

Chapter 1

Sea Urchin Ecology and Biology

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Introduction

Sea urchins are widely distributed in polar, temperate, and tropical oceans, where they are conspicuous members of most benthic marine communities. They play an important ecological role as herbivorous grazers, and their ability to alter algal community states has made them the subject of numerous ecological studies (e.g., Elner and Vadas 1990; Tegner and Dayton 2000; Witman and Dayton 2001; Uthicke *et al.* 2009). Sea urchins are also used as a model organism in developmental studies and in schools to demonstrate cell division and early development; the purple urchin, *Strongylocentrotus purpuratus*, was one of the first animal species to have its entire genome sequenced (Sea Urchin Genome Sequencing Consortium 2006). There are about 850 living species of sea urchins, and at least 17 of these are commercially valued as food (Table 1.1.), leading to significant sea urchin fisheries in many regions (Andrew *et al.* 2002; Lawrence and Guzman 2004). Because sea urchins often form dense aggregations when their populations increase, they are very vulnerable to overharvesting. Wild stocks in most regions where they are fished are greatly diminished and aquaculture has been proposed as a means to supply the continued market demand, most of which comes from Japan. The first section of this chapter discusses some of the ecological factors that affect sea urchin abundance, distribution, and vulnerability to overfishing. The second section discusses biological and physiological considerations that may be of interest to sea urchin aquaculturists, such as feeding, growth, reproductive control, and physiological adaptations relevant to intensive culture.

Natural History and Ecology

Most sea urchins are broadcast spawners, releasing eggs and sperm into the water column where fertilization takes place, followed by development into a pelagic pluteus larval stage. Environmental cues such as day length and temperature initiate gametogenesis, and spawning is triggered by environmental cues and pheromones to coordinate gamete release. Specific factors that initiate spawning of sea urchins in the field are relatively unknown, although phytoplankton blooms are considered to be an important trigger (Palmer 1937;

Table 1.1. Commercially valuable sea urchin species.

Scientific name	Common name	Country/Region
<i>Anthocidaris crassispina</i>	Japanese purple sea urchin	China, Japan, Korea
<i>Echinus esculentus</i>	European edible urchin	North Sea, NE Atlantic, Scotland
<i>Evechinus chloroticus</i>	Kina	New Zealand
<i>Glyptocidaris crenularis</i>	none	China, Japan, Korea
<i>Heliocidaris erythrogramma</i>	Purple sea urchin	Australia
<i>Hemicentrotus pulcherrimus</i>	Green sea urchin	China, Japan, Korea
<i>Loxechinus albus</i>	Chilean sea urchin	Chile
<i>Lytechinus variegatus</i>	Variegated or green sea urchin	Tropical western Atlantic
<i>Paracentrotus lividus</i>	Purple sea urchin	Mediterranean, Eastern Atlantic
<i>Psammechinus miliaris</i>	Shore or green sea urchin	North sea, Eastern Atlantic
<i>Pseudocentrotus depressus</i>	Purple sea urchin	Japan
<i>Strongylocentrotus droebachiensis</i>	Green sea urchin	North Atlantic & Pacific
<i>Strongylocentrotus franciscanus</i>	Red sea urchin	California, British Columbia
<i>Strongylocentrotus intermedius</i>	Japanese sea urchin	Japan, China
<i>Strongylocentrotus nudus</i>	Dalian purple urchin	Japan, China
<i>Strongylocentrotus purpuratus</i>	Purple sea urchin	North & Central America Pacific Coast
<i>Tripneustes gratilla</i>	Collector urchin; sea egg	Tropical pacific, Australia, Hawaii

Kanatani 1974; Cochran and Engelman 1975, 1976; Starr *et al.* 1990, 1992; Takahashi *et al.* 1990, 1991).

Gametogenesis and spawning have been well documented for the commercially valuable and widely distributed green sea urchin, *Strongylocentrotus droebachiensis*. In the Gulf of Maine, North America, the onset of gametogenesis is triggered in this species by the shorter day lengths following the autumnal equinox in September (Walker *et al.* 2007). Natural spawning of *S. droebachiensis* usually occurs over an extended period in the spring months (March to June) and there may actually be more than one spawning event for a population (Keats *et al.* 1987; Meidel and Scheibling 1998). During each spawning event, males spawn first by releasing spermatozoa, which begin swimming upon contact with seawater. Ova are then released into a cloud of actively swimming spermatozoa. In *S. droebachiensis*, both sexes spawn in response to a small-molecular-weight protein associated with phytoplankton blooms (Himmelman 1975; Starr *et al.* 1992). Studies by Levitan (1991), Levitan *et al.* (1992), and Wahle and Peckham (1999) have suggested that fertilization success requires close proximity of spawning urchins. If this is the case, then fishing removal could reduce the population density to a level that adversely affects reproduction. However, other studies suggest that factors other than proximity determine reproductive success (Meidel and Yund 2001; Yund and Meidel 2003). Normally, sea urchins tend to be cryptic in distribution and seldom aggregate in the open, which calls into question whether reproductive success requires high population densities (aggregations).

The author has observed large numbers of the sea urchin *Echinothrix sp.* releasing eggs or sperm at sunset on the Kona Coast of Hawaii; individuals were dispersed over many hundreds of meters rather than in aggregations, but the timing was coordinated.

The reproductive success of broadcast spawning invertebrates has been likened to a “recruitment sweepstakes” (Flowers *et al.* 2002). Variability in ocean conditions and high mortality rates of larvae and newly settled juveniles mean that random events can affect the reproductive success of spawning adults during each season. This makes it difficult to predict recruitment from year to year, and variable reproductive success might also influence the genetic structure and diversity of year classes (Flowers *et al.* 2002). As urchin larvae drift in the water column for 1 month or longer before settling and are not strong swimmers, the urchins that recruit to an area of bottom likely drifted in from somewhere else. Mortality due to micropredators during the initial settlement phase can be very high and recruitment appears to be more a case of differential survival rather than selective settlement (Harris *et al.* 1994; Harris and Chester 1996). In the 1980s in the southern Gulf of Maine, densities of newly settled *S. droebachiensis* on the bottom could be measured in thousands per meter square (Harris and Chester 1996), with numerous pinhead-size (<1.0 mm) urchins found on urchin barrens (Harris, personal observations); but within a couple of weeks, only scattered patches of juvenile urchins could be observed and most of the small urchins had disappeared. Breen and Mann (1976) reported that recruitment of *S. droebachiensis* was higher in urchin barren communities and seldom occurred in kelp bed communities. However, Harris *et al.* (1994) found that settlement did occur within algal-dominated environments, but survival was highest in barren communities. There is also variation in settlement by depth with higher numbers in shallower habitats (Martin *et al.* 1988; Harris and Chester 1996).

One of the most significant features of sea urchin ecology is the ability of some species to respond to a reduction in predation pressure with exploding populations that can alter community states (Tegner and Dayton 2000; Witman and Dayton 2001; Uthicke *et al.* 2009). At low population densities, most temperate sea urchin species tend to be cryptic in habitat selection. As grazers, they contribute to the detrital food web by converting drift algae and sessile colonial animals into particulates (Mamelona and Pelletier 2005; Sauchyn and Scheibling 2009a, 2009b). When predators such as fish, crustaceans, or sea otters decline in numbers due to fishing or other causes, sea urchin populations can increase and above a certain density their behavior changes from a cryptic habit to forming dense aggregations in open areas (Sala and Zabala 1996; Witman and Dayton 2001). These aggregations begin to consume most sessile algae and associated fauna, converting complex algal-dominated communities into urchin barrens dominated by bare rock and crustose coralline algae (Lawrence 1975; Witman 1985, 1987). Urchin barrens may persist for very long periods if sea urchin populations are not controlled (Witman and Dayton 2001; Steneck *et al.* 2002, 2004). Harris (personal observations) first observed a sea urchin barrens community in Eastport, Maine, in 1970; that community was still dominated by *S. droebachiensis* 44 years later in 2012. Similar patterns of overgrazing of kelp beds by *S. droebachiensis* to form sea urchin barrens have been documented along the coast of Norway (Hagen 1983, 1995; Sivertsen 2006). Outbreaks of sea urchins in the Genus *Strongylocentrotus* have also occurred along the Pacific coast of North America from California (North and Pearse 1970; Watanabe and Harrold 1991; Witman and Dayton 2001) to Alaska (Estes and Palmisano 1974; Uthicke *et al.* 2009). Sometimes, large urchin populations are controlled by naturally occurring disease outbreaks (Miller and Colody 1983). In Nova Scotia, Canada, intense tropical storms, possibly due to climate change,

create conditions that lead to mass mortality of *S. droebachiensis* from infection with *Paramoeba invadens* (Scheibling and Lauzon-Guay 2010). In other cases, abundant sea urchin populations are exploited by predators, including humans.

A classic study in the Aleutian Islands by Estes and colleagues documented how sea otter predation results in low sea urchin populations and a rich kelp bed community supporting fish and seals, whereas islands with few or no sea otters are characterized by urchin barrens with few fish or seals (Estes and Palmisano 1974; Estes and Duggins 1995). Archeological excavation of Aleut middens on several islands showed alternating layers dominated by bones of fish, seals, and sea otters grading into a layer dominated by sea urchin tests and limpet shells. This pattern was repeated over a number of layers (Simenstad *et al.* 1978). A conclusion from this study was that the Aleuts colonized islands with healthy kelp bed communities and harvested the sea otters, fish, and seals until these populations declined, allowing sea urchins to increase. As the sea urchins grazed down the kelp beds, the Aleuts moved to another island until sea otter populations recovered and reduced the sea urchin populations, allowing recovery of the kelp beds that supported fish and seal populations (Simenstad *et al.* 1978; Estes and Duggins 1995). In recent times, sea otter populations have sharply declined along the Aleutians, apparently from predation by killer whales, and sea-urchin-dominated communities have increased around many of the islands that previously supported kelp beds (Estes *et al.* 1998).

In the Caribbean, overfishing of reef fish populations allowed the sea urchin *Diadema antillarum* to become the dominant grazer on coral reefs (Hughes 1994). In the 1960s, studies by Randall (1965) documented the role of grazing fish in controlling algal populations on coral reefs, resulting in patch reefs surrounded by halos of bare area. By the 1970s, *Diadema* populations had taken over the role of dominant grazer in many regions (Sammarco 1982; Hay 1984), until a disease outbreak spread through the Caribbean in the early 1980s and decimated *Diadema* populations. The causative agent for the *Diadema* die-offs has yet to be determined (Uthicke *et al.* 2009). Recovery of *Diadema* numbers has been slow in most areas and has not happened at all in others (Lessios 1988, 1995; Miller *et al.* 2003). Without fish or urchins to control algal populations on reefs, seaweed populations have become a major threat to the health of coral reef communities in many areas of the Caribbean (Hughes 1994).

In many cases, population explosions of sea urchins have led to the rapid growth of regional fisheries, usually followed by a collapse in sea urchin numbers. This pattern can set in motion an ecological cascade that can make it difficult for sea urchin populations to recover to their former levels. A notable example of this was seen in the Northwest Atlantic, where populations of *S. droebachiensis* exploded in the 1980s, briefly supporting a major fishery in the Gulf of Maine, which dramatically declined in the subsequent decade due to overfishing (see Chapter 7). Although kelp beds recovered in this region in many of the areas that were formerly urchin barrens, populations of *S. droebachiensis* have not (Steneck *et al.* 2004, 2013). Another example can be seen in northern Chile, where the historically dominant sea urchin in shallow waters was *Loxechinus albus*. Heavy fishing pressure decimated populations of this species along much of the extensive Chilean coast (Andrew *et al.* 2002; Stotz 2004). Removal of *L. albus* led to increased numbers in many regions of another sea urchin, *Tetrapygus niger*, which has no commercial value but is able to dominate shallow water habitats and create urchin barren communities (Stotz 2004; Urriago *et al.* 2011). These examples and others have led to widespread interest in sea urchin aquaculture as a way to augment regional fisheries.

Biology and Physiology

Treatises on the biology of echinoderms, and sea urchins in particular, include Hyman (1955), Boolootian (1966), Binyon (1972), and published proceedings of the tri-annual International Echinoderm Conferences (Harris *et al.* 2010; Johnson 2012). Subscription to the web-based Echinoderm List Serve (listserv@nrm.se) provides another source of information and a number of symposium volumes related to specific aspects of echinoderm biology are available (e.g., Jangoux and Lawrence 1982), including two focusing on sea urchin fisheries and aquaculture (Lawrence and Guzman 2004; Lawrence 2007). Several aspects of sea urchin biology that may be of particular interest to aquaculturists are discussed subsequently. These include larval development, feeding and digestion, excretion, respiration, somatic and gonadal growth, and control of reproduction. Given the vast and extensive literature regarding sea urchins, only brief introductory overviews are provided of these topics.

Larval Development and Metamorphosis

Echinoderms have long been favored for embryological and developmental studies (Buznikov and Podmarev 1990; Lowe and Wray 2000). *S. droebachiensis* was the first echinoid to have its embryology fully described (Aggasiz 1864) and the larval development of echinoderms as a whole was described as early as 1921 (Mortensen 1921). Complete larval development has been elucidated for a number of sea urchin species, including *S. droebachiensis* (Stephens 1972), *Heliocidaris crassispina* (Onoda 1931), *Strongylocentrotus intermedius* and *Strongylocentrotus nudus* (Kawamura 1970), and *Lytechinus variegatus* (McEdward and Herrera 1999). Metamorphosis and settlement of sea urchins have also been extensively studied and described (e.g., Cameron and Hinegardner 1974, 1978; Kitamura *et al.* 1993). Azad *et al.* (2010) provide a good review of the factors affecting sea urchin larval development and metamorphosis in the context of hatchery production.

Following gamete release, spermatozoa are motile and respond to peptides that dissolve from the jelly coat of the ova and stimulate respiration, motility, and chemoattraction in a species-specific manner (Kinoh *et al.* 1994). Sperm follow a decapeptide gradient in seawater toward the region of higher concentration at the jelly coat of recently spawned ova. After fusion of spermatozoa and egg, radial cleavage results in the echinopluteus larva; the time scale is dependent on temperature. In *S. droebachiensis*, development from fertilized egg to the first pluteus stage requires 1 month at 0 °C and 12 days at 8 °C (Stephens 1972); at 12 °C this process requires just 6 days (Eddy, personal observation). The pluteus larvae of most sea urchin species are pelagic, feeding on plankton until they undergo metamorphosis and settlement as juveniles. In the hatchery, a combination of one or more microalgae species can be used as feed, such as *Dunaliella* spp., *Chaetoceras* spp., *Isochrysis galbana*, *Rhodomonas lens*, and *Phaeodactylum tricornutum*. Most larvae typically progress through three or four pluteus stages, characterized by the number of arms (prism, four arm, six arm, and eight arm) suspended from the cone shaped body. Duration of the larval stage depends on species and environmental conditions, such as temperature and food availability (Fenaux *et al.* 1994). The duration from spawning to settlement for *S. droebachiensis* reared at 10 °C in laboratory culture is approximately 21 days (Harris *et al.* 2003), but this is likely much

longer in the field in the Gulf of Maine, as spawning is observed in March when water temperatures may be close to 0 °C, with settlement observed about the first of June (Harris *et al.* 1994, 2001; Harris and Chester 1996; *et al.*). There is variation in the developmental cycle of sea urchins and up to 20% of species have some form of reduced development, including some with direct development to juveniles (Raff 1988).

Morphological features of the rudiment, which is visible within the body of the eight-armed pluteus, can be used to determine if the pluteus is competent for settlement. Three or more podia and several fully developed spines can be detected and the rudiment itself will usually be around the same size as the stomach (Yazaki 2002). Studies have suggested that metamorphoses and settlement in some species is stimulated by external cues such as coralline algae and bacterial biofilms (Pearce and Scheibling 1991; Huggett *et al.* 2006), but competent plutei will settle on any hard surface with which they come in contact (Harris *et al.* 1994; Harris and Chester 1996; Lambert and Harris 2000). Following settlement, there is further development into the adult form as the larval structures degenerate and become incorporated into the rudiment or used as energy stores. Therefore, the nutritional status of the larvae before metamorphosis may strongly influence post-settlement development and survival (Meidel *et al.* 1999; Byrne *et al.* 2008a, 2008b). Survival of newly settled urchins in the hatchery can be less than 1%, with most of the mortality occurring soon after settlement (Mos *et al.* 2011). The onset of endogenous feeding on microbial biofilms occurs following further development of the lantern and gut. This was found to occur on about day 10 post-settlement in *Strongylocentrotus franciscanus* and *S. purpuratus* (Miller and Emlet 1999). Biofilm species composition can vary in nutritional value and thus also affect post-settlement survival (Xing *et al.* 2007). Juveniles will begin feeding on particulates and macroalgae when they are still quite small; Devin *et al.* (2004) tested various macroalgae as feed for recently settled *S. droebachiensis* that were as small as 2.5 mm test diameter.

Feeding and Digestion

Sea urchins feed using a complex jaw apparatus known as the Aristotle's Lantern (Hyman 1955). The five teeth of the Aristotle's Lantern can chew through materials as tough as the plastic coating on lobster traps and can erode the surfaces of crustose coralline algae. The digestive tract of sea urchins is long and coiled, consisting of a pharynx, esophagus, stomach, intestine, and rectum, which opens through the anus within the periproct at the apex of the test. The stomach comprises the greatest length of the intestine, forming five pouches hanging from the body wall in an almost complete circuit. Sea urchins produce enzymes capable of digesting protein, carbohydrates, and lipids (Lasker and Giese 1954). The digestive tract of sea urchins also contains a rich flora of bacteria and protists that contribute to the digestion of a wide range of food types (Fong and Mann 1980). Although intestinal bacteria may play an important role in digestion, they are not strictly required (Farmanfarmaian and Phillips 1962).

Most sea urchins prefer kelp and other macroalgae and they can have distinct preferences for certain species, although availability is also a key factor (Larson *et al.* 1980; Dworjanyan *et al.* 2007). Broad leafed kelps such as *Laminaria sp.* and *Saccharina sp.* are often preferred, whereas other species, such as *Agarum cribrosum*, are avoided even when they are the only species available (Fuji 1967; Vadas 1977). When macroalgae are present sea urchins will eat continuously; under these conditions gut passage time is reduced and

feed may pass through the gut in as little as 8–12 h (Lasker and Giese 1954). Lawrence and Klinger (2001) reported an average gut passage time of 2 days for *S. droebachiensis*. Under food-limited conditions, gut passage slows; starved *S. purpuratus* continued ejecting feces for up to 2 weeks (Lasker and Giese 1954). A range of values has been reported for absorption efficiency, generally within 60–80% when urchins are feeding on preferred algae (Lasker and Boolootian 1960; Lawrence 1975). However, feed composition and feeding rate can affect both gut passage time and nutrient absorption. Fuji (1967) reported a gut retention time of 1 day when *S. intermedius* was fed *Laminaria japonica* and 3 days when fed *Ulva pertussa*; absorption values were about 55% and 75%, respectively. Fuji concluded that when urchins are continuously feeding, there is a larger loss of organic matter and nutrients in the feces. Boolootian and Lasker (1964) reported greater digestive efficiency in *S. purpuratus* fed *Macrocystis pyrifera* (80%) than with *Egregia laevigata* (62%), but they did not see any decline in absorption efficiency at higher consumption rates. Absorption of protein by sea urchins appears to be high regardless of the food type and most of the variation in absorption values for different foods might be a function of differences in carbohydrate quality (Fernandez and Boudouresque 2000).

Most sea urchins are capable omnivores (Briscoe and Sebens 1988; Nestler and Harris 1994) and they do best on a mixed diet that offers higher protein than a strictly vegetarian diet (Williams and Harris 1998; Lawrence *et al.* 2001; Watts *et al.* 2010). In the field, protein sources might include bryozoans and other macroalgae epiphytes, small crustaceans, and even opportunistic feeding on dead vertebrates. A number of laboratory studies have shown that sea urchins respond to the higher dietary protein levels found in formulated feeds with faster somatic growth and increased gonad production (e.g., Akiyama *et al.* 2001; Kennedy *et al.* 2005; Hammer *et al.* 2006). Protein levels of about 20% (dry weight) appear to be optimal for somatic growth under culture conditions for *S. droebachiensis* (Eddy *et al.* 2012), *Pseudocentrotus depressus* (Akiyama *et al.* 2001), and *L. variegatus* (Hammer *et al.* 2006). Unlike the pattern seen with algal feeds, consumption rates of formulated diets tend to decrease with increasing protein levels (McBride *et al.* 1998; Fernandez and Boudouresque 2000; Hammer *et al.* 2006). Absorption of the total organic matter in formulated diets can be lower than that seen for algal feeds, possibly reflecting better utilization of the increased protein (McBride *et al.* 1998).

Excretion

Unabsorbed food is excreted as feces in the form of globular pellets surrounded by a mucous envelope (Lawrence and Klinger 2001). In *S. droebachiensis*, these pellets are about 1–3 mm in diameter and negatively buoyant in seawater (Miller and Mann 1973; Sauchyn and Scheibling 2009b). Mamelona and Pelletier (2005) reported that on average, 75% of ingested algae was excreted in the fecal pellets, making them a potentially important food source for detritivores. This raises the possibility of coculturing sea urchins with detritivores such as sea cucumbers or marine worms (Brown *et al.* 2011; Yokoyama 2013). Defecation rates in sea urchins are a function of feed composition and consumption rates. Sauchyn and Scheibling (2009a) observed that defecation rates were lower for *S. droebachiensis* fed *Codium fragile* than for urchins fed kelp *Saccharina longicuris*, with a correspondingly higher digestion efficiency for the *Codium* (about 87% for *Codium* and 65% for kelp). These authors estimated a defecation rate of 0.002 g feces/g urchin/day in the field for urchins feeding on kelp. This is in close agreement with the rate reported

by Mamelona and Pelletier (2005) for the same species in the laboratory (0.003 g feces/g urchin/day). The rate at which the feces degrade is dependent on microbial action, which in turn may be affected by the carbon-to-nitrogen ratio of the feces (Sauchyn *et al.* 2011). *S. droebachiensis* grazing on *S. longicruris* excreted feces with a C:N ratio of 30.7, whereas the feces from urchins grazing on *C. fragile* had a C : N ratio of 8.5 (Sauchyn and Scheibling 2009a).

The excretion of nitrogenous wastes in sea urchins is poorly understood and they do not appear to have a specific organ for accumulation and excretion of nitrogenous compounds (Jangoux and Lawrence 1982; Arafa *et al.* 2006). There has been some speculation that phagocytic coelomocytes might transfer insoluble nitrogenous wastes, dead cells, and particles to the exterior of the test (Endean 1966). The gills may play a major function in this process by removing necrotic phagocytes (Cobb and Sneddon 1977). Lewis (1967) measured ammonia nitrogen compounds in various tissues of the sea urchin *D. antillarum* and observed the highest concentrations in the hindgut (400 µg/100 g), which might suggest that nitrogenous wastes are excreted in the feces. However, it is likely that water soluble nitrogenous wastes are excreted directly through respiratory surfaces (Endean 1966). Sea urchins are considered to be predominately ammonotelic. Ammonia comprised the majority of nitrogenous waste compounds in *D. antillarum* (Lewis 1967), *S. droebachiensis* and *S. purpuratus* (Stickle 1988), and *Pseudocentrotus lividus* (Arafa *et al.* 2006). Total nitrogen excretion rates for actively feeding *S. droebachiensis* and *S. purpuratus* were found to be 27 µg N/g organic tissue/h and 9.08 ± 3.21 µg N/g organic tissue/h, respectively (Stickle 1988). In a comparison between fed and starved *P. lividus*, it was found that there was no significant difference in ammonia efflux between the two groups, indicating that the starved urchins were continuing to metabolize nitrogen, probably by utilizing nutrient stores in the gonads (Arafa *et al.* 2006). Ammonia excretion was found to be higher in starved *A. crassispina* than in recently collected animals (Dy and Yup 2000). This was attributed to catabolism of nutrient stores in the gonads and increased metabolic activity as the animals engaged in searching behavior for food. Sea urchins are sensitive to elevated nitrogen levels in the water; Siikavuopio *et al.* (2004a 2004b) reported reduced gonad growth in *S. droebachiensis* at unionized ammonia concentrations above 0.016 mg/l¹ and nitrite levels greater than 0.5 mg N–NO₂/l.

Respiration

Sea urchins have five pairs of external gills surrounding the peristomial membrane. Interestingly, however, the gills play only a minor role in oxygen uptake; the podia are the primary means by which sea urchins exchange gases between the internal and the external environment (Farmanfarmaian 1966). The podia are extensions of the water–vascular system, which is internally lined with a ciliated epithelium responsible for maintaining the flow of water into the coelomic cavity. Sea urchins lack a well-developed system for internal oxygen transport. The various internal body tissues are suspended within the coelomic cavity, and the rate of oxygen consumption by the body tissues varies in direct proportion to the partial pressure of oxygen in the coelomic fluid (Johansen and Vadas 1967). This arrangement provides an advantage in that the spacious coelomic cavity acts as an oxygen storage reservoir, allowing urchins to survive up to 15 h out of water, possibly as an adaptation to intertidal conditions.

When sea urchin gonads increase to their maximum size, they can occupy most of the coelomic cavity. Under the aforementioned condition, this would appear to reduce the opportunity for oxygen exchange with internal tissues and with the gonads themselves, which are minimally perfused by the water vascular system. However, Bookbinder and Shick (1986) reported that up to 96% of gonad metabolism in *S. droebachiensis* was based on anaerobiosis, although gut activity was largely aerobic. Although Siikavuopio *et al.* (2007) observed that both gonad growth and feed intake were significantly reduced at oxygen levels less than 6 mg/l but they concluded that reduced feed intake at lower oxygen levels was responsible for the reduced gonad production. Lilly (1979) reported that the rate of oxygen uptake in both *Tripneustes ventricosus* and *S. droebachiensis* varied depending on the diet, with higher oxygen consumption attributed to greater food absorption of brown algae (*Sargassum* sp. or *Nereocystis* sp.), as opposed to lower oxygen uptake with reduced absorption of angiosperm plants. This raises the possibility that sea urchins fed with high quality formulated diets might consume more oxygen than those fed macroalgae, although to our knowledge this question has not been addressed. In any case, although it appears that sea urchins can survive for extended periods under hypoxic conditions, both somatic and gonadal growth rates are improved when seawater is fully saturated with oxygen (Siikavuopio *et al.* 2007, 2008). In the case of a relatively sedentary animal such as sea urchins, high water flow rates are also needed in order to maintain adequate oxygen levels in the vicinity of the animal.

Somatic Growth

Somatic growth in sea urchins occurs by expansion of the plates that comprise the test. The sea urchin test appears to be an external skeleton, but in fact it is a porous endoskeleton consisting of a CaCO₃ matrix, covered by a thin epidermal layer. The test is made up of twenty plates held together by connective tissue and sea urchins grow in size by secreting CaCO₃ at the edges of the skeletal plates. Echinoderms have a unique form of connective tissue that is under nervous control, with the ability to quickly change from an almost liquid and flexible state to a rigid state (Motokawa 1988). In sea urchins, this flexible connective tissue allows the test to quickly expand under favorable growth conditions, creating spaces between the ossicles that permit growth of the test over a longer period (Ellers *et al.* 1998; Johnson *et al.* 2002). The ability to rapidly increase their body volume may allow sea urchins to increase their internal space for higher consumption volumes or allow for rapid growth of gonads for nutrient storage. For many years it was assumed, based on studies by Ebert (1982), that urchins could grow smaller during times of stress. However, a recalculation of the earlier study indicated that urchins do not decrease the size of their ossicles (Ebert 2007).

Sea urchin growth has traditionally been measured as a function of increase in test diameter (TD), although more recently Ellers and Johnson (2009) advocated weight as a more precise measure in *S. droebachiensis*, from which TD can be reliably and accurately determined. Growth lines created by calcium deposition along skeletal structures have been used to estimate age and growth of sea urchins in the field (Pearse and Pearse 1975). Assuming annual periodicity to these growth rings, growth can be modeled based on average TD measured at each age. In the sea urchin *Hemicentrotus pulcherrimus*, annual growth rings can be observed as black bands on charred genital plates. These were used to demonstrate that growth of this species slowed during the reproductive season (Agatsuma and Nakata

2004). However, in other species, such as *S. droebachiensis*, growth rings are not always annual and cannot be used to reliably determine age (Ellers and Johnson 2009). An alternative approach is to mark skeletal structures with fluorochromes, which allows subsequent skeletal growth to be measured, while also providing a means by which the urchins can be identified at a later date (Gage 1992; Ellers and Johnson 2009).

In general, sea urchin growth is characterized by an initial lag phase following settlement, rapid growth from about 10 mm to the size of reproductive maturity (about 25–45 mm TD for most species), and then a linear decrease with increasing test size. Asymptotic growth functions, such as the von Bertalanffy equation (von Bertalanffy 1938), are often used to model sea urchin growth (Ebert 1975). However, for many species, the von Bertalanffy function does not always provide the best fit for the growth observed and a variety of other growth functions have been proposed instead, some of which do not assume asymptotic growth (Walker 1981; Lamare and Mladenov 2000; Rogers-Bennett *et al.* 2003; Ellers and Johnson 2009). Asymptotic growth implies that above a certain size, growth rates approach zero, but some sea urchin species may continue to grow throughout their lifetimes (Lamare and Mladenov 2000). Some species can live for very long periods; Russell *et al.* (1998) calculated that *S. droebachiensis* could live for more than 50 years and Ebert and Southon (2003) provided estimates for *S. franciscanus* of 120 or more years. These long-lived, slow-growing species can attain a large maximal size; *S. franciscanus* is one of the largest species and can grow to 18 cm TD.

The rate of somatic growth is one of the most critical considerations affecting species selection and economic viability of marine aquaculture. Lawrence and Bazhin (1998) compiled data on age and size at sexual maturity for a number of commercially important species. Members of the family Toxopneustidae, such as *Tripneustes gratilla* and *L. variegatus*, can reach 40 mm TD within 9–12 months, whereas Strongylocentrodids grow at a much slower rate; according to their source data, *S. droebachiensis* required 40 months to attain 29 mm TD (Siverston and Hopkins 1995). However, intraspecific growth rates observed in the field can be quite variable, depending upon location and the type of algae used as feed (Swan 1961 1966). Sea urchins may grow very slowly for long periods on minimal resources, but respond to improved conditions with rapid growth (Russell 1998; Brady and Scheibling 2006). Growth of *S. droebachiensis* in tidal pools can be ≤ 0.25 mm/year (Russell *et al.* 1998), but under laboratory conditions, growth modeling indicates that this species can grow from 4 mm TD to 50 mm in as little as 2.3 years (Ellers and Johnson 2009). Temperature, season, and diet have all been found to influence growth rates. Faster growth of *S. droebachiensis* (Devin *et al.* 2004; Pearce *et al.* 2005) and *P. lividus* (Fernandez and Pergent 1998) was seen with increased temperature, but at the upper temperature tolerance range for each species growth rates decreased and there was increased mortality. Seasonal growth effects may be related to temperature, food availability, and gonad production (Walker 1981). There is ample evidence that in culture many species can reach a reproductive harvest size of 40–50 mm TD within 2 years, if environmental conditions are optimized and the urchins are fed a high-quality feed. Agatsuma (2000) recorded an average TD of 46.9 mm TD after 30 months in culture for *S. intermedius* fed *L. japonica*. Individuals from the same hatchery cohort reared under similar conditions but fed *Sargassum confusum* grew at a slower rate and were only 36.7 mm TD after 30 months. Growth to harvest size within 2 years under culture conditions has been documented for several species, including *S. droebachiensis* (Eddy *et al.* 2012), *P. lividus* (Grosjean *et al.* 1998; Fernandez and Pergent 1998), and *T. gratilla* (Dworjanyn *et al.* 2007).

A multimodal size distribution, where a percentage of the population grows very quickly while a subset grows very slowly or almost not at all, has been observed in laboratory and field populations of *S. droebachiensis* (Harris *et al.* 2003; Hagen 2004), *Echinus esculentus* in sea cages (Gage 1992), and *P. lividus* in the laboratory (Grosjean *et al.* 1996). This presents a problem for the aquaculturist, as it means that a potentially significant percentage of hatchery juveniles may need to be culled in order to focus resources on the faster growing individuals. In the case of *P. lividus*, the multimodal distribution was attributed to environmental rather than genetic factors, as improvements in growth were seen when individuals were graded into homogenous size groups (Grosjean *et al.* 1996, 1998). However, there is evidence of genetic heterogeneity within some natural populations of sea urchins, such as *S. franciscanus* (Moberg and Burton 2000) and *S. purpuratus* (Flowers *et al.* 2002). Potentially, this provides a basis for attributing to some extent the variability observed in sea urchin growth rates to genetic factors. Indeed, measures of growth heritability in *S. nudus* (Liu *et al.* 2004) and *S. intermedius* (Liu *et al.* 2005) indicated that there was sufficient heritability to justify selective breeding of these species for faster growth in culture. Hybridization is another approach that could be used to improve growth in culture. Some species of sea urchins can be readily crossed in the laboratory to produce faster growing offspring than the parent lines, as reported by Ding *et al.* (2007) for hybrids of *S. nudus*, *S. intermedius*, and *A. crassispina*.

Gonad Growth and Its Relation with Somatic Growth

All echinoids are dioecious, and in sea urchins of both sexes the reproductive system consists of five separate gonads, each connected to the upper aboral surface by individual gonopores. The gonads, which line the interior of the test, serve both for the production of gametes and for the storage of nutrients within gonadal cells known as nutritive phagocytes (Walker *et al.* 2005). As sea urchins enter gametogenesis, the nutrients stored within the nutritive phagocytes are used to produce gametes for reproduction and the nutritive phagocytes shrink in size. Gonad quality is optimal for human consumption when the gonads are dominated by large nutritive phagocytes, before gametogenesis has fully progressed (Unuma 2002; Walker *et al.* 2007). Even when gametes are not being produced, well-fed urchins may contain large gonads, which are primarily serving as energy storage organs (Walker *et al.* 2005; Walker *et al.* 2007). Gonads can comprise as much as 20% or more of the animals' total weight in well-fed individuals, with values as high as 30% reported for the Chilean sea urchin *L. albus* (Cárcamo 2004) and 35% for *S. intermedius* (Lawrence *et al.* 2011).

Ultimately, the objective of sea urchin aquaculture is to produce high quality gonads for harvest and consumption. Gonad size and yield will depend upon body size at harvest and the time to harvest will depend upon the rate of somatic growth. In the case of sea urchin aquaculture, size restrictions imposed upon the capture fishery for management purposes may not apply. The legal harvest size varies between species and fisheries, and for conservation purposes, it is usually larger than the size at reproductive maturity. *S. droebachiensis* can be reproductively mature at about 25 mm TD, but in the state of Maine, USA, regulations limit the legal harvest size to between 52 and 72 mm TD. This allows urchins greater than 25 mm but less than 52 mm to have an opportunity to spawn before they are harvested, while also preserving larger individuals greater than 72 mm, which are more fecund than smaller individuals (Taylor 2004). In Japan, where six species are harvested,

the legal minimum harvest size for *S. nudus* is 50 mm, but they are reproductively mature at 40–45 mm (Fuji 1960; Yokota 2002). The fact that sea urchins can produce commercial quality gonads at a smaller size than what may be legally harvested from the fishery could be advantageous to the aquaculturist. The issue then becomes a matter of the minimum size that is acceptable for processing while still yielding a sufficient economic return to the grower. In Japan, *H. pulcherrimus* as small as 20 mm TD are considered economically worthwhile.

Sea urchins have indeterminate growth, that is, both gonadal and somatic growth can occur following maturation of the animal (Sebens 1987). This raises the question as to whether a conflict exists between somatic and gonadal growth. Precocious gonad growth is often observed in juvenile sea urchins fed formulated diets, including *S. droebachiensis* (Eddy *et al.* 2012), *L. variegatus* (Hammer *et al.* 2004), *P. depressus* (Akiyama *et al.* 2001), and *L. albus* (Olave *et al.* 2001). Hammer *et al.* (2004) suggested that the decreased growth rate they observed over time of *L. variegatus* fed high protein diets (after an initial period of fast growth) might have been due to precocious gonad development. However, Minor and Scheibling (1997) reported that gonadal and somatic growth in *S. droebachiensis* increased in parallel with diet quality or quantity. Lawrence (2000) gives many examples from the literature of continued somatic growth in sea urchins following gonad development and concludes that there is no convincing evidence for a conflict between gonadal and somatic growth.

Reproductive Control

Gonad development and maturation in sea urchins has been classified into four or five stages, starting with fully spent or immature gonads and progressing to fully mature gonads at spawning (Unuma 2002; Walker *et al.* 2007). Many species of sea urchins initiate vitellogenesis and gametogenesis in response to temperature and photoperiod cues, either working alone or in combination (Bay-Schmidt and Pearse 1987; Walker and Lesser 1998; Unuma 2002; Kirchhoff *et al.* 2010). Sea urchins may be able to detect light intensity via their podia, which have enervated discs at the end containing photosensitive pigments (Lesser *et al.* 2011). For many temperate sea urchin species, such as *P. miliaris* and *S. droebachiensis*, a combination of low temperature followed by lengthening days is required for completion of gametogenesis (Kelly 2001; Kirchhoff *et al.* 2010). For other species, such as *P. depressus* and *H. pulcherrimus*, temperature is more important than photoperiod for gonadal maturation (Yamamoto *et al.* 1988). The nutritional status of the urchin also plays an important role; well-fed sea urchins produce larger and more productive gonads, whereas nutritionally deprived individuals may fail to develop sufficient gonads for spawning (Garrido and Barber 2001; Fabbrocini and D'Adamo 2010). Feeding, temperature, and photoperiod regimes have all been manipulated with captive urchins to improve the market value of the gonads and/or extend the season by delaying gametogenesis (e.g., Spirlet *et al.* 2000; Vadas *et al.* 2000; Böttger *et al.* 2006) (see Chapter 12 of this book, “Sea Urchin Gonad Enhancement,” for more on this topic). These same techniques can be applied to sea urchin broodstock management. Holding mature urchins in laboratory conditioning systems allows the reproductive cycle to be decoupled from natural rhythms, to permit year round or out-of-season spawning for hatchery production (Kirchhoff *et al.* 2010).

Summary

Sea urchins play an important ecological role as a grazer of macroalgae, with the ability to significantly alter marine community composition when conditions are favorable (Uthicke *et al.* 2009). Their gonads function as nutrient storage organs as well as for gamete production, which has made a number of species attractive as food in a number of cultures (Lawrence 2007). When populations of sea urchins reach high densities, they often become the target of fisheries (Andrew *et al.* 2002). Unfortunately, maintenance of sustainable fisheries for sea urchins has proven elusive (Andrew *et al.* 2002), which has led to the development of culture techniques for sea urchin aquaculture industry (Saito 1992; Hagen 1996; Lawrence and Guzman 2004; Lawrence 2007). Sea urchins have a number of biological and physiological characteristics that make them adaptable to intensive culture conditions. These include the capacity to feed upon both vegetable and animal sourced feeds, fast growth potential, tolerance of high culture densities, high reproductive potential, a long history of hatchery production at mass scale, and high yields of nutritious and commercially valuable gonads. The cultivation of sea urchins is quite well understood (Saito 1992; Hagen 1996); however, there are still issues to be resolved before sea urchin aquaculture can become economically viable without government subsidies (Harris *et al.* 2003; Lawrence and Guzman 2004), which is one of the major themes of this present volume.

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