*, *Gymnodinium impudicum*, and *Oblea rotunda*. The suggestion was that cyst sinking was correlated to the presence of active stages in the water column and, as probably the most interesting aspect, the numbers involved in the dynamics of sinking/germination were only a small proportion of the whole cyst bank.

On the other hand, cysts of *Posoniella tricarinelloides* and *Pentapharsodinium tyrrhenicum* were collected by sediment traps throughout the year and their cyst bank was always present with light fluctuations, while their active stages were apparently absent from the water column. This was also the case of the rarest *Calciperidinium asymmetricum*, *Follisdinellum splendidum* (Figure 10), and *Melodomuncula berlinensis*, known to science only as cysts.

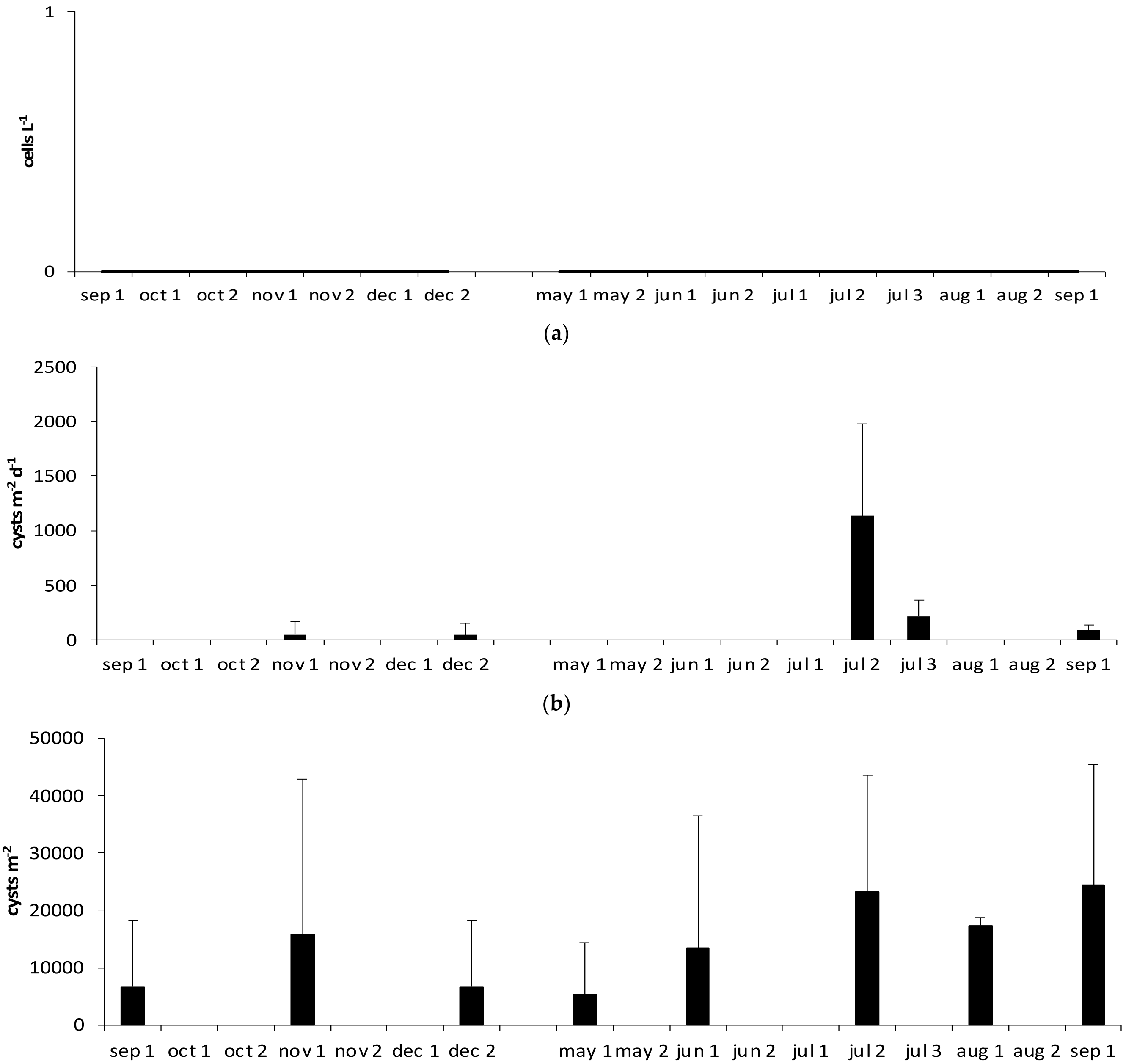


(**a**)

(**b**)

(**c**)

Figure 9. The benthic-pelagic dynamics of *Scrippsiella acuminata* in the Mar Piccolo of Taranto; (**a**) active cells in the water column, collected with a Niskin bottle at three different depths (black lin); active cells (intended as germinated) from the sediment, collected with inverted traps (grey bars); (**b**) cyst fluxes to the bottom, collected by sediment traps; (**c**) full cysts in surface sediment cores.



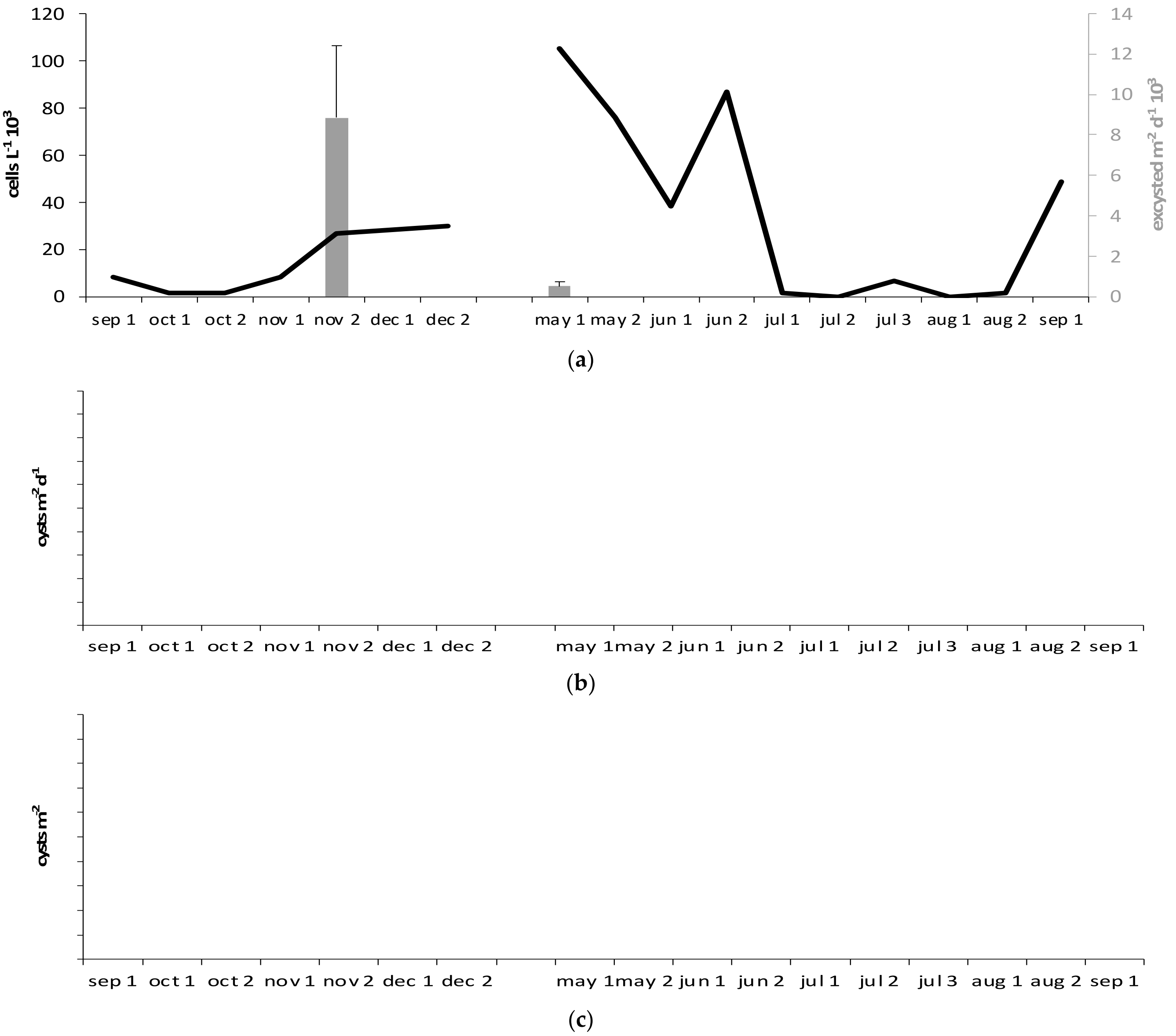
(**a**)

(**b**)

(**c**)

Figure 10. The pelagic-benthic dynamics of *Follisdinellum splendidum* in the Mar Piccolo of Taranto; (**a**) active cells in the water column; (**b**) cyst fluxes to the bottom, collected by sediment traps; (**c**) full cysts in the surface sediment cores.

The opposite pattern was also observed, with species known as resting stage producers, whose cysts were not observed or not recognized. *Akashiwo sanguinea*, for instance, showed the highest abundance among the plankton *taxa*, during spring and early summer T2, probably sustained by a preceding period of germination from the sediments, still evident in May. During T1, in addition, lower densities in the water were detected, but an important germination event was recorded in November with 8854 cells m^{-2} d^{-1} in the inverted traps (Figure 11). This fact can be interpreted as a massive germination not followed by active reproduction in the water column.



(**a**)

(**b**)

(**c**)

Figure 11. The pelagic-benthic dynamics of *Akashiwo sanguinea* in the Mar Piccolo of Taranto; (**a**) active cells in the water column, collected with a Niskin bottle at three different depths (black line); active cells (intended as excysted) from the sediment, collected with inverted traps (grey bars); (**b**) cyst fluxes to the bottom; (**c**) full cysts in surface sediment cores.

4. Discussion

The first result of the present investigation showed an important presence of cysts in the sediments of the studied site. Such a presence, with densities up to millions of cysts m^{-2} of wet sediment, is probably underestimated if we consider that the consistency of the cyst bank appeared to be even higher down to 10 cm of sediment in a study by Belmonte et al. [4]. Other studies [31,32] defined an obvious general increase in cyst content in layers below the sediment surface, which is the only involved in the injection of re-activated stages into the water column. The storage power of a deeper cyst bank still awaits better understanding. The existence of viable stocks of individuals and species, although in a resting condition, obliges us to think about the resilience of a plankton community in confined environments over a more extended time span.

Notwithstanding the fact that the unicellular plankton dominated the metazoan plankton in terms of numbers in the water column, it was not surprising that the abundance of cysts from some metazoan organisms was found to be numerically comparable (as an order of magnitude) with that of unicellular algae in the sediments. In fact, each Dinophyta cyst derives from the fusion of two swimming cells in a single zygote, while eggs of Metazoa are produced by a single individual (the mature female) at a rate of up to 100 day^{-1} female^{-1}, for up to 45 days of life length in the case of Copepoda [33,34].

The high production of cysts in the water column (see the sediment trap results, for *Scrippsiella acuminata*, July 2011), did not necessarily correspond to an accumulation in the sediment, and the recording of such an increase in our sediment samples. This could be the result of continuative encystment/excystment short cycles of resting stages not diapausal, but simply quiescent [4] as well as continuative germination events, as demonstrated for *Scrippsiella* spp. including *S. acuminata* (reported in that paper as *S. trochoidea*) in Onagawa Bay [35]. This possibility was confirmed by the finding of active stages in sediment traps (positioned to catch cysts) during the same period of cyst sinking. At this point, the sediment trap content probably deserves a more cautious determination because it represents the collection time of a fortnight, during which at least part of the collected cysts can re-germinate active stages.

The extreme variability of the rest duration is a well-known trait among Dinophyta, leading to the suggestion that encystment is the necessary by-product of sexual reproduction, and is only secondarily an adaptation to variable conditions of the environment [36–38].

In the inverted traps, the presence of active stages of organisms not producing cysts (as in the case of Copepoda juveniles) could represent proof of their chance to enter a rest phase as lethargic individuals, without encystment [39].

This possibility, probably present also in other *taxa*, together with the capacity of many dinoflagellates to produce dormant stages with different physiological features, is to be carefully considered in studies of pelagic-benthic dynamics because of the difficulty in morphologically distinguishing dormant from active stages, or even the temporary from the true resting cysts in the sediment samples [40].

The study by Belmonte et al. [11] of the zooplankton of Taranto seas showed that a single date-collection of zooplankton in the first inlet of the Mar Piccolo revealed about 30% of the species hosted by the same site over a collection of two years. The whole species list of the two-year study, furthermore, differed by about 60% from that coming from another study carried out 15 years before [23]. This suggests a strong influence of the “resting biodiversity”, if recruited in a timely manner in the water column, on the functioning and the characterization of the whole active community.

The present integrated approach allowed us to recognize species not observed in the water column, but clearly deriving from the plankton because they were collected by sediment traps as sinking cysts. This was the case of three paleontological *taxa, Calciperidinium asymmetricum*, *Follisdinellum splendidum*, and *Melodomuncula berlinensis*. They have also been found in sediments and sediment trap samples in other studies [41,42] and, moreover, in the case of *C. asymmetrivcum,* a scrippsielloid active stage was obtained in the laboratory germination experiments (Table 3). Even though it was not possible to identify it at the species level, this demonstrates the non “fossil” stage of the organism, besides the still lacking knowledge of the active stages associated with these cysts.

The finding of swimming stages of *Protoperidinium mite* (Dinophyta) and *Tintinnopsis* sp. (Ciliophora) in inverted traps (for the capture of newly germinated forms), coupled with the absence of any indication of a resting stage for them, probably suggests that these species have a resting stage morphologically indistinguishable from the swimming one, and when their rest is concluded, they simply “wake up” from the sediment, without germinating and/or abandoning a “cyst envelope”, as also hypothesized for *Protoperidinium quinquecorne* [43,44].

The most interesting suggestion, which comes from the present study of a marine cyst bank, however, is the acceptance that the biodiversity in the Mar Piccolo is higher than that assumed on the basis of standard approaches. The analysis of sediments, despite its complexity, offers an opportunity to save time in the effort of estimating biodiversity. In addition, the case of cyst morphotypes buried in the sediments, belonging to *taxa* without the corresponding active stages in the water column, suggests that a sort of "re-apparition" of species can occur sooner or later in the system, completely inserted into the framework of the *Resurrection Ecology* proposed by Kerfoot and Wider [4,8] (Figure 1). In fact, resting stages found in the sediment, without the corresponding active stages in the water column, can be produced by species either not known as resting stage producers so far, or active in the past and temporarily absent at the time of this study.

More precisely, for Dinophyta, the resting forms present in the sediment traps and sediments (62 and 53 *taxa*, respectively) largely exceeded the active forms collected in the water column (43 *taxa*). This "hidden" part of the Dinophyta community is even more important if we consider that only 17 of the 43 active stages in the water column are known to science as cyst producers. The continuous collection of samples will probably lead to the recognition of the whole community, but in any case, the present study demonstrated that integrated sampling in the different domains of the environment more than doubled the *taxa* involved in community dynamics.

The comparative measure unit adopted for all the data allowed us to sketch a picture of benthic-pelagic coupling in the Mar Piccolo of Taranto (Table 4). The fluxes of the cysts produced and that sunk to the bottom in the two periods examined suggest that the critical period for most active plankton is the winter, but encystmet also occurs in summer time for some species. During summer in fact, episodes of eutrophication and consequent oxygen depletion are possible and actually reported in the past from the Mar Piccolo [45]. A more detailed observation of the results also suggests that the benthic-pelagic coupling is quantitatively affected by the abundance of Dinophyta.

If we consider only Copepoda, in fact, the reverse trend can be recognized, with an enhanced cyst production in autumn, which suggests an overwintering strategy of these species (data not shown).

In the observed period, the total produced cysts were more abundant than the germinated ones, as revealed by the comparison between the contents of sediment traps and inverted traps (Table 4). The cyst bank of the sediments daily injects (with germination) up to 0.2% of its components into the water column, and receives cysts about 0.0014% of plankton components. This notwithstanding, the difference in volume of the two considered compartments (1 cm of sediments, vs. 11 m of water column) is enough to produce an input of cysts higher than the output due to germination. This fact simply testifies that the cyst bank has a high storage power and a content only slightly affected by germination events. This is a common strategy among highly resilient communities, where cyst accumulation surpasses the germination rate. It is not rare to find different species with germination strategies that count on different, and even very long resting periods, to spread successful germination over many time windows [46–50]. In fact, cysts can maintain their viability for a time that is largely longer than that of active stages, and this fact could also be decisive in the accumulation of resting stages in the cyst bank, and in the increase in its resilience capacity [14,51].

Little is known about the subtraction of cysts from the sediment compartment, if it is not due to germination. Predation on the cysts [21,22,52], their natural mortality/degradation [53], or their removal from the layer where benthic-pelagic exchanges take place [54] is to be ascertained, because it could be important for the success of benthic-pelagic coupling for each species. More precisely, regarding each species, the apparent lack of unison of the total number of active and resting stages must be discussed in light of some considerations of other aspects of benthic-pelagic coupling:

Many species are involved in benthic-pelagic exchanges that are different from the cyst production/germination. They are the so-called mero-plankton, spending a part of their life cycle in the benthos, but as active organisms.

Many holoplankters of the list do not produce cysts (for example, Dinophyta are known as cyst producers only in a few cases, [5,55,56]) or resolve the environmental fluctuations with alternative strategies (e.g., resting as juveniles for Harpacticoida or

Cyclopoida; or being adapted to seasonal variations as perennial/ubiquitous species that are never absent from the water column).

Some holoplankton species (as Cladocera) produce very few extra-large resting eggs that have not been collected by the method of the present study (resting stages with a diameter >200 µm were not considered). The same could also be said for morphotypes smaller than the minimum sieve mesh size used in laboratory treatments (20 µm).

The sediment cyst bank is not uniform, even in the Mar Piccolo of Taranto, since cysts are patchily distributed [57] and horizontal exchanges of sinking cysts and germinated active stages between adjacent water columns should be considered, in addition to the vertical exchanges.

In some species, the time interval of each active generation could be shorter than the sampling interval used, thus causing the absence of species in the plankton records, notwithstanding their presence as cysts.

Sediment traps collected cyst sinking at 1 m above the sea floor. Inverted traps collected germinations just on the sea floor. The 1 m gap of the two sampling devices could be important in the lacking of unison of some results.

Cyst morphology can be affected by environment and what has been described as a cyst in vitro, could perhaps not correspond to cysts in the natural environment (as in the case of *Akashiwo sanguinea* [30], abundant as an active stage in the present study, but with an in vitro obtained cyst here not found).

5. Conclusions

Many species in the Mar Piccolo of Taranto have an abundant stock of resting individuals in the sediments, which ensures the periodical re-population of the water column after adverse periods for life. This fact could represent a defensive strategy of the whole community against the unpredictability of the environment. If the production/presence of cysts could in some way represent the unpredictability of the environment, future studies could use the ratio of cysts/active stages of the whole plankton community to rank environments and/or seasons according to their instability.

It is interesting to note that the cyst morphotypes are more numerous than the active stages potentially able to produce them. The identification of cysts is still far from completed, and new cyst morphotypes are continuously added to the known system in the confined bays investigated [5,57,58].

Single-cell sequencing would assist in linking the identity of cysts to pelagic stages.

The frame in which to collocate rest–activity cycles for single species is consequently complex (see the approximate sketch of Figure 1), and deserves the maximum caution in deriving generalizations for resurrection ecology. What is not negligeable, however, is the high utility in considering cysts in any kind of study of ecosystems because, as is the case of Mar Piccolo, biodiversity and ecosystem resilience can be reliably determined only if the sediment cyst bank is considered.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/w13243619/s1, Supplementary Material 1: Active stages in the water column (Niskin bottle); Supplementary Material 2: Active stages in the water column (plankton net); Supplementary Material 3: Resting stage fluxes (sediment traps); Supplementary Material 4: In situ excystment (inverted traps); Supplementary Material 5: Cyst bank in surface sediments (sediment cores).

Author Contributions: Conceptualization, F.R.; Methodology, F.R. and G.B.; Formal analysis, F.R. and G.B.; Writing—original draft preparation, G.B. and F.R.; Writing—review and editing, G.B. and F.R.; Resources and equipment, F.R. and G.B.; All authors have read and agreed to the published version of the manuscript.

Funding: Samples were collected and analyzed in the framework of the CNR—IRSA and DiSTeBA—UniSalento basic research activities.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available as Supplementary Materials.

Acknowledgments: The authors wish to thank Giovanni Fanelli (CNR-IRSA Taranto) for their help during the sampling activities. Manuela Belmonte (CNR-IRSA Taranto) performed part of the technical analyses in the laboratory. Nicolette James usefully commented on the text to revise the English language. Particular thanks are due to the three reviewers and, overall, the Academic Editor whose suggestions greatly improved the style and the communication quality of the present paper.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Boero, F. Fluctuations and variations in coastal marine environments. *Mar. Ecol.* **1994**, *15*, 3–25. [CrossRef]
2. Giangrande, A.; Geraci, S.; Belmonte, G. Life-cycle and life-history diversity in marine invertebrates and the implications in community dynamics. *Oceanogr. Mar. Biol. Annu. Rev.* **1994**, *32*, 305–333.
3. Boero, F.; Belmonte, G.; Fanelli, G.; Piraino, S.; Rubino, F. The continuity of living matter and the discontinuities of its constituents: Do plankton and benthos really exist? *Trends Ecol. Evol.* **1996**, *11*, 177–180. [CrossRef]
4. Belmonte, G.; Castello, P.; Piccinni, M.R.; Quarta, S.; Rubino, F.; Geraci, S. Resting stages in marine sediments off the Italian coast. In *Biology and Ecology of Shallow Coastal Waters*; Eleftheriou, A., Hansell, A.D., Smith, C.J., Eds.; Olsen & Olsen: Frederborg, Denmark, 1995; pp. 53–58.
5. Belmonte, G.; Rubino, F. Resting cysts from coastal marine plankton. *Oceanogr. Mar. Biol. Annu. Rev.* **2019**, *57*, 1–88.
6. Marcus, N.H.; Boero, F. Minireview: The importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnol. Oceanogr.* **1998**, *43*, 763–768. [CrossRef]
7. Anderson, D.; Alpermann, T.; Cembella, A.; Collos, Y.; Masseret, E.; Montresor, M. The globally distributed genus *Alexandrium*: Multifaceted roles in marine ecosystems and impacts on human health. *Harmful Algae* **2012**, *14*, 10–35. [CrossRef] [PubMed]
8. Kerfoot, W.C.; Weider, L.J. Experimental paleoecology (resurrection ecology): Chasing Van Valen's Red Queen hypothesis. *Limnol. Oceanogr.* **2004**, *49*, 1300–1316. [CrossRef]
9. Moscatello, S.; Rubino, F.; Saracino, O.D.; Fanelli, G.; Belmonte, G.; Boero, F. Plankton biodiversity around the Salento Peninsula (South East Italy): An integrated water-sediment approach. *Sci. Mar.* **2004**, *68* (Suppl. 1), S85–S102.
10. Rubino, F.; Saracino, O.D.; Moscatello, S.; Belmonte, G. An integrated water/sediment approach to study plankton (a case study in the southern Adriatic Sea). *J. Mar. Sys.* **2009**, *78*, 536–546. [CrossRef]
11. Belmonte, G.; Vaglio, I.; Rubino, F.; Alabiso, G. Zooplankton composition along the confinement gradient of the Taranto Sea System (Ionian Sea, south-eastern Italy). *J. Mar. Sys.* **2013**, *128*, 222–238. [CrossRef]
12. Belmonte, G.; Pati, A.C. Hatching rate and diapause duration in eggs of *Paracartia latisetosa* (Copepoda: Calanoida). *J. Plankton Res.* **2007**, *29*, i39–i47. [CrossRef]
13. Hairston, N., Jr.; Van Brunt, R.; Kearns, C. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* **1995**, *76*, 1706–1711. [CrossRef]
14. Ribeiro, S.; Berge, T.; Lundholm, N.; Ellegaard, M. Phytoplankton growth after a century of dormancy illuminates past resilience to catastrophic darkness. *Nat. Commun.* **2011**, *2*, 311–317. [CrossRef]
15. Bravo, I.; Figueroa, R. Towards an ecological understanding of dinoflagellate cyst functions. *Microorganisms* **2014**, *2*, 11–32. [CrossRef]
16. Pati, A.C.; Belmonte, G. Disinfection efficacy on cyst viability of *Artemia franciscana* (Crustacea), *Hexarthra fennica* (Rotifera) and *Fabrea salina* (Ciliophora). *Mar. Biol.* **2003**, *142*, 895–904. [CrossRef]
17. Pati, A.C.; Belmonte, G. Effect of aquaculture disinfectants on the germination of a Dinophyta cyst. *Thalass. Salentina* **2007**, *30*, 129–142.
18. Stabili, L.; Miglietta, A.M.; Belmonte, G. Lysozyme-like and trypsin-like activities in the cysts of *Artemia franciscana* Kellog, 1906: Is there a passive immunity in a resting stage? *J. Exper. Mar. Biol. Ecol.* **1999**, *237*, 291–303. [CrossRef]
19. Marcus, N.H. Recruitment of copepod nauplii into the plankton: Importance of diapause eggs and benthic processes. *Mar. Ecol. Progr. Ser.* **1984**, *15*, 47–54. [CrossRef]
20. Ichimi, K.; Montani, S. Effects of deposit feeder ingestion on the survival and germination of marine flagellate cysts. *Fisheries Sci.* **2001**, *67*, 1178–1180. [CrossRef]
21. Zonneveld, K.A.; Versteegh, G.J.; de Lange, G.J. Preservation of organic-walled dinoflagellate cysts in different oxygen regimes: A 10,000 year natural experiment. *Mar. Micropaleontol.* **1997**, *29*, 393–405. [CrossRef]
22. Persson, A. Possible predation of cysts—A gap in the knowledge of dinoflagellate ecology? *J. Plankton Res.* **2000**, *22*, 803–809. [CrossRef]
23. Rubino, F.; Saracino, O.D.; Fanelli, G.; Belmonte, G.; Boero, F. Plankton dynamics in the Mar Piccolo of Taranto: A pilot plan. *Giorn. Bot. Ital.* **1996**, *130*, 1032–1036. [CrossRef]
24. Pastore, M. *Mar Piccolo*; Nuova Editrice Apulia: Martina Franca, Italy, 1993; p. 164.

25. ARPA Puglia. Mar Piccolo of Taranto—Scientific technical report on the interaction between the environmental system and contaminants flow from primary and secondary sources. *Tech. Rep.* **2014**, *4*, 175.
26. Belmonte, G.; Rossi, V. Resurrection and time travelling. Resurrection in crustaceans (and others). *Trends Ecol. Evol.* **1998**, *13*, 4–5. [CrossRef]
27. Zingone, A.; Totti, C.; Sarno, D.; Cabrini, M.; Caroppo, C.; Giacobbe, M.G.; Lugliè, A.; Nuccio, C.; Socal, G. Fitoplancton: Metodiche di analisi quali-quantitativa. In *Metodologie di Studio del Plancton Marino, ISPRA—Istituto Superiore per la Protezione e la Ricerca Ambientale*; Socal, G., Buttino, I., Cabrini, M., Mangoni, O., Penna, A., Totti, C., Eds.; Institute for Environmental Protection and Research (ISPRA): Rome, Italy, 2010; pp. 213–237.
28. Montresor, M.; Bastianini, M.; Cucchiari, E.; Giacobbe, M.; Penna, A.; Rubino, F.; Satta, C.T. Stadi di resistenza del plancton. In *Metodologie di Studio del Plancton Marino, ISPRA—Istituto Superiore per la Protezione e la Ricerca Ambientale*; Socal, G., Buttino, I., Cabrini, M., Mangoni, O., Penna, A., Totti, C., Eds.; Institute for Environmental Protection and Research (ISPRA): Rome, Italy, 2010; pp. 271–285.
29. Belmonte, G.; Moscatello, S.; Rubino, F. Forme di resistenza dello zooplancton. In *Metodologie di Studio del Plancton Marino, ISPRA—Istituto Superiore per la Protezione e la Ricerca Ambientale*; Socal, G., Buttino, I., Cabrini, M., Mangoni, O., Penna, A., Totti, C., Eds.; Institute for Environmental Protection and Research (ISPRA): Rome, Italy, 2010; pp. 507–518.
30. Tang, Y.Z.; Gobler, C.J. Sexual resting cyst production by the dinoflagellate *Akashiwo sanguinea*: A potential mechanism contributing to the ubiquitous distribution of a harmful alga. *J. Phycol.* **2015**, *51*, 298–309. [CrossRef] [PubMed]
31. Hairston, N.G., Jr.; Fox, J.A. Egg banks. In *Plankton of Inland Waters*; Likens, G.E., Ed.; Elsevier: San Diego, CA, USA, 2010; pp. 247–254.
32. Sichlau, M.H.; Hansen, J.L.S.; Andersen, T.J.; Hansen, B.W. Distribution and mortality of diapause eggs from calanoid copepods in relation to sedimentation regimes. *Mar. Biol.* **2011**, *158*, 665–676. [CrossRef]
33. Ianora, A. Copepod life history traits in subtemperate regions. *J. Mar. Syst.* **1998**, *15*, 337–349. [CrossRef]
34. Drillet, G.; Jeppesen, P.M.; Højgaard, J.K.; Jørgensen, N.O.G.; Hansen, B.W. Strain-specific vital rates in four *Acartia tonsa* cultures II: Life history traits and biochemical contents of eggs and adults. *Aquaculture* **2008**, *279*, 47–54. [CrossRef]
35. Ishikawa, A.; Taniguchi, A. Contribution of benthic cysts to the population dynamics of *Scrippsiella* spp. (Dinophyceae) in Onagawa Bay, northeast Japan. *Mar. Ecol. Prog. Ser.* **1996**, *140*, 169–178. [CrossRef]
36. Rengefors, K. Seasonal succession of dinoflagellates coupled to the benthic cyst dynamics in Lake Erken. *Arch. Hydrobiol. Sp. Iss. Adv. Limnol.* **1998**, *51*, 123–141.
37. Olli, K.; Anderson, D.M. High encystment success of the dinoflagellate *Scrippsiella* cf. *lachrymosa in culture experiments. J. Phycol.* **2002**, *38*, 145–156. [CrossRef]
38. Figueroa, R.I.; Bravo, I.; Garcés, E. Effects of nutritional factors and different parental crosses on the encystment and excystment of *Alexandrium catenella* (Dinophyceae) in culture. *Phycologia* **2005**, *44*, 658–670. [CrossRef]
39. Williams-Howze, J. Dormancy in the free-living copepod orders Cyclopoida, Calanoida, and Harpacticoida. *Oceanogr. Mar. Biol. Ann. Rev.* **1997**, *35*, 257–321.
40. Kremp, A.; Parrow, M.W. Evidence for asexual resting cysts in the life cycle of the marine peridinioid dinoflagellate *Scrippsiella hangoei*. *J. Phycol.* **2006**, *42*, 400–409. [CrossRef]
41. Meier, K.J.S.; Willems, H. Calcareous dinoflagellate cysts in surface sediments from the Mediterranean Sea: Distribution patterns and influence of main environmental gradients. *Mar. Micropaleontol.* **2003**, *48*, 321–354. [CrossRef]
42. Rubino, F.; Moncheva, S.; Belmonte, M.; Slabakova, N.; Kamburska, L. Resting stages produced by plankton in the Black Sea—Biodiversity and ecological perspective. *Rapp. Comm. Int. Mer. Medit.* **2010**, *39*, 399.
43. Satta, C.T.; Anglés, S.; Garcés, E.; Lugliè, A.; Padedda, B.M.; Sechi, N. Dinoflagellate cysts in recent sediments from two semi-enclosed areas of the Western Mediterranean Sea subject to high human impact. *Deep. -Sea Res. Part II* **2010**, *57*, 256–267. [CrossRef]
44. Rubino, F.; Belmonte, M.; Galil, B.S. Plankton resting stages in recent sediments of Haifa port, Israel (Eastern Mediterranean)—Distribution, viability and potential environmental consequences. *Mar. Poll. Bull.* **2017**, *116*, 258–269. [CrossRef]
45. Alabiso, G.; Cannalire, M.; Ghionda, D.; Milillo, M.; Leone, G.; Caciorna, O. Particulate matter and chemical-physical conditions of an inner sea: The Mar Piccolo in Taranto. A new statistical approach. *Mar. Chem.* **1997**, *58*, 373–388. [CrossRef]
46. Moscatello, S.; Belmonte, G. Egg banks in hypersaline lakes of the South East Europe. *Saline Syst.* **2009**, *5*, 3. [CrossRef]
47. Cohen, D. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.* **1966**, *12*, 119–129. [CrossRef]
48. Philippi, T.; Seger, J. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **1989**, *4*, 41–44. [CrossRef]
49. Menu, F.; Roebuck, J.P.; Viala, M. Bet-hedging diapause strategy in stochastic environment. *Am. Nat.* **2000**, *155*, 724–734. [CrossRef] [PubMed]
50. Ślusarczyk, M.; Starzyński, J.; Bernatowicz, P. How long to rest in unpredictably changing habitats? *PLoS ONE* **2017**, *12*, e0175927-16. [CrossRef]
51. Viitasalo, S. Effects of bioturbation by three macrozoobenthic species and predation by necto-benthic mysids on cladoceran benthic eggs. *Mar. Ecol. Prog. Ser.* **2007**, *336*, 131–140. [CrossRef]
52. Persson, A.; Rosenberg, R. Impact of grazing and bioturbation of marine benthic deposit feeders on dinoflagellate cysts. *Harmful Algae* **2003**, *2*, 43–50. [CrossRef]

53. Shul, D.H.; Kremp, A.; Mayer, L.M. Bioturbation, germination and deposition of *Alexandrium fundyense* cysts in the Gulf of Maine. *Deep. -Sea Res. Part II* **2014**, *103*, 66–78. [CrossRef]
54. Dale, B. Dinoflagellate resting cysts: Benthic plankton. In *Survival Strategies of the Algae*; Frixell, G.A., Ed.; Cambridge University Press: Cambridge, UK, 1983; pp. 69–136.
55. Taylor, F.J.R. General group characteristics, special features of interest, short history of dinoflagellates study. In *The Biology of Dinoflagellates*; Taylor, F.J.R., Ed.; Blackwell Science Publications: Boston, MA, USA, 1987; Volume 21, pp. 1–23.
56. Ferraro, L.; Rubino, F.; Belmonte, M.; Da Prato, S.; Greco, M.; Frontalini, F.A. Multidisciplinary approach to study confined marine basins: The holobenthic and merobenthic assemblages in the Mar Piccolo of Taranto (Ionian Sea, Mediterranean). *Mar. Biodivers.* **2017**, *47*, 887–911. [CrossRef]
57. Rubino, F.; Moscatello, S.; Belmonte, M.; Ingrosso, G.; Belmonte, G. Plankton Resting Stages in the Marine Sediments of the Bay of Vlorë (Albania). *Intern. J. Ecol.* **2013**, *2013*, 3–14. [CrossRef]
58. Rubino., F.; Belmonte, G. A new cyst morphotype from recent sediments of the Mar Piccolo of Taranto (Southern Italy, Ionian Sea). *Progr. Aqua Farm. Mar. Biol.* **2019**, *2*, 180015.