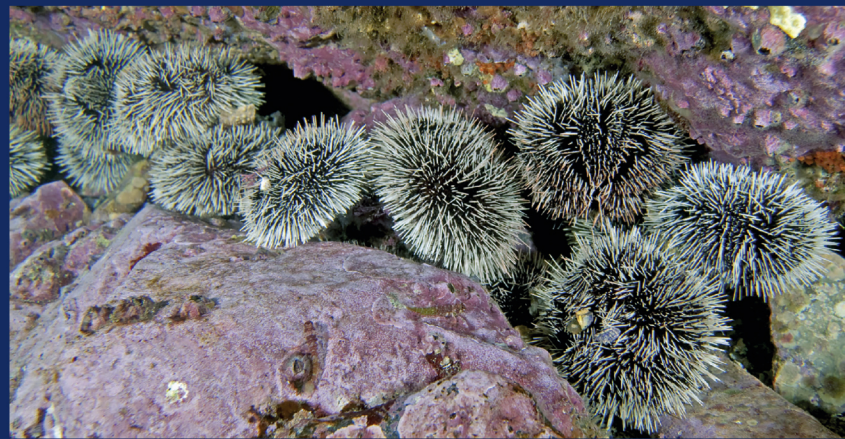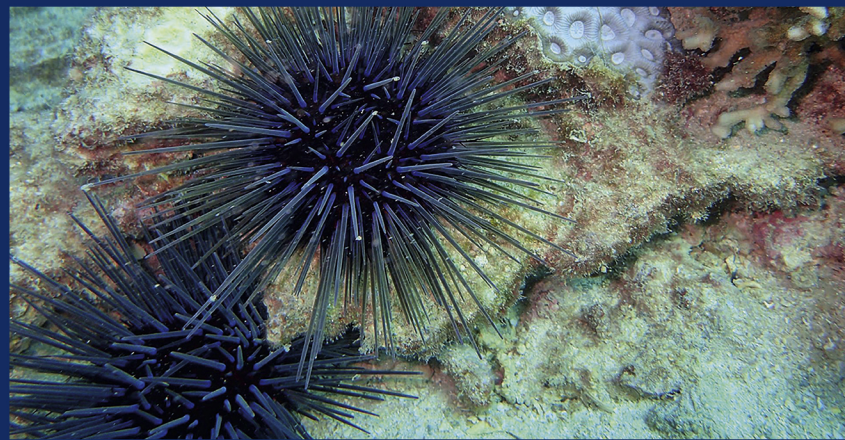# Sea Urchins: Biology and Ecology

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Chapter 24

Arbacia

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1 Species of *Arbacia*

John Edward Gray named the regular sea urchin genus *Arbacia* (family Arbaciidae, order Arbacioida) in 1835. According to Agassiz (1842) and Mortensen (1935), *Arbacia* was a "nonsensical" name for a sea urchin genus. Harvey (1956) gave the most plausible explanation for the name, considering it a derivation of *Arbaces*, a secondary character in the historical poem *Sardanapalus* by Lord Byron, which was published in 1821, a few years before Gray's work. *Arbacia* is a small genus well known from Miocene age (Smith, 2005). All the members of this genus show morphological similarities (Mortensen, 1943). The test, formed from regularly arranged plates, is rather stout, flattened below, and gently domed above. The test has primary spines and tubercles; secondary spines are absent in the genus (Tortonese, 1965). The spines are moderate to long in length, often showing size and shape pattern differences with reference to body regions. In particular, those nearest to the mouth have enameled flattened tips. On the aboral side, there are usually conspicuous naked areas in the upper portions of the interambulacra. A large, more or less soft and membranous peristome, with an undulating edge characterizes the genus. The peristome may be naked, but it usually has small spines and pedicellariae and contains embedded plates that support the buccal podia. The periproct is largely covered by four subtriangular and subequal plates. The apical system has four large periproctal plates forming an anal valve. The size of *Arbacia* species ranges from approximately 15 to 50 mm in diameter (test without spines).

The various species of *Arbacia* are usually colored uniformly, most commonly green, brown, purple, or black. *Arbacia* species occur in tropical, temperate, and sub-Antarctic zones. Six species of *Arbacia* have been described by Mortensen (1943): *Arbacia punctulata* (LAMARCK, 1816), *Arbacia lixula* (LINNAEUS, 1758), *Arbacia crassispina* (MORTENSEN, 1910), *Arbacia dufresnii* (BLAINVILLE, 1825), *Arbacia spatuligera* (VALENCIENNES, 1846), and *Arbacia stellata* (as *incisa*) (BLAINVILLE, 1825; GMELIN, 1791). Recently, renewed interest in this genus has arisen from its evolution and phylogeography (Metz et al., 1998; Lessios, 2011; Hart, 2012, Pérez-Portela et al., 2019). Unlike other sea urchin genera, members of this genus occur in both temperate and tropical waters and in three different ocean basins (Pacific, Atlantic, Mediterranean). This is not in line with the tendency of marine species to arise in the tropics and then spread into the temperate zones (Lessios et al., 2012). *Arbacia* could be an evolutionary oddball consisting of very old species (Mayr, 1954), or a taxonomic artifact, or the exception that proves a rule. So, although *Arbacia* is a small genus of just six nominal species, the study of its phylogeographic history has had a disproportionate reward. According to Lessios (2011) *Arbacia* seems to have originated relatively recently (<5 Mya) in the Eastern Pacific and four different fossil species have been described from the Late Miocene.

During the first speciation event, the more northern *A. stellata* was separated from the southern clade, which subsequently split into *A. dufresnii* and *A. spatuligera*. *A. dufresnii* is present in both the Southern Pacific and Atlantic oceans. *A. spatuligera* occurs along the Southern Pacific coasts. These were then isolated from the Atlantic by the Isthmus of Panama, approximately 3 Mya, and the mid-Atlantic barrier separated two additional species: *A. lixula* and *A. punctulata*. The same work suggests that *A. crassispina* and *A. dufresnii* are not separate species, as the two morphs are not distinct in the phylogeny of either the mitochondrial or the nuclear genome and Lessios et al. (2012) did not formally synonymize the two species. Thus they are not treated as synonyms here, even if Pérez-Portela et al. (2019) cited Lessios et al. (2012) as saying there are five extant species and suggested the synonymy of *A. crassispina* within *A. dufresnii*.

1.1   Biogeography and large-scale distribution

Arbacia is a genus with a discontinuous allopatric distribution, except for some range overlap among *A. spatuligera*, *A. stellata*, and *A. dufresnii* on the west coast of South America. The purple *A. punctulata* occurs in the shallow waters of the Northern Hemisphere of the Western Atlantic. It occurs from Massachusetts to Cuba and the Yucatan Peninsula, from Texas to Florida in the Gulf of Mexico, from the coast of Panama to French Guiana, and in the Lesser Antilles (Serafy, 1979). This species is rare in the Caribbean (Mortensen, 1935). The black *A. lixula* is a common inhabitant of shallow-water hard grounds throughout the Mediterranean, the Atlantic coast of Spain, Portugal, and Northwestern Africa. This species occurs also in the Azores, Cape Verde Islands, the Canaries, and Madeira. It is also found on the other side of the Atlantic, but only in the Southern Hemisphere, off the coast of Brazil. *A. stellata* is found in the Eastern Pacific Ocean from Baja California to Peru (Mortensen, 1935). *A. spatuligera* occurs from Ecuador to Southern Chile. The green *A. dufresnii* is one of the most abundant echinoids along the Argentinean coast (Brogger et al., 2010). It is distributed around South America from the Rio de la Plata on the Atlantic Ocean to Puerto Montt in the Pacific and is also near islands of the South Atlantic Ocean (Bernasconi, 1953). This is the only species of *Arbacia* found off both the Atlantic and Pacific coasts of South America. It also occurs at Booth (Wandel) Island on the coast of Antarctica. *A. crassispina* is considered endemic to Tristan da Cunha, half-way between South America and South Africa (Mortensen, 1935).

1.2   Local distribution and abundance patterns

Bathymetrical distribution of *Arbacia* species ranges from the intertidal to 315 m. The purple *A. punctulata* occurs on rocky, sandy, and rubble bottoms from shallow water to 255 m (Serafy, 1979; Hill and Lawrence, 2003). The average density ranges from approximately 0.06 to 1.25 ind. m^{-2} (Hill and Lawrence, 2003).

The black sea urchin *A. lixula* has a tropical affinity (Stefanini, 1911; Mortensen, 1935; Tortonese, 1965) and probably spread through the Mediterranean in the Upper Pleistocene (Wangensteen et al., 2012). Phylogeographic genetic evidence indicates that this species is a recent thermophilous (warm-tolerant sensu Kempf, 1962; Francour et al., 1994) colonizer of the Mediterranean (Wangensteen et al., 2012, 2013). This species has experienced population increases in the Mediterranean (Petit et al., 1950; Francour et al., 1994). It may reach high population densities of more than 10 ind. m^{-2} (Guidetti and Dulĉić, 2007). This is probably due to the fact that its reproduction is enhanced by high temperatures (Gianguzza et al., 2011; Wangensteen et al., 2013) and larval development features indicate that warming, modulated by other factors such as pH and food availability, may favor *A. lixula* development (Privitera et al., 2011; Wangensteen et al., 2013; Gianguzza et al., 2014; Visconti et al., 2017). This species shows a great resistance to water motion and is well adapted to the turbulent waters of the first few meters of the upper infralitoral. *A. lixula* is common on vertical substrata. It is considered a main grazer of encrusting coralline algae (Benedetti-Cecchi et al., 1998; Bulleri et al., 1999). In spite of the fact that *A. lixula* can live on barren grounds and vegetated rocky shores (Gianguzza et al., 2010), data have shown a positive correlation between barren areas and sea urchin densities (Fanelli et al., 1994; Guidetti and Dulĉić, 2007; Gianguzza et al., 2010). In the barren habitat *A. lixula* reaches an average density of 4.5 ind. $m^{-2}\pm0.05$ S.E. (Gianguzza et al., 2006). On the Brazilian subtropical rocky reefs of Santa Caterina, *A. lixula* represented 20.7% (1.67 ± 06.5 ind. m^{-2}) of the local total abundance and was linked to higher depths and complexity of the reefs (Labbé-Bellas et al., 2016). In a subtidal population from Northeast Spain, large individuals of *A. lixula* (>50 mm) contributed to 65% of the total abundance of sea urchin species in Arraial do Cabo (Cordeiro et al., 2014). The highest density and biomass of large *A. lixula* were observed at intermediate depths and was positively correlated with the number of crevices.

The geographic range of *A. stellata* extends along the Pacific coast of North, Central, and South America from Southern California to Peru, and includes the Galapagos Islands and the mainland and peninsular coasts of the Gulf of California (Mortensen, 1935; Clark, 1948; Brusca, 1980; Houston, 2006). The species is rarely distributed in the shallow water of Panama (Lessios, 2005). Burcham and Caruso (2015) showed that *A. stellata* was significantly more abundant and larger at Laguna Beach, Southern California (test diameter 52 mm) than in Baja California (test diameter 25 mm). These authors have reported the absence of small and large *A. stellata* in the Laguna Beach, suggesting that possibly *A. stellata* may not be successfully reproducing in Southern California and their presence may be the result of a recruitment event from warmer waters (Lessios, 2005).

A. spatuligera occurs from Guayaquil in Ecuador to Puerto Montt in Southern Chile at depths of <25 m (Lessios et al., 2012). No data are available on the density and preferred habitat of the last two species.

The green *A. dufresnii* is distributed around South America at depths between 0 and 315 m. In Golfo Nuevo, Patagonia, individuals of *A. dufresnii* live on mixed gravel and sandy bottoms and among Macrocystis blades and holdfasts

(Bernasconi, 1953). In the Magellanic region of Southern Chile, *A. dufresnii* is the numerically dominant sea urchin (5.5 ind. m^{-2} ± 0.01 average ± S.E.)**** on deeper bed rocky reefs (Newcombe et al., 2012). Recent field observations conducted in North Patagonian gulfs, correlated the population parameters of *A. dufresnii* to the presence of the invasive seaweed *Undaria pinnatifida* (Harvey) Suringar, 1873 (Epherra et al., 2015). Results provided evidence that *A. dufresnii* density and biomass was higher in the invaded sites and varied with the seaweed cycle. The invasive algae probably affects sea urchin populations because it is a new source of food that changes environmental structure (it provides microhabitat for new recruits) and affects the native benthic community (Epherra et al., 2015).

2 Population biology

2.1 Reproductive cycles

Arbacia is a gonochoric genus and hermaphroditism is rare (Harvey, 1956). No sexual dimorphism has been detected in *Arbacia* species. As with other sea urchins, the reproduction of *Arbacia* species is controlled by a suite of endogenous and environmental factors, which interact in a complex synergistic way (Byrne, 1990; Levitan, 1991). Gonads of sea urchins contain somatic (nutritive phagocytes) and germinal cells, and during the reproductive cycle, a sequence of changes in these cells can be observed (Walker et al., 2013). Usually, the timing of the different stages of the reproductive cycle varies among species. Sea urchin gametogenesis involves nutrient accumulation in the gonads, transfer of the accumulated nutrients from nutritive cells to gametogenic cells, storage of the accumulated gametes, and broadcast spawning of sperm and eggs into the water column with external fertilization. This process is considered to be controlled principally by seasonal changes in photoperiod sea temperature, lunar periodicity, phytoplankton, and food availability (Pearse et al., 1986; Bay-Schmith and Pearse, 1987; Byrne, 1990; Gianguzza et al., 2011; Visconti et al., 2017). Reproductive cycles of these echinoids are typically annual or semiannual.

A. *dufresnii* from Golfo Nuevo (Argentina) has an annual reproductive cycle with two spawning events, one in spring and another one in summer (Brogger et al., 2010, 2013). In the field, *A. dufresnii* has a small size and low gonad biomass and gamete production. Under laboratory conditions a high-quality formulated food produces in this species a remarkable increase in biomass production and gonad yield, probably due to high assimilation efficiency of protein and lipids in the culture conditions (Rubilar et al., 2016). Two different populations of *A. dufresnii* along the coast of Patagonia showed an annual cycle, with gametogenesis occurring mainly in the autumn and winter and an extended spawning period took place during the spring and the summer (Epherra et al., 2015). Brogger et al. (2010) showed two spawning peaks for *A. dufresnii* in Golfo Nuevo, Patagonia. The first spawning event occurred during spring and a second major spawning occurred in summer. In this species, proliferation and differentiation of gametes, and the presence of mature gonads were synchronous among males and females. Briefly, *A. dufresnii* displays spatial and temporal differences in its reproductive cycle. This high plasticity may be responsible for the wide distribution of this species in different environments. The color of the ovaries ranges from light to dark purple (Brogger et al., 2013).

The reproductive cycle of *A. lixula* can be continuous or restricted and varies spatially. Wangensteen et al. (2013) studied the reproductive cycle over 4 years of *A. lixula* in a population from Northeast Spain. They found that its gonadosomatic index (GSI) follows a seasonal cycle which peaks in May–July and attains its lowest values in October–November every year. Gonad histology was also in agreement with a single gametogenic cycle per year in this species. The final picture that emerged is that GSI of *A. lixula* shows a remarkable correlation with photoperiod. Temperature acted as an enhancer of the gametogenic process, but probably not as a trigger signal for spawning. In a pioneer study on ecological consequences of increased mean temperature in the Mediterranean, Francour et al. (1994) observed that in the Scandola marine reserve, Corsica, the abundance of *A. lixula* increased more than 12 times over a time span of 9 years, from densities of 8 ind. m^{-2} in 1983 to 100 ind. m^{-2} in 1992, with higher recruitments after hot summers. Spawning events were observed in the summer for *A. lixula* along the French Mediterranean coast (Harvey, 1956). However, observations in the Marine Protected Area (MPA) of Ustica Island (Southwestern Mediterranean) show males and females of *A. lixula* spawn throughout the year (P. Gianguzza, unpublished data). According to Ernst et al. (1973) *A. lixula* reaches sexual maturity between 9.0- and 14-mm test diameter, although Tommasi (1964) reported sexual maturity in a Brazilian population in specimens of 6 mm. The color of its ovaries is generally dark purple.

In the Pacific Ocean, a single spawning period in spring is reported for the carnivorous *A. spatuligera* (Bay-Schmith, 1981). Among a multiple choice experiments with six food items offered (the red algae *Iridaea ciliate* KIITZING, the green algae *Ulva lactuca* LINNAEUS, 1753, and the brown algae *Durvillea antarctica* CHAMISSO) to the canned mackerel flesh *Trachurus symmetrycus* AYRES, 1855, the clam flesh *Protothaca thaca* MOLINA, 1782, and the scallop flesh *Tagelus dombeii* LAMARCK, 1818 or *Ensis macha* MOLINA, 1782, Silva et al. (2004) showed that female *A. spatuligera* from

Central Chile had a clear feeding preference for the clam *P. theca*. Both sexes showed almost a twofold increment in the average gamete production of laboratory animals under the high ration treatment compared to the reference group of sea urchins from the field (Silva et al., 2004).

The breeding season for *A. punctulata* is from June to August and varies from year to year depending on the sea temperature (Harvey, 1956). Maturity in this species is typically very early, with fully mature specimens of only 7-mm test diameter (Harvey, 1956). During May and early June, the gonads are small and it is often difficult to distinguish ovaries and testes. The sex ratios observed for *A. dufresnii*, *A. punctulata*, and *A. lixula* were different from 1:1 and might reflect ambient conditions that influence sex determination (Brogger et al., 2010).

The reproductive cycle of *A. stellata* in Punta Banda, Baja California, Mexico shows semicontinuous pattern with an increase in the reproductive activity at the end of summer and onset of autumn. Only the photoperiod was significant and positively related to the GSI (Díaz-Martínez, 2015). No data are available on the reproductive cycles of *A. crassispina*.

2.2   Larval dynamics and recruitment

Data available on larval supply, settlement, and recruitment of *Arbacia* species are very few and relate only to *A. lixula*. A great amount of effort on *Arbacia* species showed the great sensitivity of early-life stages of their offspring to the toxicity of different contaminants (Riveros et al., 1996; Martino et al., 2017; Giannetto et al., 2018).

George et al. (1990) found that significant variations in the egg quality (protein and lipid contents) and survivorship of *A. lixula* larvae within Mediterranean populations are related to different parental nutrition. Pedrotti and Fenaux (1992) reported a major peak of planktonic larval abundance of this species during October and November in the Ligurian Sea. García-Sanz et al. (2014) showed one main recruitment peak in late winter-early spring (February, March, and April) for *A. lixula* in Gran Canaria Island. This recruitment peak coincides with the lower temperatures observed during the year (<18°C) and the period of maximum primary production in the study area. This optimal recruitment at 18°C clearly contrasts with the temperature of 22°C identified in the Mediterranean at which larvae optimize survivorship through metamorphosis (Privitera et al., 2011). These discrepant outcomes could highlight potential differences at which recruits reach optimum competence across the species' distribution range. In the Northwestern Mediterranean, its recruitment rate may be remarkably different across space (hundreds of meters) and consecutive years (Sala et al., 1998). Size frequency distributions of *A. lixula* suggest that recruitment, except over barren grounds, may not take place every year but is greater in hot summers (Francour et al., 1994; Sala et al., 1998). Privitera et al. (2011) showed that competent larvae metamorphosed on bare stones and calcareous algae: the two main components of barren habitats. Recruitment is rarely reported. This is due to a habitat partitioning between recruits and adults. Kroh et al. (2012) found recruits and small individuals of *A. lixula* under boulders, whereas large individuals typically occur in more exposed habitats. The reason for this segregation may lie in the different morphology of small and large individuals. Unlike large individuals, small individuals have weak phylloides, few suckered tube feet, and flattened spines. Thus they are not able to withstand turbulence and wave action and select sheltered microhabitat. Furthermore, Sala et al. (1998) suggested that small *A. lixula* (<10 mm test diameter) may occur in shallow nursery areas and support the adult stock via migration.

Wheeler et al. (2016) exposed two different larval stages (four- and six-armed plutei) of *A. punctulata* to three environmentally relevant turbulent flow regimes. The swimming speed and vertical velocity of larval urchins changed significantly with age and turbulence regime. The six-armed larval urchins had higher swimming speeds than the four-armed larvae. This increase is consistent with earlier hydromechanical model predictions that weight-carrying capacity is proportional to total arm length. This study highlights the importance of turbulence to planktonic larvae, not just during settlement but also in earlier stages through morphology-flow interactions and this is important for understanding the population dynamics of sea urchin species.

The relationship between egg size and development time in *A. punctulata*, *Strongylocentrotus purpuratus*, and *Dendraster excentricus* was tested by Allen (2012) by manipulating the food concentration given to larvae. Development time increased exponentially as egg size reduced. This confirmed that for species of planktotrophic echinoids with small eggs, one cost of reduced egg size is a prolonged development time.

3   Ecology

3.1   Functional traits

Functional traits are defined as measurable properties of organisms that strongly influence their performance. Functional traits may be useful to predict species-specific contribution to multispecies interactions in the community, and give

information about the potential responses of organisms to environmental changes (Van Der Linden et al., 2012). Regarding sea urchins, studies have principally focused on functional traits that have been proven to influence their (1) local distribution; (2) vulnerability to predators; (3) grazing effect; (4) competitive and mutualistic interaction; and (5) response to food storage. These traits encompass morphological features, attachment tenacity, locomotor capacity, behavior, and feeding habit.

The genus *Arbacia* is characterized by a fairly flattened test with a round ambitus. The peristome is large and covered by a naked membrane. The primary spines are robust and sharp, and their height up to half of the test diameter. The tips of the oral spines are flat and have a small cap of cortex. The genus lacks suckered tube feet on the aboral surface. Within the genus, the functional traits of *A. lixula* have been studied most, probably due to the important ecological role of the species in the dynamics of Mediterranean rocky reef (Hereu et al., 2012 and references therein).

A. lixula is characterized by a low test height to diameter ratio, wide sutures between the plates (constituted by mesenchyme and calcareous trabecules which represents a stress breaker of mechanical forces) and high attachment tenacity. These traits provide a great resistance to wave motion (Chelazzi et al., 1997; Tuya et al., 2007). These morphological features, along with the long spines and the great robustness of the test, make adult *A. lixula* also structurally resistant to predatory attacks by fish (Guidetti, 2004; Guidetti and Mori, 2005). These features (test morphology, attachment tenacity, and spine length) allow this species to live on exposed vertical or subvertical rocky substrates at depths between 2 and 15 m (Gianguzza et al., 2010 and references therein).

A. lixula reaches high densities only in barren areas which are dominated by encrusting organisms (Micheli et al., 2005; Guidetti and Dulĉić, 2007; Gianguzza et al., 2010; Privitera et al., 2011). Work has shown that *A. lixula* prefers barren patches due to its feeding habit and locomotor capacity (Wangensteen et al., 2011; Agnetta et al., 2015). The adaptation of *A. lixula* to barrens is evident by its large and strong Aristotle's lantern, great functional capacity to scrape off corallines, and to consume the associated endolithic fauna (an important food source of this species). Moreover, the movement of *A. lixula* is impaired by erect algae (Maggiore et al., 1987; Scianna et al., 2007; Agnetta et al., 2013) probably due to the weakness of the tube feet, the length of their spines, and the reduced number of tube feet on the adoral portion (Santos and Flammang, 2007; Gianguzza et al., 2010). Other species of *Arbacia* (e.g., *A. punctulata*) show a superior clinging power which gives them a greater ability to withstand high hydrodynamic forces (Sharp and Gray, 1962).

3.2   Feeding habit

All species of *Arbacia* are omnivorous with a strong tendency to carnivory. They are able to scrape fleshy algae, sea grasses, encrusting algae, barnacle shells, and hard calcareous tubes of polychaetes from the substrata, thanks to their large Aristotle's lantern, indicative of a durophagic habit (Fernandez and Boudouresque, 1997; Hill and Lawrence, 2005; Agnetta et al., 2013). *A. punctulata* consumes a variety of food such as algae, sea grasses, sponges, coral polyps, dead fish, hydrozoans, sand dollars, mussel, and bryozoans (Lawrence, 1975; Wahl and Hay, 1995). In particular, Cobb and Lawrence (2005) found that *A. punctulata* may change its feeding habit in relation to the availability of food in the field, being a general omnivore when algae are abundant and carnivorous when algal availability is moderate or low. Inspired by the latitudinal decline in seaweed chemical defenses, Craft et al. (2013) tested for the presence of phylogenetic and biogeographic effects on the feeding behavior of different subtropical and temperate species such as *A. punctulata*. They found that subtropical species displayed greater feeding resistance than the temperate species. Similarly, the subtropical population of *A. punctulata* had greater feeding resistance for *Dictyota* and *Stypopodium* extracts relative to temperate *A. punctulata*. The strong influence of evolutionary history on marine plant-herbivore interactions detected by Craft et al. (2013) implies that evolution may play important roles in species range expansion.

Over 50% of the gut contents of *A. dufresneii* from the coastal beds of *Macrocystis pyrifera* near Southern Chile are invertebrates such as serpulid polychaetes, barnacles, and sponges (Vásquez et al., 1984). It is considered a main carnivorous species on the Argentinian coast (Penchaszadeh and Lawrence, 1999). Under laboratory conditions, *A. spatuligera* showed a marked preference for animals (Silva et al., 2004). This confirms the carnivorous habit of the genus.

A. lixula has a considerable trophic plasticity, ranging from omnivory to strict carnivory (Wangensteen et al., 2011; Agnetta et al., 2013, 2015). Its scraping predatory behavior can play a dominant role in driving switches between one complex state dominated by a stratified assemblage of several erect macroalgae to a simpler one dominated by few encrusting algae, the so-called barren ground (Bonaviri et al., 2011; Wangensteen et al., 2012; Agnetta et al., 2013, 2015; Piazzi and Ceccherelli, 2019).

Corresponding to the omnivorous/carnivorous feeding habit of *Arbacia* species, Trenzado et al. (2012) found high proteolytic ad lipase activity in *A. lixula*. They considered the enzymes found in the gut of this species as "suitable enzymatic machinery" for the digestion of nutrients of animal origin. Conversely, *A. lixula* has little cellulase activity, suggesting

that it is unable to efficiently digest plant material. These results confirm those obtained by the isotopic signatures (Agnetta et al., 2013; Wangensteen et al., 2011). No data are available on the food of *A. stellata*.

3.3   Interaction with other sea urchins

Different species of sea urchins can coexist in numerous habitats. Competition can be avoided by differentiating resources and microhabitats (Vásquez et al., 1984). *A. punctulata* and *Lytechinus variegatus* (LAMARCK, 1816) occur throughout the Gulf of Mexico and the Caribbean in a variety of environments. These species usually occupy distinct microhabitats: *A. punctulata* is abundant on hard substrata whereas *L. variegatus* is usually on sand bottoms (Hill and Lawrence, 2003). Their great difference in morphology and feeding habit might explain the little overlap in the diet of these two occurring species. *A. punctulata* tends to consume large quantities of animals while *L. variegatus* primarily consumes plants and algae (Cobb and Lawrence, 2005).

Hill and Lawrence (2005) evaluated the effect of two types of stress (high temperature and starvation) on gonad production and scope for growth in *A. punctulata* and *L. variegatus*. They hypnotized that *A. punctulata* has a stress-tolerant life strategy and would be more tolerant to stress than *L. variegatus*, considered a species with competitive-ruderal strategy, and thus less tolerant to stress. Relative changes in the gonad indexes and outcomes for the energy budget with stress support the suggestion that *A. punctulata* and *L. variegatus* have different life history strategies**.**

In the Mediterranean, the high wave action resistance of *A. lixula* allows it to occur on exposed shores and on vertical walls in the shallow water (Kempf, 1962; Régis, 1978), in contrast to the cooccurring *P. lividus* which is limited to horizontal or gently sloping surfaces (Chelazzi et al., 1997). When barren grounds are formed, *P. lividus* and *A. lixula* coexist (Privitera et al., 2008; Bonaviri et al., 2011). Gut contents and isotopic signatures support the hypothesis of well-separated trophic niches for *P. lividus* and *A. lixula,* both in vegetated and barren areas of the Mediterranean (Chiantore et al., 2008; Privitera et al., 2008; Agnetta et al., 2013, 2015; Wangensteen et al., 2011). *A. lixula* shows a strong feeding preference for encrusting corallines and their associated invertebrates, whereas *P. lividus* prefers erect fleshy algae. Interestingly, it is possible that *P. lividus* facilitates *A. lixula* by consuming erect fleshy algae and creating barren patches, because *A. lixula* needs encrusting algae to settle (Privitera et al., 2011) and a smooth surface to move (Maggiore et al., 1987; Scianna et al., 2007; Gianguzza et al., 2010). In contrast to *A. lixula, P. lividus* can settle in areas with erect algae and also easily moves on "bumpy" substrata (Privitera et al., 2011). Therefore, it is possible that the "bulldozing" effect of *P. lividus* on erect macroalgae clears foraging grounds for *A. lixula* (Maggiore et al., 1987; Bonaviri et al., 2011). At this stage, recolonization of barren grounds by erect macroalgae can be prevented through intense grazing by the populations of *A. lixula* found in this habitat (Micheli et al., 2005; Guidetti and Dulĉić, 2007; Bonaviri et al., 2011; Privitera et al., 2011; Agnetta et al., 2013). This evidence suggests facilitative interactions (Duggins, 1981), in contrast to the traditional hypothesis of a competitive scenario among cooccurring sea urchin species. In agreement with this hypothesis, the decrease in *P. lividus* recorded in the recent years at Ustica MPA did not trigger any increase in *A. lixula* (Gianguzza et al., 2006; Bonaviri et al., 2009; Agnetta et al., 2013).

In Golfo Nuevo, Patagonia, *A. dufresnii* live on mixed gravel and sandy bottoms and among Macrocystis blades and holdfasts, where they live with another sea urchin, *Pseudechinus magellanicus* (Philippi, 1857) (Bigatti et al., 2004; Marzinelli et al., 2006). The latter species is omnivorous whereas *A. dufresnii* is mainly carnivorous (Penchaszadeh et al., 2004).

3.4   Response to climate change

A pressing challenge in ecology is to understand and predict the effects of global warming on the marine realm. The global increase in mean temperature is expected to profoundly alter temperate communities, with cascading effects for the biodiversity and function of coastal ecosystems (Burrows et al., 2011; Molinos et al., 2016). The mean global surface temperature has increased by 0.76°C in the past 150 years and is predicted to rise an additional 1.1–6.4°C by the end of the 21st century (IPCC, 2007; Fabry et al., 2008). Ocean acidification scenarios project a $\Delta pH = -0.3$ to -0.5 units by the end of the century.

Temperature may regulate sea urchin populations as it regulates reproduction success, larval development, settlement, and growth (Hammond and Hofmann, 2010; Byrne, 2011). Many studies have shown that each species of sea urchin has an optimal fertilization temperature based on the average temperature found in its natural habitat (Sewall and Young, 1999). This optimal temperature is necessary for the successful development of the embryos and larvae (Yamada and Mihashi, 1998). Moreover, temperature increase may induce faster larval growth and urchin reproduction (Hoegh-Guldberg and Pearse, 1995; Ling et al., 2008).

Direct impacts of ocean acidification on sea urchins are mostly negative and sublethal. These include slower somatic and gonadal growth and reflect a shift in energy budgets linked to additional costs for extracellular pH (pHe) and intracellular pH (pHi) regulations rather than direct impact on calcification (Dupont and Thorndyke, 2013). Increased temperature and reduced pH can have additive, both significant and nonsignificant interaction, synergistic—increased stress greater than the sum of the effects, or antagonistic (decreased stress) effects on the developmental processes in marine invertebrates (Byrne and Przeslawski, 2013; Przeslawski et al., 2015). The influence of temperature and pH on echinoderms is well documented as single stressors (e.g., Byrne, 2011; Dupont and Thorndyke, 2013).

Data on the impact of global warming on the different life stages of *Arbacia* species are generally lacking. The exception is studies on *A. lixula*. A single stressor study of *A. lixula* from the Northeast Spain NWM involving three temperatures at control pH showed that the larvae generated from parents held at $\sim 20°C$ are tolerant to cooler conditions ($\Delta 6°C$) but larval growth and survival was highest at $19°C$ (Wangensteen et al., 2013). At $19°C$ and pH_T 7.7 larvae were smaller but had a high survival rate to metamorphosis and the early juvenile (Wangensteen et al., 2013). Interestingly, although the larvae were smaller, development was not delayed as those reared at low pH metamorphosed at the same time as controls, albeit producing smaller juveniles (Wangensteen et al., 2013).

A recent study on the effects of simultaneous exposure to warming and lower pH on the development of *A. lixula* showed that larval growth was positively correlated with increased temperature and was negatively correlated with decreased pH (Visconti et al., 2017). This ameliorating effect of temperature was particularly evident in the high-temperature ($26°C$) treatments. Thus, the hypotheses tested by the authors that warming and acidification would alter larval body growth and that increased temperature would reduce the negative effects of acidification were supported. As expected, the larvae of *A. lixula* were resilient to warming and developed over a relatively wide ($6°C$) temperature range. For the larvae of Southern Mediterranean population investigated by Visconti et al. (2017), $24°C$ appears to approximate the optimal temperature for development. These data, together with the study of Wangensteen et al. (2013) in the Northwestern Mediterranean and García et al. (2018) indicated that the thermal window for the normal development of *A. lixula* could be as large as $\sim 10°C$ (from 16 to $26°C$), with local differences influenced by the thermal history of the gametes prior to spawning due to genetic differences (Wangensteen et al., 2012; Pérez-Portela et al., 2019) that influence gamete performance. In parallel with having a broad thermotolerance, *A. lixula* is also more robust to pH variation than *P. lividus* as shown in the Mediterranean CO_2 vent systems at Vulcano (Tyrrhenian Sea) where *A. lixula* was more prevalent at higher pCO_{2sw} sites compared with *P. lividus* (Calosi et al., 2013; Bray et al., 2014). This is probably due to the fact that *A. lixula* is better able to adjust its acid–base balance by ionic regulation in naturally fluctuating pCO_{2sw} conditions than the cooccurring *P. lividus* (Calosi et al., 2013). This capacity of *A. lixula* to maintain acid–base homeostasis appears to be due to the naturally higher levels of protein in the coelomic fluid of *A. lixula* (Small et al., 2015). However at the Ischia (Tyrrhenian Sea) vent system, Kroeker et al. (2013) noted a decline in both species along a pH gradient. This difference in the response of these species at the two vent systems in the Mediterranean may be due to the location-specific effects and potentially trophic considerations because *A. lixula* and *P. lividus* differ greatly in their diet. The natural pH gradients at the CO_2 vent sites of Ischia have been used as a model system by Foo et al. (2018) to provide insights into the impact of ocean acidification (−0.3 to 0.5 pH_T units) on the egg jelly coat of *A. lixula*. For the vent sea urchins, there was a significant positive relationship between the egg and jelly coat size, a relationship not seen for the eggs of females from the control site. As the egg and jelly coat size was similar between both populations, vent *A. lixula* jelly coats are likely to be chemically fine-tuned for the low pH environment. That the egg jelly coat of sea urchins from the vent site was robust to low pH shows intraspecific variation in this trait. This may be a maternal adaptive strategy or plastic response of the species.

Most studies on the impacts of temperature on echinoids have focused on upper thermal thresholds of embryos and larvae, but it is also important to understand thermal thresholds in large individuals to predict how marine species may respond to changing ocean conditions (Hoegh-Guldberg and Pearse, 1995).

Recently, Diaz et al. (2017) have determined the preferred temperature and critical threshold limits in *A. stellata*, a species that experiences seasonal fluctuations of temperature, ranging from 19 to $25°C$ in summer and from 15 to $23°C$ in winter (Olguin, 2004). Individuals were held at 16, 19, 22, and $25°C$. The temperature interval of $22–25°C$ coincided with the preferred temperature obtained for *A. stellata* ($25.1°C$). The optimum temperature coincides with the temperature range at which large *A. stellata* had a smaller Q_{10} value. These results seem to be an adaptive responses to changing temperatures that sea urchins experienced in their natural habitat. Diaz et al. (2017) concluded that *A. stellata* was able to regulate its body temperature using behavioral thermoregulation. This may partially explain their pattern of spatial distribution in the intertidal and subtidal zone northern limit of distribution along the coast of Baja California.

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