

Seasonal variation in the effects of food availability on gametogenesis in the purple urchin (*Strongylocentrotus purpuratus*)

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Abstract The amount of food and when it is available affect both the timing of reproduction and the number of gametes produced by purple sea urchins, *Strongylocentrotus purpuratus*. To investigate this further, the effects of food availability on feeding rates, gonad growth, and gamete development were examined in *S. purpuratus* collected from the Point Loma kelp forest near San Diego, California, USA (32.69° N, 117.26° W) in September (Fall) 2007, and February (Spring) and July (Summer) 2008, using laboratory mesocosms. Each seasonal laboratory feeding experiment lasted 3 months, and different levels of food availability were established with different feeding frequencies (from 1 to 7 days week⁻¹). Gonad tissues of male and female urchins were staged at the end of each experiment using histological analyses. Reduced food availability resulted in increased daily consumption rates, especially in the Fall when gamete development began. Food limitation at this time resulted in failure to produce viable gametes, suggesting there is a critical period early in gonad development when food limitation affects reproductive competency. Food limitation later in gonad development did not stop viable gamete production, although it did reduce gamete output.

Introduction

Reproduction in marine invertebrates is a multistage process that begins with either storing nutritional resources or directly allocating them to reproduction in order to initiate gametogenesis, and ends with the spawning of mature gametes. When individuals become food limited, they may cease allocating nutritional energy to gamete production and redirect energy to growth and survival (Wade and Jones 2004). While organisms in these situations may still reproduce, the number and size of their offspring are often diminished, resulting in lowered fecundity (Moehrlein and Juliano 1998). However, in some cases, organisms will spawn even when it results in their immediate mortality, especially when the chances of surviving to the next reproductive period are low (Siems and Sikes 1998; Stockmann and Garton 2001), but if a critical amount of resources is acquired and stored early in gametogenesis, reproduction proceeds although possibly augmented by future changes in the parent's nutritional condition (as in the green urchin *Strongylocentrotus droebachiensis*, e.g., Garrido and Barber 2001). In species with “fixed” development, the buildup and storage of nutritional resources early in gametogenesis determines whether and when individuals spawn, but the quantity of gametes they produce is influenced more by nutritional changes occurring later in gametogenesis (Moehrlein and Juliano 1998). In contrast, in species with “flexible” development, changes in nutritional condition following the early buildup of nutritional resources determine the quantity of gametes produced as well as whether and when the individuals spawn, or gametes can be reabsorbed and used for growth and maintenance. In both strategies, it is essential that individuals buildup and store a minimum amount of energy during early gametogenesis, because without this they

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cannot allocate resources to gamete development (Moehrlin and Juliano 1998).

Sea urchins are conspicuous components of many coastal ecosystems where they are important resources for fisheries that harvest them for their gonad tissue (reviewed by Lawrence 2007). They are also important grazers in nearshore ecosystems where they are integral in controlling algal communities. Given the inherent spatial and temporal variability in macroalgal abundance in many coastal ecosystems, these urchins can be exposed to high spatial and temporal variability in their food supply (e.g., Ebert 1968; Harrold and Reed 1985). As a result, numerous studies examining the effects of food variability on urchin populations have found positive relationships between both food availability (e.g., Thompson 1982; Minor and Scheibling 1997; Walker and Lesser 1998; Guillou and Lumingas 1999) and/or food quality (Himmelman and Steele 1971; Larson et al. 1980; Lemire and Himmelman 1996; Meidel and Scheibling 1999) and gonad mass. Likewise, other studies have found that environmental factors such as temperature and photoperiod may also be important in controlling the timing of gamete development (e.g., Cochran and Engelmann 1975; Pearse and Walker 1986; Ito et al. 1989; Sakairi et al. 1989), although these may be more important during later stages of gametogenesis (Walker and Lesser 1998).

Urchin gonads have two main cell types, nutritive phagocytes (NP) and gametes (oocytes in females and spermatogenic cells in males). These two main cell types are inversely correlated with both number and size throughout an urchin's reproductive cycle (Holland and Giese 1965; Chatlynnne 1969; Gonor 1972; Wourms 1987; Garrido and Barber 2001). During early gametogenesis, NPs increase in both size and number as nutrients are sequestered in the gonad tissue (review by Lawrence 2007). As gametogenesis continues, these nutrients are transferred from the NPs to the gametes, and the NPs become thin and vacuolated. Once the gametes mature, they are spawned through the gonadopores and the gonad tissue begins the cycle again with nutritional buildup (Chatlynnne 1969). Although this process can occur throughout the year under land-based aquaculture conditions (Shpigel et al. 2004), it is usually annual under natural conditions (Garrido and Barber 2001; Shpigel et al. 2004; Walker et al. 2007) with gonad development divided into six stages of gametogenesis, which are identified using histological analysis (Fuji 1960; Byrne 1990). These stages are: Stage 1—pre-gamete, Stages 2 and 3—immature gametes, Stages 4 and 5—mature gametes, and Stage 6—post-spawn, no gametes left (Appendix 1 in ESM). The critical period of nutritional buildup (*sensu* Wilbur and Collins 1973) occurs in Stage 1 when the NPs are accumulating polysaccharides and lipids (Garrido and Barber 2001). While numerous studies have

examined the relationship between food availability and overall gonad growth (e.g., Ebert 1968; Minor and Scheibling 1997; Meidel and Scheibling 1999; Vadas et al. 2000; Scheibling and Anthony 2001; Lester et al. 2007), few have examined how food availability affects gonad development and maturation, thereby limiting information on the condition of the gonad tissues (Holland and Giese 1965; Chatlynnne 1969; Gonor 1972; Wourms 1987). Here, we examine the effects of food availability on consumption rates and gonad development in the purple urchin, *Strongylocentrotus purpuratus*, during three different seasons in its reproductive cycle.

Strongylocentrotus purpuratus is widely distributed in intertidal and subtidal habitats along the west coast of North America where it is an important herbivore in the subtidal kelp forest communities (Ebert and Russell 1988). As with other urchin species in this region, individuals often remain hidden under boulders, in cracks and crevices, or under low overhangs and feed on drift algae resulting from the natural senescence of nearby algae or from the fragmentation of algae by hydrodynamic forces (Harrold and Reed 1985). Consequently, their food availability varies seasonally and geographically due to differences in nearby algal abundance and wave action (Ebert 1968; Dayton et al. 1984; Harrold and Reed 1985). This, in turn, can have significant impacts on reproduction and on how quickly food is consumed once it is obtained. For example, *S. purpuratus* in habitats where food is scarce tend to consume drift algae more quickly than those in areas where food is abundant (Ebert 1968). This has also been observed in laboratory studies where individuals fed only once a week consume algae more quickly than those fed *ad libitum* (Minor and Scheibling 1997; Meidel and Scheibling 1999). Also, Ebert (1968) noted that the gonad buildup in different *S. purpuratus* populations was asynchronous, occurring earliest in areas where food was most abundant, followed by areas where food was less abundant, and last in areas where food was scarce. In contrast, populations exposed to similar levels of food availability spawned synchronously. Annual peak gonad index (GI), measured as percent of total body mass made up of gonad tissue, also varies based on food availability and appears to be correlated with spawning time (Lester et al. 2007). However, while urchin GI is useful for comparing relative levels of gonad mass among populations, it does not provide sufficient information on the type of gonad tissue present (Gonor 1972; Beninger 1987; Barber and Blake 1991; Garrido and Barber 2001). Consequently, a more detailed understanding of the effects of food availability on *S. purpuratus* reproductive condition requires information on both gonad mass (GI) as well as its developmental condition, which requires histological analysis (Thompson 1982; Garrido and Barber 2001; Byrne 1990).

Materials and methods

Sexually mature (>24 mm test diameter; Gonor 1972) *S. purpuratus* were collected from the center of the Point Loma kelp forest, San Diego California (32.69° N, 117.26° W) on three occasions, September 2007, and February and July 2008. The urchins were collected from the same 15-m deep site on each occasion and transported to the laboratory in coolers filled with seawater where they were placed in 568-l mesocosm tanks at 16–18°C. The tanks were near a large window that supplied lighting with a natural photoperiod, which is a strong component of seasonality. To examine the effects of food availability on urchin gonad growth and development, we conducted three, three-month-long feeding experiments in a flow-through water table following each collection. The three experiments were thus initiated in different seasons when the urchins were in different stages of their annual reproductive cycle (Chatlynne 1969; Walker et al. 2007). The “Fall” experiment was conducted from September to December 2007, when the urchins were in the early stages of gametogenesis, the “Spring” experiment was conducted February–May 2008, when the urchins were in the late stages of gametogenesis or were spawning, and the “Summer” experiment was conducted from July to September 2008, when the urchins were post-spawn and in a period of nutritional recovery (Chatlynne 1969). A subset ($n = 20$) of the urchins collected during each season were immediately dissected and their stomachs examined for the presence of food. All remaining urchins were then starved for 2 weeks prior to the start of each experiment in order to standardize their nutritional condition following Scheibling and Anthony (2001). Some of the urchins died during this starvation period due to water quality problems in our newly built seawater system resulting in different sample sizes for each experiment. These issues were resolved prior to the initiation of the feeding experiments. Following this, urchins (Fall $n = 29$, Spring $n = 71$, Summer $n = 40$) were allocated to seven different cages housed in flow-through water tables (Appendix 2 in ESM). The tanks were cleaned twice a week when all feces were removed using a siphon, and dead urchins were removed and not replaced.

To examine whether food consumption rates varied as a function of food availability, urchins in the seven cages were subjected to different feeding treatments in which blades of the giant kelp (*Macrocystis pyrifera*) were added to each cage in increasing one-day increments. This resulted in seven feeding treatments ranging from “fed 1 day week⁻¹” to “fed 7 days week⁻¹” (hereafter ad libitum), except for the Fall experiment when treatments ranged from fed twice per week to fed ad libitum. Before being added to the cages, the kelp was blotted dry and weighed. After the urchins had been allowed to graze for

24 h, the kelp was removed, blotted dry and reweighed to assess how much had been consumed. To determine how much kelp tissue was lost due to natural deterioration, an experimental control where kelp was added to a cage without urchins was established. This revealed that loss due to deterioration over the course of the feeding experiments was negligible. Therefore, kelp tissue loss due to consumption was determined as grams of kelp consumed urchin⁻¹ day⁻¹.

At the end of each three-month experiment, all urchins were weighed and dissected in order to examine their gonad tissue. Gonadal indices (GI) were calculated as the ratio of total gonad tissue wet weight to total body wet weight and expressed as a percentage. The middle third of gonad tissue was then taken from each urchin and used for histological analysis in order to determine its gametogenic stage. Each gonad tissue sample was fixed in 10% buffered formalin for 4 weeks. The tissue samples were then embedded in paraffin, cut into 7 μm sections using a microtome (Microm HM 355, Waldorff, Germany), stained with hematoxylin and eosin and mounted on glass microscope slides. The slides were examined under a compound microscope at both 10 \times and 40 \times magnification, and the gonads classified into one of the six stages of gametogenesis (Fuji 1960). The numbers of urchins in each stage of gametogenesis were compared among feeding treatments for each experiment using separate Goodman–Kruskal Gamma tests (Chen and Kianifard 1999). Males and females were grouped together in order to increase sample sizes for statistical comparison. For statistical analysis, the six stages of gametogenesis presented by Fuji (1960) were reduced to four groups based on similarities in gamete development as follows: Stage 1—gonads were pre-gametogenic and had only nutritional buildup, Stages 2 and 3 (combined)—gonads had immature gametes, Stages 4 and 5 (combined)—gonads had mature gametes, and Stage 6 gonads were post-spawn with no gametes left (Appendix 1 in ESM).

All statistical analyses were carried out using Systat (version 12). Prior to testing, all data were evaluated for homogeneity of variances and normality. Variation in feeding rates (g kelp urchin⁻¹ day⁻¹) among seasons and feeding treatments was analyzed using an ANCOVA, with season as a categorical factor and food treatment as the covariate. Because the feeding rate \times season interaction was significant (see “Results”), three separate linear regressions were used to analyze the relationship between g kelp urchin⁻¹ day⁻¹ and food treatment for each seasonal experiment. To examine how food availability affected total amount of gonad tissue in the urchins, the average GI was calculated for each feeding treatment and compared among seasons using an ANCOVA, with season as the categorical factor and food treatment as the covariate.

Results

Both giant kelp and drift algae were abundant in the Point Loma kelp forest throughout the study (C. Dodge pers. obs.). All urchins collected at the beginning of each experiment had algae in their guts suggesting that the urchins used in our experiment were not food limited prior to the start of the seasonal experiments. Following this, the urchins were starved for 2 weeks and then assigned to the different feeding treatments. With the exception of one treatment (urchins fed 4 days week⁻¹) in the Summer experiment when all urchins died due to unknown reasons, urchins were observed consuming kelp when fed. In general, consumption rates were negatively related to food availability though this relationship varied significantly among the three seasons (ANCOVA, season \times feeding rate interaction; $F_{(2,14)} = 5.27$, $P = 0.02$). Consequently, the relationships between consumption rates and feeding rates were assessed within each season separately using independent regressions. This revealed a negative relationship between consumption rates and the number of times the urchins were fed per week in both the Fall ($P = 0.026$) and Spring ($P = 0.001$) experiments, though the effect of feeding rates on consumption rates was greater in the Fall (slope = -0.670 , $r^2 = 0.75$) than in the Spring (slope = -0.39 , $r^2 = 0.91$) (Fig. 1). In contrast, consumption rates were not impacted by food treatment in the Summer ($P = 0.58$), as all urchins ate at similar rates regardless of the number of times they were fed per week.

Overall, although there was a general trend in which the urchins in the Fall experiment had higher GI's than those in either the Spring or Summer experiments (Fig. 2), urchin GIs did not vary significantly among the three seasons (ANCOVA, $F_{(2,15)} = 2.25$, $P = 0.14$). GIs were positively

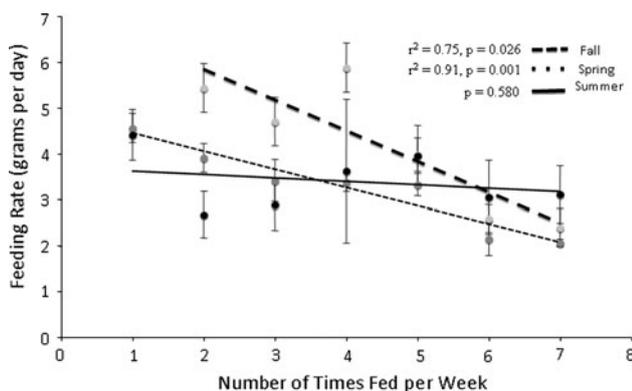


Fig. 1 Relationship between food availability (number of times fed per week) and *S. purpuratus* feeding rates (grams of kelp consumed per day) for all three seasonal experiments (Fall $n = 29$, Spring $n = 71$, Summer $n = 40$). Feeding rates vary significantly depending on how often urchins are fed during Fall and Spring experiments. During Summer, there was no effect of food availability on feeding rates

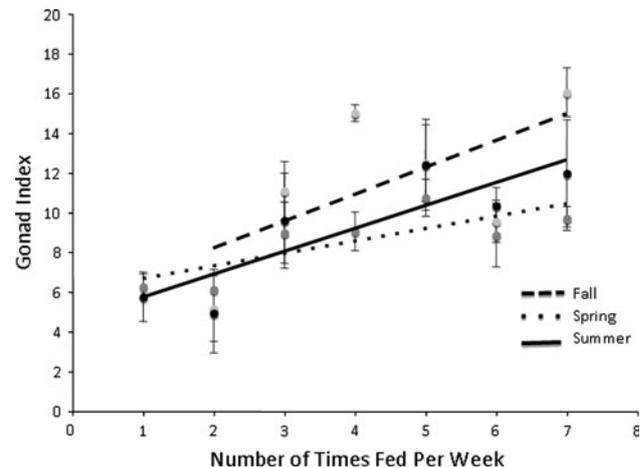


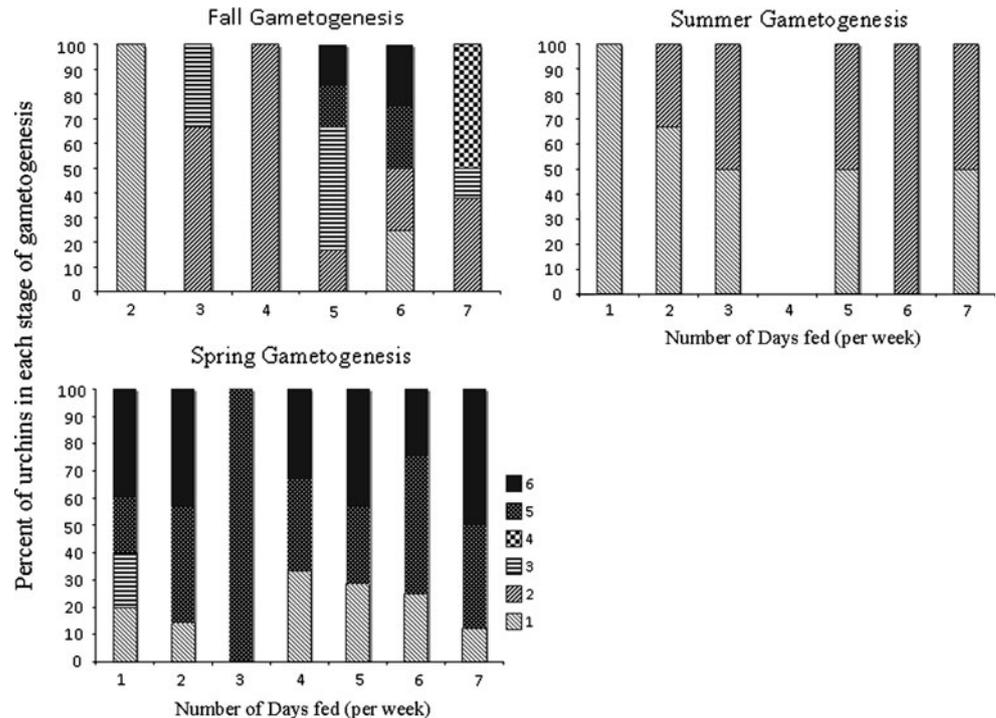
Fig. 2 Relationship between food availability (number of times fed per week) and *S. purpuratus* gonad index at the end of each of the three seasonal experiments (Fall $n = 29$, Spring $n = 71$, Summer $n = 40$). Gonad index is positively correlated with increasing food availability in all three experiments

influenced by food availability in each season (ANCOVA, $F_{(1,15)} = 15.32$, $P = 0.001$), though this relationship did not vary among the three seasons (ANCOVA, season \times feeding rate interaction, $P = 0.528$, $F_{(2,3)} = 0.14$) (Fig. 2). Similarly, food availability had a significant positive effect on gamete development in both the Fall and Summer experiments, with the gonads of urchins fed more often per week generally being in later stages of gametogenesis than those fed less often per week (Goodman–Kruskal Gamma tests, Fall, $\gamma = 0.88$, $P < 0.001$, Summer, $\gamma = 0.65$, $P = 0.012$, Fig. 3). Food availability had a greater effect on gonad development in the Fall when urchins fed only twice per week lacked any developing gametes, only NPs (Stage 1), while those fed three times per week had immature gametes (Stages 2 and 3), and those fed four to seven times per week had mature gametes or had begun to spawn (Stages 4, 5 and 6) (Appendix 1 in ESM). During the Summer, although there were no mature gametes observed in any of the feeding treatments, urchins that were fed more often tended to have more individuals in the beginning stage of gametogenesis (Stage 2), while urchins fed less often were less likely to have begun gametogenesis and remained in Stage 1. In contrast, there were no significant effects of food availability on gamete development in the Spring experiment ($\gamma = 0.048$, $P = 0.843$) when all urchins had mature gametes or were partially spawned (Stages 4 and 5) regardless of food availability.

Discussion

Our experiments show that food availability plays a strong role in determining both the feeding rate and the

Fig. 3 Gametogenic stage of urchins in all three seasonal experiments (Fall $n = 29$, Spring $n = 71$, Summer $n = 40$) for all seven feeding treatments. Food limitation delayed gametogenesis and caused differences between treatments in terms of maturation in Fall and Summer experiments. There was no difference between treatments in Spring



reproductive status of purple urchins, *S. purpuratus*. Urchin gonad mass (GI) was positively influenced by increased food availability, which is consistent with results reported for urchin species in other parts of the world; e.g., *S. franciscanus* in the San Juan Islands (e.g., Vadas 1977), *S. droebachiensis* along the coast of Nova Scotia (Thompson 1982; Minor and Scheibling 1997; Walker and Lesser 1998; Meidel and Scheibling 1999; Garrido and Barber 2001), *Paracentrotus lividus* along the coasts of Ireland and Israel (Byrne 1990; Shpigel et al. 2004, respectively) and *Sphaerechinus granularis* along the coast of France (Guillou and Lumingas 1999), as well as *S. purpuratus* along the west coast of North America (reviewed by Lawrence 2007). This is also consistent with observations from the Aleutian Islands describing *S. droebachiensis* in barren grounds as having significantly smaller gonads than those inside dense kelp stands just a few meters away (e.g., Konar and Estes 2003) and with *S. purpuratus* in habitats of varying food availability exhibiting corresponding patterns of reproduction (Ebert 1968). If urchins in barren grounds are unable to access food during critical periods, gametogenesis will likely be reduced and conventional gonad indices may be a poor indicator of actual reproductive status in different habitats (e.g., Ling and Johnson 2009). In contrast, if these urchins are able to take advantage of periodic influxes of drift algae, this may be disproportionately important for their reproduction (e.g., Britton-Simmons et al. 2009). However, while food availability may be essential to initiating gametogenesis, other factors such as temperature and photoperiod are likely

critical in determining both the timing and overall fecundity of the individuals (Walker and Lesser 1998; Byrne 1990; Lawrence 2007). Abundant food in times when the urchins are not normally releasing gametes may result in out-of-season reproduction and may explain why some urchins (e.g., *S. droebachiensis*) lack annual reproductive cycles when kept in laboratory mesocosms and fed regularly (Shpigel et al. 2004).

While urchin gonad mass may be useful for assessing relative levels of overall gonad growth, it does not provide sufficient information on the type of gonad tissue present or its developmental state (Gonor 1972; Beninger 1987; Barber and Blake 1991; Garrido and Barber 2001). In contrast, histological analysis of their gonad tissue provides more detailed information on gonad development and thus a better measure of reproductive status. In our study, histological analysis of urchin gonads indicated when purple urchins were food limited relative to their annual reproductive cycle, and this may be far more important to reproduction than food availability alone. Specifically, urchins that were experimentally food limited during the early stages of their reproductive cycle (i.e., our Fall and Summer experiments) had small gonads (low GIs), remained in earlier stages of gametogenesis, and did not produce viable gametes. In contrast, when urchins were not food limited during the early stages of their reproductive cycle, but instead were food limited after gametogenesis had already begun (i.e., our Spring experiment), they still produced viable gametes. Food availability during the later stages of their reproductive cycle then affected only gonad

mass and gamete number, not whether or not gametes were produced. This suggests that these urchins have “fixed” development (sensu Wilbur and Collins 1973), as production of viable gametes appears to be most strongly controlled by food availability early in their reproductive cycle. In the case of *S. purpuratus* in Point Loma, California, adequate food resources in the Summer and Fall are needed to begin gametogenesis and to produce mature gametes for spawning in the Spring. Interestingly, this timing coincides with the highest annual abundances of drift algae due to senescence of *Macrocystis pyrifera* and low water motion, which result in high levels of drift accumulation on the forest floor (Harrold and Reed 1985).

In addition to impacting gonad development, urchins can respond to variability in food supply by changing their feeding rates once food is available. Our results show that urchins that were food limited generally consumed algae more quickly once that food was available than urchins that were not food limited. This is consistent with other studies examining the effects of high versus low food availability on feeding rates in *S. droebachiensis* (e.g., Minor and Scheibling 1997) and with field observations that urchins had higher grazing rates on drift algae experimentally added to urchin barren grounds relative to those in established kelp forests (e.g., Estes et al. 1998). However, our results also show that feeding rates vary with intermediate levels of food availability and that the nature of this relationship itself varies according to the season. Specifically, during the Fall, food availability strongly influenced feeding rates as urchins that were fed less often consumed food more rapidly once it was captured than urchins fed more often. A similar but weaker relationship was observed in Spring, but no effect of food availability on feeding rates was observed in the Summer. Possible explanations for this are that nutritional requirements in purple urchins may vary seasonally with their reproductive cycle as observed in *S. droebachiensis* (Vadas 1977; Meidel and Scheibling 1999; McBride et al. 2004) or that purple urchin gut size itself varies seasonally as observed by Lawrence et al. (1965). In addition, feeding rates may increase when gonads are post-spawn or during early stages of gametogenesis when nutritional demands for gonad development are highest, as has been observed in red urchins, *S. franciscanus* (e.g., McBride et al. 1997, 2004). Regardless of the underlying causation, our results indicate that feeding rates in purple urchins respond to food availability strongly in the Fall when the urchins are in their early stages of development, only weakly in the Spring when the urchins are in their late stages of development, and not in the Summer when urchins are in post-spawning condition.

In conclusion, our study supports previous work showing that urchins exhibit a strong degree of plasticity in

reproduction and feeding rates in response to food availability (e.g., Guillou and Lumingas 1999). While this may be an important adaptation to surviving in environments where food availability is highly variable, it is also important for commercially harvested species where markets prefer gonads that are not only near maximum mass, but that are also comprised mainly of NPs (Lawrence 2007). Thus, how food availability impacts gonad development can be of paramount importance not only to patterns of urchin reproduction, but also to their viability as a fisheries species.

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