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Analysis of time-lapse images as a tool to study movement in situ in four species of sea urchins and one limpet from North Patagonia and the South Shetland Islands

Abstract

Time lapse photography closes a gap to other benthic studies, where the community and its structure is often investigated by estimates of percentage cover and abundance of epibenthic organisms. We realized preliminary experiments of the movement patterns of the three Southern Chilean sea urchin species, *Arbacia dufresnii*, *Loxechinus albus*, *Pseudechinus magellanicus* and the Antarctic species *Sterechinus neumayeri* in shallow water (10 m depth). Additionally, we included the Antarctic limpet *Nacella concinna* from a subtidal location in our study. The maximum movement activity of single specimen of all four species varied between 22.5 cm and 62.5 cm h⁻¹ during day time. Both Antarctic species *N. concinna* and *S. neumayeri* were much more active compared to the species from North Patagonia. They were in movement at 44 % and 49 % of all observations, which were recorded in intervals of 1 min. Stop intervals were more pronounced in the species from Northern Patagonia. They were only active between 5 % (*L. albus*), 20 % (*A. dufresnii*) and 30 % (*P. magellanicus*) of all observation intervals. We compared our results with literature data from other echinoids and gastropods, worldwide. Our preliminary results indicate that all species fit well in the activity range known from other species. We have found no evidence that the movement of animals from polar regions differ during austral summer significantly from animals of temperate or tropical zones.

Keywords: time lapse, limpet, sea urchin, Antarctica, Chile, locomotion

1 Introduction

The study of interactions between species in a benthonic community contains methodology of different difficulties (Brinkhurst 1975, Peckarsky 1979). Although useful, laboratory studies cannot fully replicate natural conditions. However, these studies can contribute to examining the frequency and impact of every interaction that could be replicated in the community. Therefore, to assess the biological importance of several populations in the field it is necessary to perform in situ measurements in the field. Some techniques used to assess in situ interaction and movement include study of colonization, caging experiment and visual observations (Peckarsky 1979). Although visual observation is intuitively the most attractive method of assessing benthonic populations, it has some limitations, such as the size of the organism, the disturbance of the observer and the difficulty of underwater observation.

For a scientific diver, in situ observations of macroepibenthic organisms for periods exceeding the allowed time range present a variety of technical challenges. A comprehensive review of the status and trends in underwater videometric measurement techniques for the last century is given by Shortis et al. (2007). Nowadays, battery energy demands as well as the recording capacity system is not any longer a limit for autonomous long-term operations. Due to the fact that the time scales of biological and ecological processes are often in the order of hours or days. These days, camera systems can cover the respective time course and pattern of the phenomenon in question.

The first time-lapse studies were realized by simply observing a specimen by eye and noting its behaviour at regular time intervals. This method was used in an upright microscope (Carey & Pettengill 1967), in aquaria and in the field. Drawing layouts and taking images at regular intervals demonstrated the whole range of dynamics, from a single cell to population (Paddock 2001). Most probably, Kenneth Read was in 1967 the first diver who accomplish time-lapse photography on sea urchins with a motion picture camera designed by Harold E. Edgerton (Marx 1990). Rupert Riedl mentioned already in 1963 and in 1967 the need for time-lapse photography to replace scuba divers and consequently, he designed a variety of housings for this purpose (Riedl 1963, Riedl 1967). In the 1970s, underwater time-lapse studies became in demand for answering, both, behavioural questions and interactions between benthic organisms in shallow water as well in the deep sea (Fedra & Machan 1979). Paul et al. (1978) used a Bottom Ocean Monitor developed by Gerard and Thorndike in 1974 to take time-lapse photographs in the deep-sea at 4873 m water depth. Innumerous studies have been conducted since that time.

Time-lapse photography closes a gap to other benthic studies, where the community and its structure is often investigated by estimates of percentage cover and abundance of macroepibenthic organisms (Beuchel et al. 2010), adding by this method its dynamic over a certain time period. Motion studies not only allow the analysis of the displacement of benthic organisms between its start and endpoint over long time periods (Creese 1982, McClintock & Lawrence 1986, Andrew et al. 2002) but they can also track the total distance travelled by the organisms including their inactivity, mobility time and velocity in detail. Here we present primarily in situ experiments about movement patterns of sea urchins and a limpet with two camera systems used under cold-water conditions, together with a comparison of these data with other species.

In our primarily study we focused on five species. Two species are found in the Antarctic region. The limpet *Nacella concinna* (Strebel 1908) is distributed from the intertidal to about 110 m depth in decreasing abundances (Powell 1951, Powell 1973,

Clarke et al. 2004), whereas the sea urchin *Sterechinus neumayeri* (Meissner 1900) occurs from the shallow subtidal down to 1200 m (Brey & Gutt 1991, Jacob et al. 2003). Both species are omnivorous, scratching among other microbial films, algae, and bryozoans from the ground (Brey & Gutt 1991, Clarke et al. 1994). There is only limited information about the activity patterns of both species. Walker (1972) mentioned the movement of a subtidal population to the intertidal during the austral summer. A similar vertical movement within the intertidal is known for several species.

The three Southern Chilean sea urchin species that were tracked in our survey are *Arbacia dufresnii* (Blainville 1825), *Loxechinus albus* (Molina 1782), *Pseudechinus magellanicus* (Philippi 1857). Their distributional patterns and diets were studied in a giant kelp forest (*Macrocystis pyrifera*) at Puerto Toro, Navarino Island, Chile by Vásquez et al. (1984). *Arbacia dufresnii* is a common sea urchin inhabiting both coasts of South America (Lessios et al. 2012) with a distribution from Puerto Montt, Chile (41°S) to Río de la Plata, Argentina (35°S). Around Tierra del Fuego is vertically distributed from 0 to at least 315 m water depth (Brogger et al. 2013), mainly on hard substrates. *L. albus* has a distribution from the Galapagos islands along the South American coast up to the Magellan Strait and in the Southern Atlantic up to the Islas de los Estados (Fenucci 1967). In Chile, it is present from shallow water down to 340 m and it is heavily exploited by local fishermen between 0 and 40 m depth (Arana 2005). *P. magellanicus* is a small but very abundant echinoid in Argentinean and southern Chilean waters. It is distributed along the South American coast from off Río de la Plata (35°S) in the Atlantic Ocean to Puerto Montt (41°S), Chile, in the Pacific Ocean; it is also found in islands of the Antarctic Sea (Bernasconi 1953). In Reloncaví Fjord, it lives in habitats of mixed gravel, sandy bottoms, rock, and clam deposits, occurring at depths of five to 20 meters.

Activity patterns like movement and stop intervals have never been recorded in any of the five species in situ before. Displacement and velocity studies were done before on several sea urchin species from temperate and tropical waters (Mattison et al. 1977, James 2000, Duggan & Miller 2001, Dumont et al. 2004, Tuya et al. 2004, Lauzon-Guay et al. 2006), whereas studies in the polar environment are scarce. Here we present primarily in situ experiments about movement patterns of sea urchins and a limpet with two camera systems used under cold-water conditions, together with a comparison of these data with other species. Our main objective is to compare whether polar species are less active than their relatives from temperate or tropical waters. In addition to our goal, we carried out an extensive comparison with literature data.

2 Study site

Time lapse photography studies of *S. neumayeri* and *N. concinna* were realized at King George Island (KGI) (62°02'S, 58°21'W), South Shetland islands, situated at ca. 120 km off the northern coast of the Antarctic Peninsula (Fig. 1). Images were taken at Fildes Bay, a 16 km long bay, opened in south-east direction, and lying between King George and Nelson Islands. The Chilean Antarctic research base Escudero, from where diving operations were realized, is located at the innermost, eastern part of the bay. The study area can be shortly described as follows: SHOA rock (62°12'12"S, 58°56'37"W), a small, vertical rock, down to 8 m depth, then with moderate slope down to 40m, bottom with pebbles and rocks, becoming mainly soft below 40 m. The camera was placed in a depth of about 10 m. Calcareous red algae of the genera

Lithothamnium and *Lithophyllum* were the most prominent representatives of bottom algae.

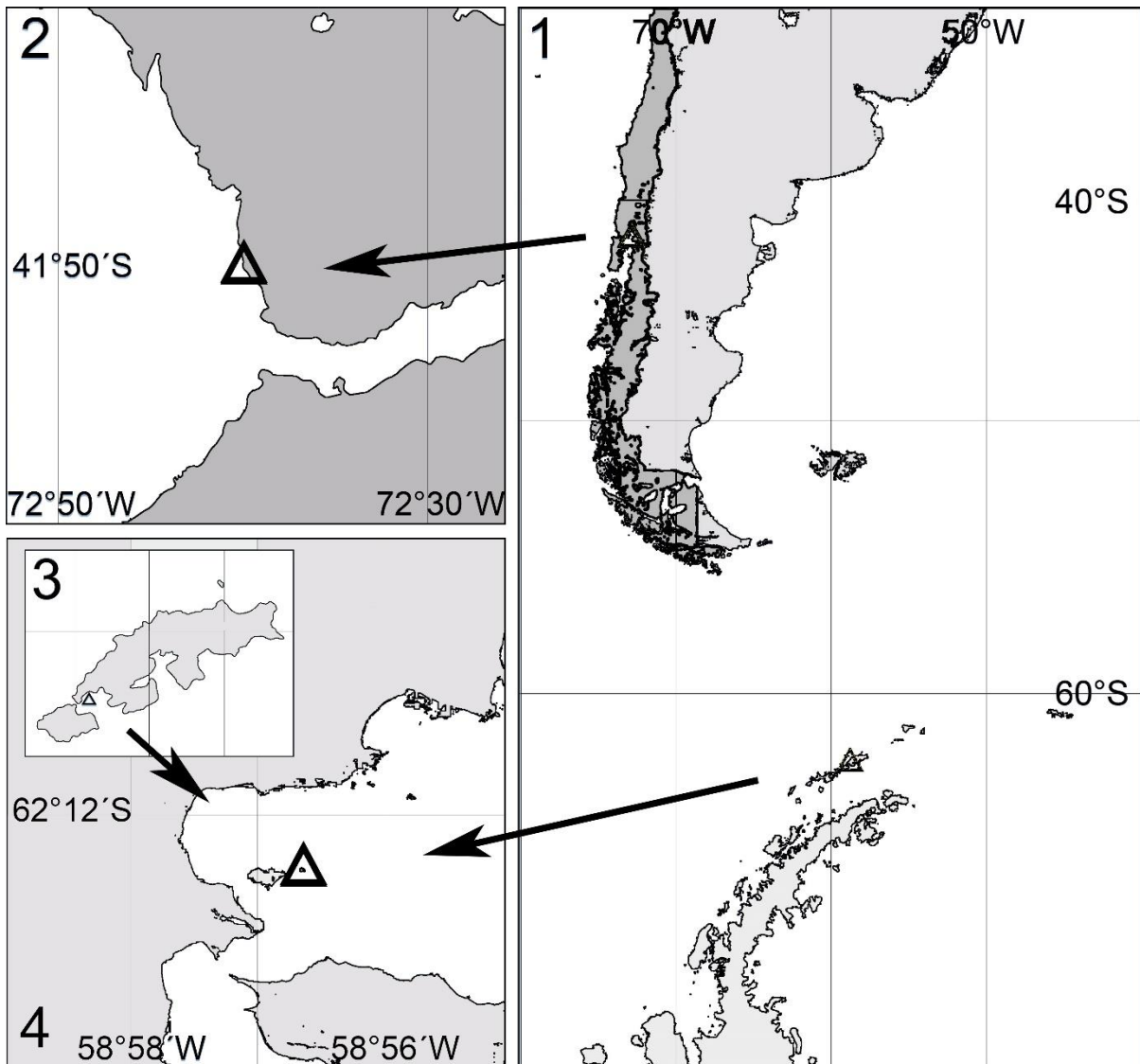


Fig. 1: Stations: (1) Map of continental Chile and Southern South America, Drake Passage and Antarctic Peninsula; (2) Caleta Yervas Buenas, Reloncaví Fjord, Chile; (3) King George Island, South Shetland Islands; (4) Fildes Bay. Triangles indicate station position.

The other part of the study was conducted in southern Chile, in the Lake District, in Caleta Yervas Buenas ($41^{\circ}40.3915' S$, $72^{\circ}39.4404' W$). It is located 35 km south of Puerto Montt, in the direction of the Reloncaví Fjord. This area has an average annual rainfall of 2,342 mm, having a maximum in the month of June (Di Castri & Hajek 1976). The average air temperature in summer is $15.1^{\circ}C$, while in winter the average drops to $7.7^{\circ}C$ (Di Castri & Hajek 1976). The temperature of the water column at a depth of 20 m, tends to vary between $10^{\circ}C$ and $11^{\circ}C$. This study site is under the influence of heavy shellfish exploitation by artisanal fisheries. Sea urchin fishery is not conducted in this area because of the small diametric size of the species. Maximum measured differences between low and high tide are close to 7 m. The camera was placed at 10 m depth (mean tide level). Images of *L. albus* and *A. dufresnii* were taken on rocks,

whereas time lapse sequences of *P. magellanicus* were taken in a habitat covered with shells and sand.

3 Methods

We conducted two different camera settings to measure the activity of sea urchins and limpets. Time lapse video recording was used in the Antarctic Region, whereas additional high resolution image sequences were taken in the Reloncaví Fjord. The daily movements of the Antarctic sea urchin *S. neumayeri* and the limpet *N. concinna* were studied in the Fildes Bay (King George Island, Antarctica) in situ. A camera (Sony DCR-TRV 900) in an underwater housing was mounted on a tripod about 1.2 m above bottom and set to record 1 second of video every minute. The recording was made between February 21 and 26, 2011 between 12:30 – 18:30 hrs. In total five recordings were made. A Bitmap image of the first frame of each video sequence was extracted and selected for analysis. The number of urchins and limpets analyzed per video sequence varied in dependency of their abundance for each recording date. Position of urchins and limpets were recorded every minute for the length of each video or until they left the field of view with the software ImageJ vers. 1.44 and the manual tracking plugin. From these data, we calculated individual speed (total distance travelled divided by total time of observation) and proportion of time spent moving (number of time intervals during which an urchin moved divided by the total number of intervals).



Fig. 2: Installation of a SONY TVR 995 video camera near Caleta la Arena, Reloncaví Fjord, 10 m depth

We used the same analysis and experimental design in Reloncaví Fjord (Fig. 2), but we made additional recordings with a high resolution photo camera (NIKON D70s) to record especially the activity of the small sea urchin *P. magellanicus*. Images of *L. albus* and *A. dufresnii* were recorded together, whereas time-lapse images of *P. magellanicus* were taken separately. The NIKON D70s was mounted 0.5 m above bottom. Image distortion was corrected with the freeware Hugin-2011.4.0.

In total nine recordings were made between July 2010 and November 2011. Recording time varied between 60 min and 6:40 hrs depending on camera settings and technical issues.

We used an external self-built interval recording control for the NIKON D70s that used the camera's remote control input to execute the time-lapse recordings.

Six additional quantitative samples were taken to estimate density and size of urchins and limpets close to the recording spots. Due to the more complex habitat in the Reloncaví Fjord we estimated the density of the sea urchins on sand and rock and checked their densities also with increasing depth.

We present the data for this primarily study as pooled data over all recording intervals due to the different recording times and densities of individuals. Additional descriptive data are shown as mean values \pm 1 SD.

4 Results

4.1 Size and density

At both study sites all species' mean diameter or length were below 5 cm. The biggest species was *L. albus*. The specimens of *L. albus* reach commercial size after 8 years and reproduce at 7 cm, but at the Reloncaví Fjord its mean diameter was only 4.51 ± 1.10 cm (Tab. 1). None of the measured individuals reached commercial size. The abundance of *L. albus* at 10 m depth was the lowest of all species on hard substrate with 7 ± 8 ind. m^{-2} , on shelly sand abundance at 10 m depth was 2 ± 4 ind. m^{-2} . The species was absent on both habitats between 20–40 m depth (Tab. 2).

Arbacia dufresnii was relatively small at the Reloncaví Fjord with a mean diameter of 2.87 ± 1.14 cm. It reached densities of up to 131 ind. m^{-2} on rock in 10 m depth, where we tracked the individuals, with a mean value of 41 ± 29 ind. m^{-2} . Its abundance on shelly sand was 95 ± 52 ind. m^{-2} . In 20 m depth *A. dufresnii* showed nearly the same abundance on rock surface as in 10 m depth, but it was scarce on shelly sand. In 40 m depth the species was found only sporadically on hard bottom.

P. magellanicus was the smallest species in this study with a mean diameter of 1.13 ± 0.20 cm but with very high abundances on shelly sand in all depths down to 40 m and with low abundances in 20 m depth on rock. Its abundance was in 10 m depth on shelly sand 135 ± 233 ind. m^{-2} and 775 ± 374 ind. m^{-2} in 20 m, respectively. Even still in 40 m depth it had an abundance of 51 ± 103 ind. m^{-2} (Fig. 3).

The Antarctic species *S. neumayeri* had a mean size of 3.30 ± 0.75 cm, individual size ranged between 1.80 and 6.40 cm. As for all other species its density showed huge variations with a mean value 9 ± 8 ind. m^{-2} in 10 m depth.

N. concinna was really abundant in the subtidal. Its average shell length was 1.92 ± 0.45 cm. The smallest individual was 1.00 cm in length, the biggest one 4.20 cm. Its density was 46 ± 16 ind. m^{-2} .

Tab. 1: Number of specimen for mean length /diameter calculation (size); number of individuals tracked for the movement studies (activity); N observations between intervals (total number of images taken); mean size in cm; min. / max. size of specimen; mean density in the area; maximum distance moved by a single individual; extrapolated mean daily inactivity per species.

	A. <i>dufresnii</i>	L. <i>albus</i>	P. <i>magellanicus</i>	S. <i>neumayeri</i>	N. <i>concinna</i>
n (size)	57	217	44	307	227
n (activity)	12	209	44	53	90
N (observations)	2518	13803	2684	2470	4328
size cm	2.87 ± 1.14	4.51 ± 1.10	1.13 ± 0.20	3.30 ± 0.75	1.92 ± 0.45
size range	1.23 – 5.92	1.23 – 5.92	0.75 – 1.79	1.80 – 6.40	1.00 – 4.20
density m ⁻²	41 ± 29	7 ± 8	135 ± 233	9 ± 8	46 ± 16
Max distance h ⁻¹	52.5	62.5	22.5	35.28	42.24
daily inactivity (h)	19h 13min	22h 43min	16h 48min	12h 18min	13h 28min

Tab. 2: Mean abundance of *A. dufresnii*, *L. albus* and *P. magellanicus* m⁻² in dependency of depth and substrate, Caleta Yervas Buenas

Depth	A. dufresnii		L. albus		P. magellanicus	
	sand	rock	sand	rock	sand	rock
10	95 ± 52	41 ± 29	2 ± 4	7 ± 8	135 ± 233	0
20	0 ± 1	42 ± 32	0	0	774 ± 373	27 ± 69
40	0	3 ± 6	0	0	51 ± 103	0

4.2 Locomotion

Different aspects of locomotion were studied: a) relationship between movement and stop intervals; b) mean & maximum velocity min⁻¹; c) maximum distance moved hr⁻¹; d) percentage of individuals without any activity hr⁻¹ (Tab. 1, Fig. 4, Fig. 5).

In total 209 individuals of *L. albus* were tracked and 13 803 time intervals were analyzed. In nearly 95 % of all observations *L. albus* did not move. This percentage did not change when we included movements shorter than 0.5 cm min⁻¹. The maximum distance travelled by one individual was 8.0 cm min⁻¹, however we never observed specimens moving more than 62.5 cm hr⁻¹. The activity of different specimens showed big variations. We observed specimens that did not move at all, whereas another specimen moved during 41 of 61 observation intervals.

Arbacia dufresnii was rare in the video sequences taken at the Reloncaví Fjord, although this species was in general more abundant than *L. albus* in the area. We gave preference for our camera settings to the observation of *L. albus*, because of its commercial value. Therefore, tracking of small *A. dufresnii* individuals was not possible. We could only track 12 individuals in all video sequences together. The maximum distance travelled by one individual was 3.2 cm min⁻¹, however we never observed specimens moving more than 52.5 cm hr⁻¹. In more than 97 % of 2518 observations *A. dufresnii* did not move. During tracking time, which varied between

1 hr and 3 hrs, 10 specimen showed at least in a single observation interval movement whereas two specimen remained all the time inactive. Tracking for these two specimen was 1:37 hrs.



Fig. 3: High densities of *P. magellanicus* on shelly sand at 10 m depth, Caleta Yerbos Buenas, May 05, 2011.

Pseudechinius was the smallest species in our study. We tracked a total of 45 individuals and analyzed 2684 time intervals. In 70 % of these time intervals *P. magellanicus* did not move at all, in 9 % the individuals moved less than 0.2 cm min^{-1} . In 93 % of all observations *P. magellanicus* did not move at all or moved less than 0.5 cm min^{-1} . The maximum movement observed was 1.3 cm min^{-1} . A single individual moved 22.5 cm h^{-1} .

Compared to the activity patterns of the temperate species from the Reloncaví Fjord, the cold water urchin *S. neumayeri* and the limpet *N. concinna* were more active in our study. *S. neumayeri* was inactive at 51 % of all observation intervals, in 14 % of 2470 observations ($n = 53$) it moved less than 0.2 cm min^{-1} , whereas in 22 % of our tracking intervals the species moved at least 0.5 cm min^{-1} . We never observed an individual of *S. neumayeri* moving faster than 2.8 cm min^{-1} . Individual differences were pronounced, in one case a specimen only moved at one of 59 observations, whereas another individual were active in 44 of 49 observations.

97 individuals of *N. concinna* were tracked and all specimens moved at least once during the observation interval. Highest activity was 26 movements of 39 observations before the specimen disappeared from the field of view. As for all other species in our study, individual activity patterns differ extremely between specimens (Fig. 6). In total *N. concinna* was inactive in 56 % of 4328 observations, in 17 % of all observations *N. concinna* was active but moved less than 0.2 cm min^{-1} . In 91 % of all observations

for *N. concinna* the species did not move more than 0.5 cm min^{-1} . However, *N. concinna* is able to move much faster. In one observation an individual moved 3.1 cm min^{-1} . The longest distance one individual moved was 42.2 cm h^{-1} .

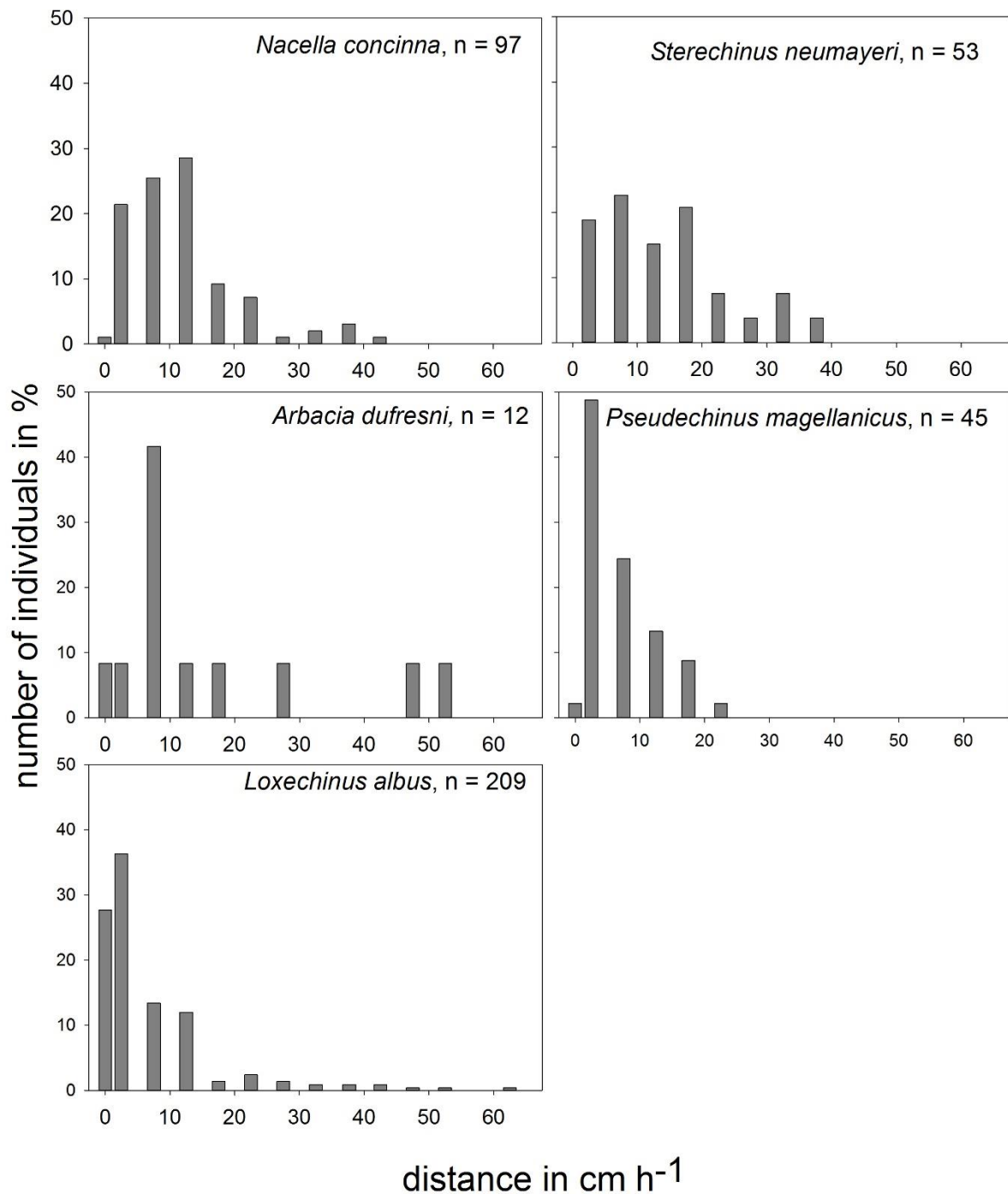


Fig. 4: Individual movement of the 4 sea urchins *A. dufresnii*, *L. albus*, *P. magellanicus*, *Sterechinus* and the limpet *N. concinna* in 10 m depth, values are given in cm h^{-1} .

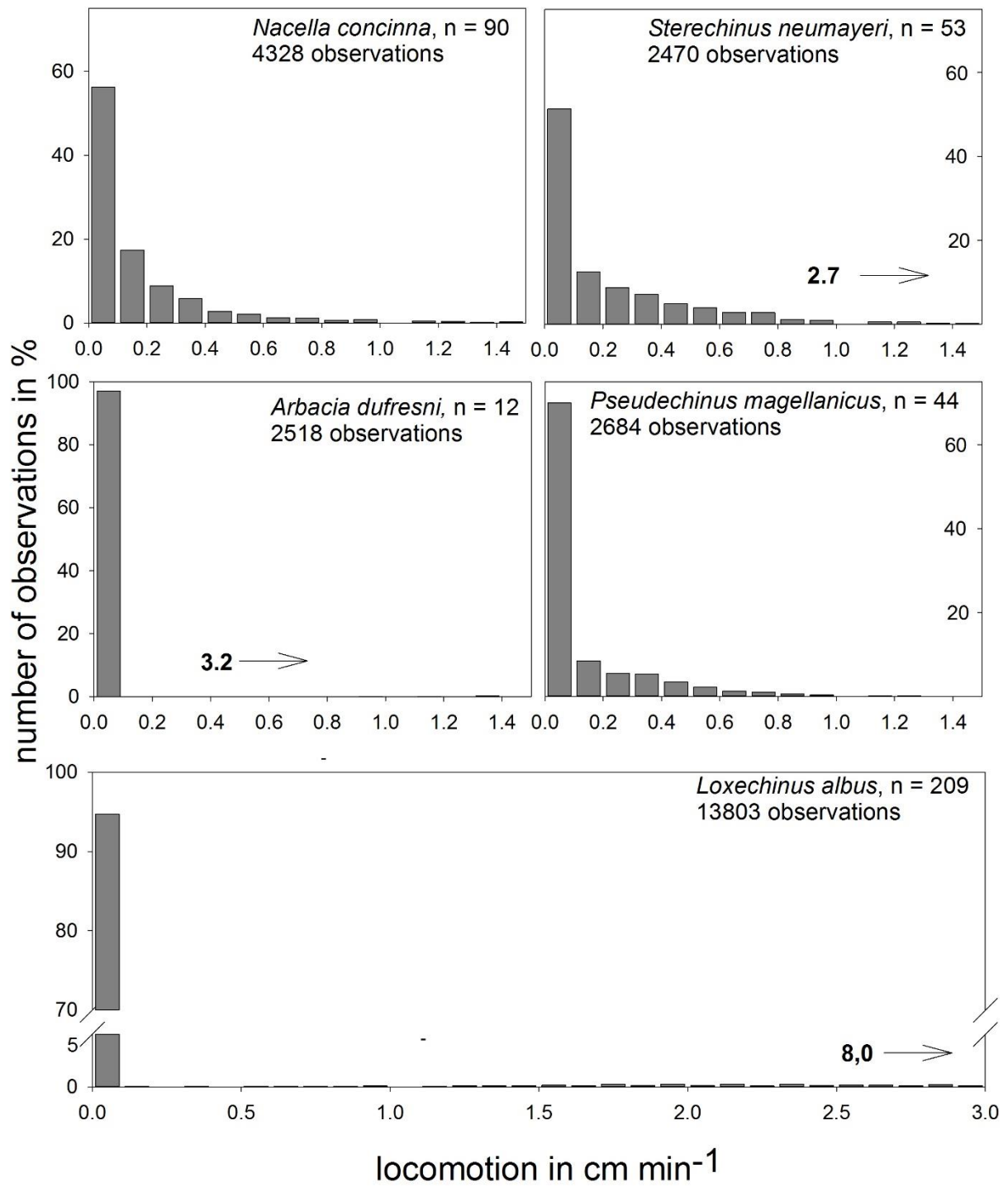


Fig. 5: Total number of observations in relation to the movement of the 4 sea urchins *A. dufresnii*, *L. albus*, *P. magellanicus*, *Sterechinus* and the limpet *N. concinna* in 10 m depth, values are given in cm min⁻¹. Specimens were tracked every minute.

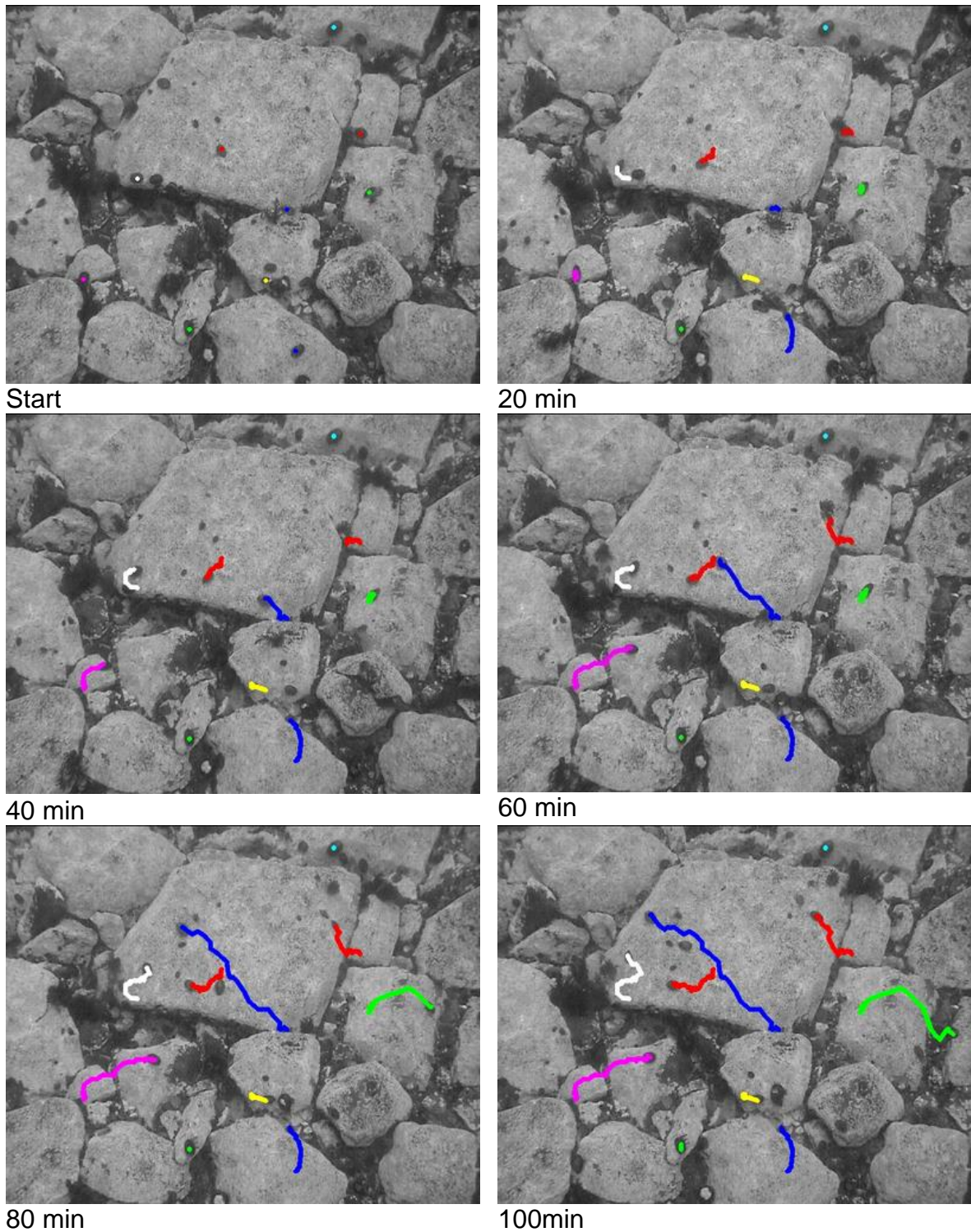


Fig. 6: Movement of 10 randomly selected specimens of *N. concinna* in course of time. Activity was recorded every minute.

5 Discussion

Movement studies of marine intertidal and subtidal gastropods and echinodermata are done since nearly 200 years, sometimes together with physiological studies (Lukis 1831, Romanes & Ewart 1881, Villee & Groody 1940). What started as first observations in the field followed by aquaria studies, has developed further in the

intertidal and shallow subtidal with different tagging methods, so that displacement studies could be done with limpets and sea urchins over days or weeks. However, tagging is at least for sea urchins not easy. It does not exist any reliable universal tagging procedures for these animals in the field. Each tagging method has its advantages and disadvantages (Dance 1987, Tuya et al. 2004) and depends on the sea urchin's morphology. External tags or marks (Sinclair 1959, Gamble 1965, Dix 1970, Shepherd & Boudouresque 1979, Hagen 1996, James 2000) can effectively be used to study short-term movements, but they have not proved to be worthy on a long-term basis. Authors who anchored tags in a hole in the test (Dix 1970, Nelson & Vance 1979, Duggan & Miller 2001) noticed that the hole did not recalcify and often resulted in up to 50 % mortality of the marked individuals. In contrast, tagging limpets is quite more simple and individuals can be marked individually with numbered commercial bee tags. For our studies it was not necessary to mark the animals, because the high image frequency enabled us to identify each individual in every photo, although it has moved a short distance.

Displacement studies gave new insights in the homing behavior of several species and the radius in which a species is active (Test 1945, Hazlett 1984). However, these studies give only limited information how active the animals are during a couple of hours or even days, so that in the following years several other innovative techniques have been developed to study the behavior and activity of marine organisms (Parpagnoli & Chelazzi 1995). Distances given as daily displacement of an individual might be only a small percentage of the total route moved by an animal within this time interval. Mattison et al. (1977) showed that the red sea urchin *Strongylocentrotus franciscanus* moves faster outside kelp forests than inside, but only daily displacement rates were noticed during the study by scuba divers and the total activity of this species remained unknown. For slow moving animals time lapse photography can close this gap, because by a more frequent data logging – in our studies one picture per minute – the complete movement of a limpet or sea urchin can be visualized and measured (Fig. 6 & 7). Other techniques are required for animals which move in the range of several meters or kilometers per day.

Ideas of observing and tracking animals in the field by time lapse photography, goes back to the time, when Scuba diving became a popular tool in marine science (Riedl 1963, Riedl 1967). Investigations of the mobility and behavior of aquatic organisms by time-lapse recordings have also been widely used in laboratory experiments (Schütz & Taborsky 2003). However, Thompson & Riddle (2005) showed that results obtained from organisms kept in an aquarium can be significantly different compared to experiments performed in situ. The authors studied the mobility of the sea urchin *Abatus ingens* for a period of 24 hrs in situ and in the aquarium. In the field during one day the sea urchins did not move for most the time (16.7 h), while specimen observed in the aquarium spent half the time moving. In addition, the average speed of the animals was faster in the aquarium than in situ. This shows the advantage of in situ time lapse observations like we did it. There is no handling stress and the organisms stay in their accustomed environment, the only unfamiliar thing might be the regularly flash of the camera.

Tables 3 & 4 summarize the activity of various sea urchin and gastropod species showing the range in which these species move. All these studies give a first insight in the activity patterns of the species and a lot of similarities can be found. Although some species move faster than others, there was no observation that a single species moved extraordinary fast over a longer time interval in comparison to the others. With $15.24 \text{ cm min}^{-1}$ the sea urchin *Echinus esculentus* moved faster than all other species

shown in tables 3 & 4, but its movement is based on a historical aquarium study and may not be representative for the mobility of this species in the field (Romanes & Ewart 1881). In comparison to *E. esculentus* the species *A. dufresnii*, *L. albus*, *P. magellanicus* and *S. neumayeri* observed in this study moved much more slowly, but this might also depend on their smaller size. Compared to others our results agree well with former studies. Obviously, the daily activity of the species in our study combined with their relatively high abundances in the field have a strong impact on habitat structuring. Figure 7 and also the image of *P. magellanicus* (Fig. 2) clearly demonstrate why erect algae did not have any possibility to develop under this high grazing and activity pressure. *S. neumayeri* and *N. concinna* are abundant in Fildes bay at depths between 3 and 10 m, *S. neumayeri* also on hard bottom up to 40 m depth (Sakurati et al. 1996). The vertical distribution of both species extends down to several hundred meters depth (Brey & Gutt 1991, Aldea & Troncoso 2008). However, we suppose that all organisms studied have their highest impact to benthic communities in shallow water, when densities can reach extraordinary high values. In our study *P. magellanicus* showed densities of 135 ± 233 ind. m^{-2} .

Davenport (1997) carried out a laboratory experiment with *N. concinna* at water temperatures of 2 °C and measured a movement of 0.6 cm h^{-1} . This accords somehow to our measurements. Our preliminary results demonstrate that the observed movement of the Antarctic limpet *N. concinna* varied in situ between total inactivity and a maximum movement of 18 cm h^{-1} . In the vast majority of all observations the animals did not move more than 0.5 cm min^{-1} . Although in one observation an individual moved 3.1 cm min^{-1} . This shows the complexity of movement studies.

Several environmental factors like tide level, daytime and food availability (Dix 1970), presence and absence of enemies (Beckett 1968) and seasonality (Walker 1972) influence the activity of animals, which makes mobility studies very complex and limits the transferability of results. Beckett (1968) observed in the field that escape reaction of the limpet *Cellana radians* to a predator can result in quadrupling its speed from 2.5 cm min^{-1} during feeding to 10 cm min^{-1} . Studies about escape response were also done by Espoz & Castilla (2000) with the intertidal limpets *Lottia orbigny* and *Scurria viridula* in presence of a predator. Both species showed fast movements 6.3 ± 1.8 cm min^{-1} SD and 8.6 ± 2.6 SD, but reaction did not last for more than a few minutes. This may demonstrate the limitations of the species to cover long distances in a short time. Dix (1970) noticed in aquarium experiments that the sea urchin *Evechinus chloriticus* is more active during night time than during day time and that activity depends on food availability. The effects of food and competitors on movement patterns in *Patella caerulea* limpets were studied by Keasar & Safriel (1994). Their experiments demonstrated when food is abundant, the benefit of foraging is higher than the costs of locomotion. We suppose that this was also the case for *S. neumayeri* and *N. concinna* during austral summer in Antarctica. Fraser et al. (2002) showed that *N. concinna* is feeding throughout the year. Faecal egestion was 10-fold from summer to winter and tissue ash-free dry mass decreased by 47 %. Also metabolic rates decreased significantly in winter.

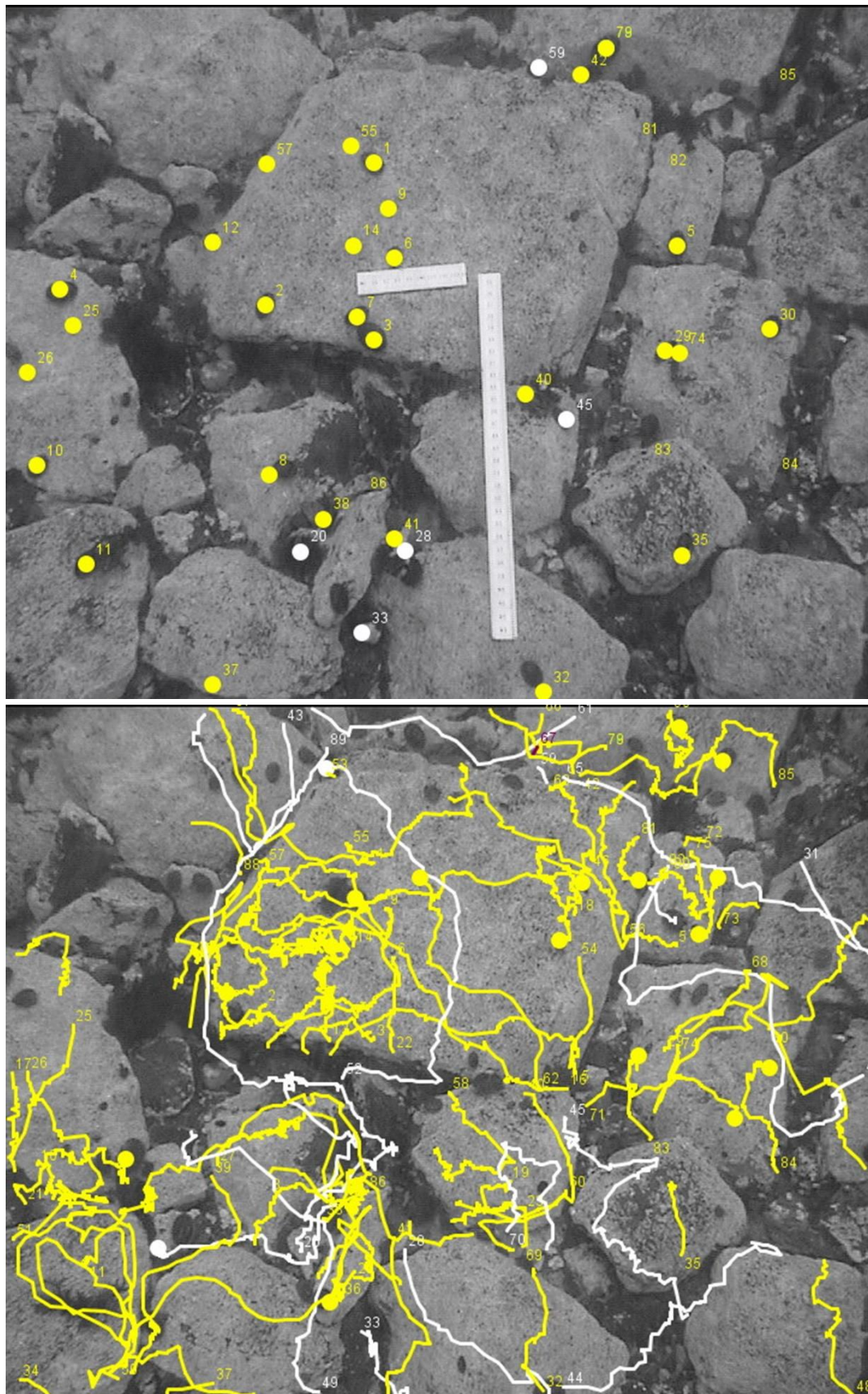


Fig. 7: Activity patterns of *S. neumayeri* (white lines) and *N. concinna* (yellow) at the beginning and after 6:40 hrs of time lapse recordings. Length of the larger tape measure = 30 cm. Note, that not all specimens in the images were tracked.

In our study our longest recordings lasted about 6:40 hrs. We do not have any information yet, if activity peaks in dependency of daytime exist or how the activity varies between seasons, especially if activity drops down in winter time when food availability is limited. Shabica (1976) showed that *N. concinna* has very high annual growth rates indicating high food availability. However, the magnitude how growth and activity varies between summer and winter months is unknown.

In our study the three sea urchin species from Northern Patagonia showed lower activity than their Antarctic counterpart. As mentioned above, the factors that influence movement of benthic sea urchins and limpets are too diverse to present a simple answer to our observations.

Tab. 3 Individual movement and displacement of different sea urchin species; (1) = velocity in cm min⁻¹; (2) = cm h⁻¹; (3) cm d⁻¹; \bar{x} = mean; SE = standard error; SD = standard deviation

Species	Velocity	Remarks	Author
<i>Abatus ingens</i> (2)	\bar{x} 1.95 ± 1.20 SD	Laboratory	Thompson & Riddle (2005)
<i>Abatus ingens</i> (2)	\bar{x} 0.30 ± 0.30 SD	In situ	Thompson & Riddle (2005)
<i>Arbacia punctulata</i> (1)	0.30	Laboratory	Harvey (1956)
<i>Arbacia punctulata</i> (1)	\bar{x} 2.22 3.50 - 4.00	undisturbed (Laboratory) disturbed (Laboratory)	Jackson (1939)
<i>Diadema antillarum</i> (2)	\bar{x} 33±26 SE	In situ, night time	Tuya et al. (2004)
<i>Echinarachnius parma</i> (1)	\bar{x} 0.84; max 1.8	Laboratory, on sand	Parker (1927)
<i>Echinus esculentus</i> (1)	15.24	Laboratory, on sand	Romanes & Ewart (1881)
<i>Lytechinus variegatus</i> (1)	\bar{x} 8.2; max 13.7	Lab. on sand, horizontal	Parker (1936)
<i>Lytechinus variegatus</i> (1)	\bar{x} 0.18; max 1.2	Lab. on sand, vertical	Parker (1936)
<i>Paracentrotus lividus</i> (3)	6 – 220	In situ	Hereu (2005)
<i>Paracentrotus lividus</i> (3)	\bar{x} 49 0 – 240	Displacement, in situ	Andrew et al. (2002)
<i>Strongylocentrotus droebachiensis</i> (2)	\bar{x} 15.1 ± 2.6 SE	In situ	Lauzon-Guay et al. (2006)
<i>Strongylocentrotus droebachiensis</i> (1)	0.25 – 0.48	In situ	Dumont et al. (2007)
<i>Strongylocentrotus franciscanus</i> (3)	\bar{x} 7.5 ± 3.3 SE	Displacement, in situ Inside <i>Macrocystis</i> kelps	Mattison et al. (1977)
<i>Strongylocentrotus franciscanus</i> (3)	\bar{x} 52.2 ± 6.5 SE	Displacement, in situ Outside <i>Macrocystis</i> kelps	Mattison et al. (1977)
<i>Toxopneustes roseus</i> (2)	\bar{x} 6.6 – 11.7		James (2000)

Tab. 4: Individual movement and displacement of different gastropod species.; (1) = velocity in cm min⁻¹; (2) = cm h⁻¹; (3) cm d⁻¹; \bar{x} = mean; SE = standard error; SD = standard deviation.

Species	Velocity	Remarks	Author
<i>Astraea tecta</i> (3)	\bar{x} 11	In situ, displacement over several months	Hazlett (1984)
<i>Cellana grata</i> (1)	\bar{x} 0.22 ± 0.06 SE \bar{x} 0.36 ± 0.03 SE	In situ, different months	Davies et al. (2006)
<i>Cellana ornata</i> (1)	0.2 – 1.5	In situ, feeding movements	Beckett (1968)
<i>Cellana radians</i> (1)	0.5 – 2.5	In situ, feeding movements	Beckett (1968)
<i>Cellana radians</i> (1)	8.0 – 10.0	In situ, escape response	Beckett (1968)
<i>Cerithium eburneum</i> (3)	\bar{x} 70	In situ, displacement over several months	Hazlett (1984)
<i>Cerithium litteratum</i> (3)	\bar{x} 53	In situ, displacement over several months	Hazlett (1984)
<i>Columbella mercatoria</i> (3)	\bar{x} 28	In situ, displacement over several months	Hazlett (1984)
<i>Lottia asmi</i> (1)	1.28	Laboratory	Test (1945)
<i>Nacella concinna</i> (1)	0.6	Laboratory at 2°C	Davenport (1997)
<i>Patella rustica</i> (1)	\bar{x} 0.42	In situ, last part of trail	Santina (1994)
<i>Patella vulgata</i> (1)	\bar{x} 0.64 \pm 0.26	In situ, increasing tide, movement to feeding habitats	Hartnoll & Wright (1977)
<i>Patella vulgata</i> (1)	\bar{x} 0.08 \pm 0.04	In situ, at feeding habitat	Hartnoll & Wright (1977)
<i>Patella vulgata</i> (1)	\bar{x} 0.55 \pm 0.21	In situ, returning home	Hartnoll & Wright (1977)
<i>Patelloida latistrigata</i>	25 (8 d) 64 (84 d)	In situ, displacement	Creese (1982)
<i>Phyllonotus pomum</i> (3)	\bar{x} 27	In situ, displacement over several months	Hazlett (1984)
<i>Scutellastra flexuosa</i> (1)	\bar{x} 0.14 ± 0.04 SD	Foraging speed, spring tide	Iwasaki (1999)
<i>Scutellastra flexuosa</i> (1)	\bar{x} 0.12 ± 0.06 SD	Foraging speed, neap tide	Iwasaki (1999)
<i>Siphonaria lateralis</i> (1)	0.9 max	Lab. Exp. at 15°C	Davenport (1997)
<i>Siphonaria lateralis</i> (3)	\bar{x} 21.3 \pm 30.2	In situ, minimum displacement	McClintock & Lawrence (1986)
<i>Siphonaria lateralis</i> (3)	\bar{x} 7.9 \pm 9.5	In situ, minimum displacement High intertidal site	McClintock & Lawrence (1986)
<i>Siphonaria lateralis</i> (3)	\bar{x} 5.0 \pm 2.6	In situ, minimum displacement Low intertidal site	McClintock & Lawrence (1986)
<i>Stramonita haemastoma</i> (1)	\bar{x} 9.61 \pm 1.26	Aquarium, sand	Papp & Duarte (2001)
<i>Stramonita haemastoma</i> (1)	\bar{x} 9.38 \pm 1.04	Aquarium, rock	Papp & Duarte (2001)
<i>Tegula fasciata</i> (3)	\bar{x} 13	In situ, displacement over several months	Hazlett (1984)
<i>Terebralia palustris</i> (3)	\bar{x} 79,8	In situ	Vannini et al. (2008)
<i>Testudinalia testudinalis</i> (1)	0.12	In situ	Miller (1974)

6 Outlook

Manual tracking of individuals as realized in this study is a very time-consuming process and should be omitted whenever possible. However, when organisms are not crawling any longer on plan surfaces but on pebbles, body form of the organism of interest may change and may not be recognized by automatic tracking software. Obviously movement distances of species are underestimated when they are crawling on inclined surfaces like pebbles or boulders. A comparison of different tracking methods was done by Chenouard et al. (2014) but there is still a need to improve automatic tracking analysis.

All results shown in tables 3 & 4 are more or less of the same magnitude, but we should not forget that in all time lapse studies the field of view is limited. Animals that simply disappear after a certain time from the field of vision cannot be tracked any longer. Here we have a knowledge gap; we must develop technologies that are able to track animals in a range of several meters up to a kilometer per day.

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Literatur

- Aldea, C. & Troncoso, J. S., 2008. Systematics and distribution of shelled molluscs (Gastropoda, Bivalvia and Scaphopoda) from the South Shetland Islands to the Bellingshausen Sea, West Antarctica. *Iberus* 26: 43–117.
- Andrew, N. L., Agatsuma, Y., Ballesteros, E., Bazhin, A. G., Creaser, E. P., Barnes, D. K. A., Botsford, L. W., Bradbury, A., Campbell, A. Dixon, J., Einarsson, S., Gerring, P., Hebert, K., Hunter, M., Hur, S. B., Johnson, C., Juinio-Meñez, M., Kalvass, P., Miller, R. J. & Xiaoqi, Z., 2002. Status and management of world sea urchin fisheries. *Oceanography and Marine Biology*, Vol 40 40: 343–425.
- Arana, P. M., 2005. Demography and fishery of the sea urchin *Loxechinus albus* (Echinodermata: Echinidae) in south-austral Chile region. *Revista de Biología Tropical* 53: 367–382.
- Beckett, T., 1968. Limpet movements. *Tane* 14: 43–65.
- Bernasconi, I., 1953. Monografía de los Equinoideos Argentinos. *Anales del Museo de Historia Natural de Montevideo*. 2a Serie 6: 1–38.
- Beuchel, F., Primicerio, R., Lønne, O. J., Gulliksen, B. & Birkely, S. R., 2010. Counting and measuring epibenthic organisms from digital photographs: A semiautomated approach. *Limnology and Oceanography: Methods* 8: 229–240.
- Brey, T. & Gutt, J., 1991. The genus *Sterechinus* (Echinodermata, Echinoidea) on the Weddel Sea shelf and slope (Antarctica) – distribution, abundance and biomass. *Polar Biology* 11: 227–232.
- Brinkhurst, R. O., 1975. *The benthos of lakes*. London: Macmillan International Higher Education.
- Brogger, M. I., Gil, D. G., Rubilar, T., Martínez, M. I., de Vivar, M. E. D., Escolar, M., Epherra, L., Pérez, A. F. & Tablado, A., 2013. Echinoderms from Argentina: Biodiversity, distribution and current state of knowledge. In: Alvarado, J. J. & Solís-Marín, F. A. (Eds), *Echinoderm Research and Diversity in Latin America*. Springer Verlag, Berlin Heidelberg, pp. 359–402.

- Carey, F. J. & Pettengill, O. S., 1967. A time-lapse study of effects of anticellular antibody on membrane mobility and phagocytic activity of hela cells. *Cell Biology* 33: 709 – 712.
- Chenouard, N., Smal, I., De Chaumont, F., Maška, M., Sbalzarini, I. F., Gong, Y., Cardinale, J., Carthel, C., Coraluppi, S., Winter, M., Cohen, A. R., Godinez, W. J., Rohr, K., Kalaidzidis, Y., Liang, L., Duncan, J., Shen, H., Xu, Y., Magnusson, K. E. G., Jaldén, J., Blau, H. M., Paul-Gilloteaux, P., Roudot, P., Kervrann, C., Waharte, F., Tinevez, J.-Y., Shorte, S. L., Willemsse, J., Celler, K., van Wezel, G. P., Dan, H.-W., Tsai, Y.-S., de Solórzano, C. O., Olivo-Marin, J.-C. & Meijering, E., 2014. Objective comparison of particle tracking methods. *Nature methods* 11: 281.
- Clarke, A., Prothero-Thomas, E., Beaumont, J. C., Chapman, A. L. & Brey, T., 2004. Growth in the limpet *Nacella concinna* from contrasting sites in Antarctica. *Polar Biology* 28: 62 – 71.
- Clarke, A., Prothero-Thomas, E. & Whitehouse, M. J., 1994. Nitrogen excretion in the Antarctic limpet *Nacella concinna* (Strebel, 1908). *Journal of Molluscan Studies* 60: 141 – 147.
- Creese, R., 1982. Distribution and abundance of the acmaeid limpet, *Patelloida latistrigata*, and its interaction with barnacles. *Oecologia* 52: 85 – 96.
- Dance, C., 1987. Patterns of activity of the sea urchin *Paracentrotus lividus* in the Bay of Port-Cros (Var, France, Mediterranean). *Marine Ecology* 8: 131 – 142.
- Davenport, J., 1997. Comparisons of the biology of the intertidal subantarctic limpets *Nacella concinna* and *Kerguelenella lateralis*. *Journal of Molluscan Studies* 63: 39 – 48.
- Davies, M. S., Edwards, M. & Williams, G. A., 2006. Movement patterns of the limpet *Cellana grata* (Gould) observed over a continuous period through a changing tidal regime. *Marine Biology* 149: 775 – 787.
- Di Castri, F. & Hajek, E. R., 1976. *Bioclimatología de Chile*. Santiago de Chile: Editorial de la Universidad Católica de Chile.
- Dix, T. G., 1970. Biology of *Evechinus chloroticus* (Echinoidea: Echinometridae) from different localities: 2. Movement. *New Zealand Journal of Marine and Freshwater Research* 4: 267 – 277.
- Duggan, R. E. & Miller, R. J., 2001. External and internal tags for the green sea urchin. *Journal of Experimental Marine Biology* 258: 115 – 122.
- Dumont, C., J. H. Himmelman & M. P. Russell, 2004. Size specific movement of green sea urchins *Strongylocentrotus droebachiensis* on urchin barrens in eastern Canada. *Marine Ecology Progress Series* 276: 93 – 101.
- Dumont, C. P., Himmelman, J. H. & Robinson, S. M., 2007. Random movement pattern of the sea urchin *Strongylocentrotus droebachiensis*. *Journal of Experimental Marine Biology and Ecology* 340: 80 – 89.
- Espoz, C. & Castilla, J., 2000. Escape responses of four Chilean intertidal limpets to seastars. *Marine Biology* 137: 887 – 892.
- Fedra, K. & Machan, R., 1979. A self-contained underwater time-lapse camera for in situ long-term observations. *Marine Biology* 55: 239 – 246.
- Fenucci, J. L., 1967. Contribución al conocimiento de crustaceo decapodo braquiro *Pinnaxodes chilensis* (M. Edwards) comensal de *Loxechinus albus* (Molina) (Echinodermata, Echinoidea). *Physis, Buenos Aires* 27: 125 – 133.
- Fraser, K. P. P., Clarke, A. & Peck, L. S., 2002. Feast and famine in Antarctica: seasonal physiology in the limpet *Nacella concinna*. *Marine Ecology Progress Series* 242: 169 – 177.
- Gamble, J. C., 1965. Some observations on the behaviour of two regular echinoids. In: Lythgoe, J. N. & Woods, J. D. (Eds), *Proceedings of the Symposium of the Underwater Association for Malta, Malta*, pp. 47 – 50.
- Hagen, N. T., 1996. Tagging sea urchins: a new technique for individual identification. *Aquaculture* 139: 271 – 284.
- Hartnoll, R. & Wright, J., 1977. Foraging movements and homing in the limpet *Patella vulgata* L. *Animal Behaviour* 25: 806 – 810.
- Harvey, E. B., 1956. *The American Arbacia and other sea urchins*: Princeton University Press.
- Hazlett, B. A., 1984. Daily Movements of Some Tropical Marine Gastropods. *Marine Behaviour and Physiology* 11: 35 – 48.
- Hereu, B., 2005. Movement patterns of the sea urchin *Paracentrotus lividus* in a marine reserve and an unprotected area in the NW Mediterranean. *Marine Ecology* 26: 54 – 62.

- Iwasaki, K., 1999. Short-and long-term movements of the patellid limpet *Patella flexuosa* within gaps in intertidal mussel beds. *Journal of Molluscan Studies* 65: 295 – 301.
- Jackson, H. W., 1939. Notes on marine aquarium animals. *Am. Midland Nat.* 22: 654 – 659.
- Jacob, U., Terpstra, S. & Brey, T., 2003. High-Antarctic regular sea urchins – the role of depth and feeding in niche separation. *Polar Biology* 26: 99 – 104.
- James, D., 2000. Diet, movement, and covering behavior of the sea urchin *Toxopneustes roseus* in rhodolith beds in the Gulf of California, México. *Marine Biology* 137: 913 – 923.
- Keasar, T. & Safriel, U., 1994. The establishment of a territory: effects of food and competitors on movement patterns in *Patella caerulea* limpets. *Ethology Ecology & Evolution* 6: 103 – 115.
- Lauzon-Guay, J.-S., Scheibling, R. E. & Barbeau, M. A., 2006. Movement patterns in the green sea urchin, *Strongylocentrotus droebachiensis*. *Journal of the Marine Biological Association of the United Kingdom* 86: 167 – 174.
- Lessios, H. A., Lockhart, S., Collin, R., Sotil, G., Sanchez-Jerez, P., Zigler, K. S., Perez, A. F., Garrido, M. J., Geyer, L. B., Bernardi, G., Vacquier, V. D., Haroun, R., Kessing, B. D., 2012. Phylogeography and bindin evolution in *Arbacia*, a sea urchin genus with an unusual distribution. *Molecular Ecology* 21: 130 – 144.
- Lukis, F. C., 1831. Remarks on the locomotion and habits of the limpet. *Annals & magazine of natural history*: 346 – 351.
- Marx, R. F., 1990. *The history of underwater exploration*. New York: Dover Publications.
- Mattison, J. E., Trent, J. D., Shanks, A. L., Akin, T. B. & Pearse, J. S., 1977. Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. *Marine Biology* 39: 25 – 30.
- McClintock, J. B. & Lawrence, J. M., 1986. Movement patterns of the sub-Antarctic pulmonate limpet *Kerguelenella lateralis* (Gould) (Mollusca: Gastropoda). *Polar Biology* 5: 135 – 138.
- Miller, S. L., 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. *Journal of Experimental Marine Biology and Ecology* 14: 99 – 156.
- Nelson, B. V. & Vance, R. R., 1979. Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. *Marine Biology* 51: 251 – 258.
- Paddock, S., 2001. A brief history of time-lapse. *BioTechniques* 30: 283 – 289.
- Papp, M. G. & Duarte, L. F., 2001. Locomotion of *Stramonita haemastoma* (Linnaeus) (Gastropoda, Muricidae) on a mixed shore of rocks and sand. *Revista brasileira de Zoologia* 18: 187 – 195.
- Parker, G. H., 1927. Locomotion and righting movements in echinoderms, especially in *Echinarachnius*. *American Journal of Psychology* 39: 167 – 180.
- Parker, G. H., 1936. Direction and means of locomotion in the regular sea-urchin *Lytechinus*. *Memoirs of the Royal Institute of Natural Sciences of Belgium : second series*: 197 – 208.
- Parpagnoli, D. & Chelazzi, G., 1995. An automatic technique for recording grazing activity of limpets. *J. Moll. Stud.* 61: 339 – 346.
- Paul, A. Z., Thorndike, E. M., Sullivan, L. G., Heezen, B. C. & Gerard, R. D., 1978. Observations of the deep-sea floor from 202 days of time-lapse photography. *Nature* 272: 812.
- Peckarsky, B. L., 1979. Biological interactions as determinants of distributions of benthic invertebrates within the substrate of stony streams. *Limnology and Oceanography* 24: 59 – 68.
- Powell, A. W. B., 1951. Antarctic and subantarctic mollusca: Pelecypoda and Gastropoda. *Discovery Reports* 26: 47 – 196.
- Powell, A. W. B., 1973. The patellid limpets of the world (Patellidae). *Indo-Pacific Mollusca* 3: 75 – 206.
- Riedl, R., 1963. Probleme und Methoden der Erforschung des litoralen Benthos. *Zoologischer Anzeiger (Suppl.)* 26: 505 – 567.
- Riedl, R., 1967. Die Tauchmethode, ihre Aufgaben und Leistungen bei der Erforschung des Litorals; eine kritische Untersuchung. *Helgoländer wissenschaftliche Meeresuntersuchungen* 15: 294.
- Romanes, G. J. & Ewart, J. C., 1881. Observations on the locomotor system of Echinodermata. *Philosophical Transactions of the Royal Society* 172: 829 – 885.
- Sakurati, H., Sato, T., Arai, H., Takasaki, A., Taga, S., Hori, H., Kimpara, I., Matsuyama, T. & Kodama, M., 1996. Habitats of fish and epibenthic invertebrates in Fildes bay, King George island, Antarctica. *Proceedings of the NIPR Symposium on Polar Biology* 9: 231 – 242.

- Santina, P. D., 1994. Homing pattern, activity area and trail following of the high shore Mediterranean limpet *Patella rustica* L.(Mollusca Gastropoda). *Ethology Ecology & Evolution* 6: 65 – 73.
- Schütz, D. & Taborsky, M., 2003. Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyroneta aquatica*. *Evolutionary ecology research* 5: 105 – 117.
- Shabica, S. V., 1976. The natural history of the Antarctic limpet *Patinigera polaris* (Hombron and Jacquinot).
- Shepherd, S. & Boudouresque, C., 1979. A preliminary note on the movement of the sea urchin *Paracentrotus lividus*. *Parc national de Port-Cros* 5: 155 – 158.
- Shortis, M., Harvey, E. & Seager, J., 2007. A review of the status and trends in underwater videometric measurement. In: SPIE Videometrics IX, San Jose, California, USA, pp. 1 – 26.
- Sinclair, A. N., 1959. Observations on the behaviour of sea urchins. *Australian Museum Magazine* 13: 3 – 8.
- Test, F. H., 1945. Substrate and Movements of the Marine Gastropod *Acmaea-Asmi*. *American Midland Naturalist* 33: 791 – 793.
- Thompson, B. A. & Riddle, M. J., 2005. Bioturbation behaviour of the spatangoid urchin *Abatus ingens* in Antarctic marine sediments. *Marine Ecology Progress Series* 290: 135 – 143.
- Tuya, F., Martin, J. A. & Luque, A., 2004. Patterns of nocturnal movement of the long-spined sea urchin *Diadema antillarum* (Philippi) in Gran Canaria (the Canary Islands, central East Atlantic Ocean). *Helgoland Marine Research* 58: 26 – 31.
- Vannini, M., Cannicci, S., Mrabu, E., Rorandelli, R. & Fratini, S., 2008. Random walk, zonation and the food searching strategy of *Terebralia palustris* (Mollusca, Potamididae) in Kenya. *Estuarine, Coastal and Shelf Science* 80: 529 – 537.
- Vásquez, J. A., Castilla, J. C. & Santelices, B., 1984. Distributional patterns and diets of four species of sea urchins in giant kelp forest (*Macrocystis pyrifera*) of Puerto Toro, Navarino Island, Chile. *Marine Ecology Progress Series* 19: 55 – 63.
- Villee, C. A. & Groody, T. C., 1940. The behavior of limpets with reference to their homing instinct. *American Midland Naturalist*: 190 – 204.
- Walker, A. J. M., 1972. Introduction to the ecology of the antarctic limpet *Patinigera polaris* (Hombron and Jacquinot) at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin* 28: 49 – 69.