

REPRODUCTIVE TACTICS OF CALIFORNIA HALIBUT (*PARALICHTHYS CALIFORNICUS*): COMBINING SPAWNING SEASON, INTERSPAUNING INTERVAL, AND BATCH FECUNDITY TO ESTIMATE ANNUAL REPRODUCTIVE OUTPUT FOR A MULTIPLE-BATCH SPAWNING FISH

CHERYL L. BARNES

Moss Landing Marine Laboratories
8272 Moss Landing Road
Moss Landing, CA 95039
ph: (831) 334-3484
cheryl.barnes@alaska.edu

RICHARD M. STARR

Moss Landing Marine Laboratories
8272 Moss Landing Road
Moss Landing, CA 95039
starr@mlml.calstate.edu

ABSTRACT

Baseline reproductive information is crucial to identifying species responses to spatiotemporal variation and changing environmental conditions. We collected 205 central California halibut (2012 and 2013) to better understand the reproductive tactics of a batch spawner with indeterminate fecundity. We used histology to identify subphases of actively spawning fish, approximated spawning duration based on weekly proportions of reproductive females, calculated daily spawning fractions to estimate interspawning intervals, and quantified batch fecundity using the hydrated oocyte method. The spawning season lasted approximately 10 weeks. Interspawning intervals were 1.3 to 2.7 d, depending upon the spawning marker (i.e., hydrated oocytes or POFs) used. Mean batch fecundity for fish in the late hydration subphase of spawning was $597,445 \pm 318,419$ eggs, resulting in annual fecundities that ranged from 5.2×10^6 to 8.1×10^7 eggs per fish. These findings provide a preliminary assessment of reproductive output for California halibut and foundation data for future spatiotemporal analyses.

INTRODUCTION

The need to assess variation in reproductive characteristics across size and age classes (e.g., Fitzhugh et al. 2012), at several spatial and temporal scales (e.g., Ganas et al. 2004; Lowerre-Barbieri et al. 2011), and under different environmental conditions (e.g., Pecquerie et al. 2009) has been thoroughly conveyed in the scientific literature. However, we still lack basic information about the reproductive biology of many species, thus preventing more extensive investigations into the mechanistic relationships among specific reproductive tactics and demographic, spatiotemporal, or environmental factors. A poor understanding about how one generation is connected to the next is especially problematic for species targeted in commercial and recreational fisheries because changes in reproductive output are amplified by size-selective fishing (Trippel et al. 1997; Wright and Trippel 2009).

California halibut (*Paralichthys californicus*) has long been valued in commercial and recreational fisheries

along the west coast of North America (Frey 1971). Although a number of researchers have assessed variation in life history traits of California halibut (e.g., multiple studies in Haugen 1990; MacNair et al. 2001; Barnes et al. 2015), relatively few have reported information about the reproductive characteristics of wild-caught fish. Macroscopic assessments of California halibut ovaries have indicated that 50% of females reach sexual maturity by 47 cm (4.0 yr) off southern California (Love and Brooks 1990), whereas 50% of females reach sexual maturity by 62.8 cm (4.9 yr) off central California (Lesyna and Barnes 2016). Pelagic eggs are found year-round off the coasts of southern California and Mexico, with peak spawning taking place nearshore in spring and early summer (Haaker 1975; Lavenberg et al. 1986; Allen 1988; Barnes et al. 2015). Changes in mean gonadosomatic index suggest peak spawning in midsummer north of Point Conception (Barnes et al. 2015).

California halibut are batch spawners that exhibit indeterminate fecundity and undergo asynchronous ovarian development (Caddell et al. 1990; Murua and Saborido-Rey 2003; Lesyna and Barnes 2016). A study of captive females held under environmental conditions typical for southern California indicated interspawning intervals (i.e., the time elapsed between individual spawning events) between 7 and 14 d. Spawning frequencies from that study were 12 to 13 times per year and batch fecundity (i.e., the number of eggs produced per female per spawning event) ranged from 455,000 to 589,000 eggs (Caddell et al. 1990). This equated to a mean annual fecundity of 5.5×10^6 to 7.7×10^6 eggs per female.

The primary objective of our study was to estimate annual fecundity for California halibut found north of Point Conception. To do so, we quantified the duration of the spawning season, daily spawning fraction (S), interspawning interval (ISI), spawning frequency (F), and batch fecundity of wild-caught fish. We also identified subphases of actively spawning females to more accurately estimate batch fecundity using an opportunistic sampling design. Our goal was to provide a preliminary assessment of the reproductive output of California halibut, establish baseline data for future demographic or

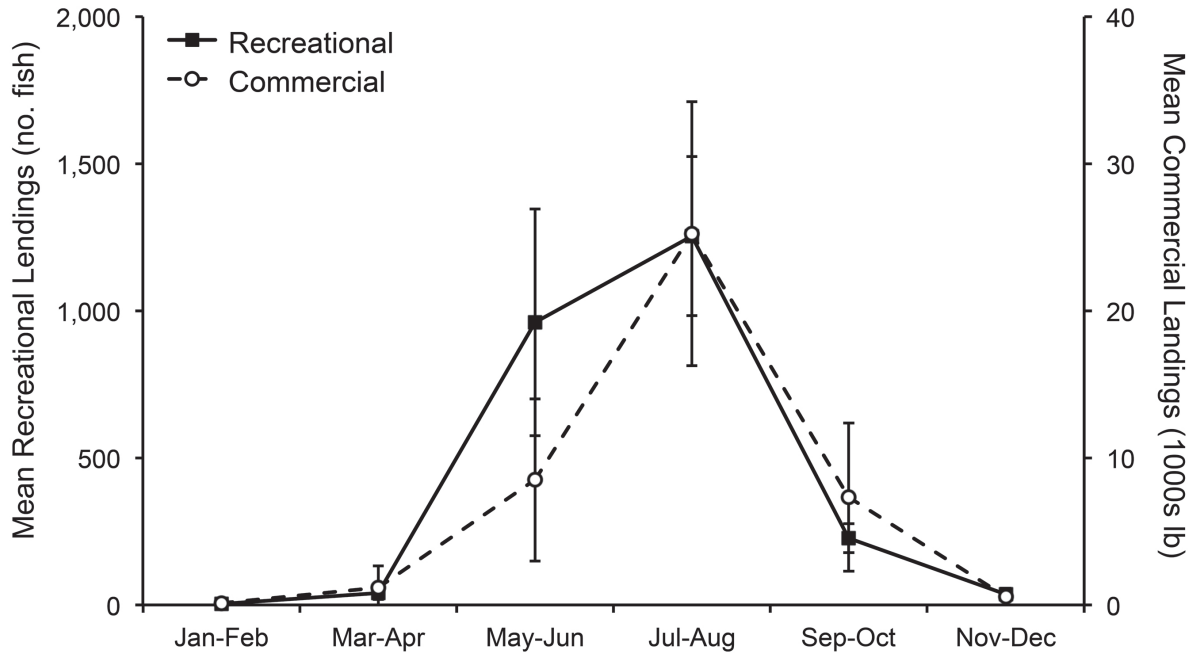


Figure 1. Bimonthly mean landings of California halibut for Santa Cruz, Monterey, and San Luis Obispo counties (2004 to 2013). The solid line and filled squares represent recreational landings (numbers of fish). The dashed line and open circles represent commercial landings (1000s lb). Errors bars denote one standard error. Recreational landings data were obtained from the Recreational Fisheries Information Network (RecFIN, <https://www.recfin.org/>), which is managed by the Pacific States Marine Fisheries Commission. Summarized commercial landings data were provided by the California Department of Fish and Wildlife (CDFW, unpublished data).

spatiotemporal comparisons, and enhance our understanding about the reproductive biology of an economically important multiple-batch spawner with indeterminate fecundity.

METHODS

We collected adult California halibut females as filleted carcasses from commercial and recreational hook-and-line fishers, seafood processors, and spearfishers between late May and mid-September (2012 and 2013), when California halibut are known to reproduce near-shore (Love and Brooks 1990; Barnes et al. 2015). We also collected a few individuals in October and November of 2013. We were unable to sample during the winter months because landings from central California fisheries are consistently low from November to April (CDFW unpublished data, fig. 1). Sampled fish were caught in shallow (<40 m) coastal waters near five primary locations: Santa Cruz, Moss Landing, Monterey, Morro Bay, and Port San Luis (fig. 2). One additional female was caught near Half Moon Bay, approximately 50 miles north of Santa Cruz. In 2012, we sampled wharfs and harbors in and around Santa Cruz four to five times per week. All other locations were sampled two to three times per month. We also processed carcasses donated from port samplers and private anglers as they became available. In 2013, we sampled all sites two times per week from mid-May to September. All fish were placed

on ice immediately after filleting and kept cold until fully processed in the laboratory (typically within 12 hr; maximum 24 hr period).

We recorded capture date, location, pre-fillet fork length (FL, mm), and body weight (W, g). When samples were received as filleted carcasses, we recorded post-fillet fork lengths (mm) and converted to pre-fillet fork lengths (mm) using the linear relationship described by Barnes et al. (2015). We extracted and thin-sectioned sagittal otoliths to age fish following methods described by the Committee of Age-Reading Experts (CARE 2006). We preserved ovaries in 10% buffered formalin and removed prepared transverse sections for histological processing, which involved dehydrating the tissue, embedding it in paraffin wax, thin-sectioning and mounting it to a microscope slide, and staining it with hematoxylin and eosin (Luna 1968; Hunter and Macewicz 1980; Hunter and Macewicz 1985). We identified stages of ovarian development as developing, spawning capable, actively spawning, regressing (i.e., spent), or regenerating (i.e., resting) according to histological characteristics described by Lesyna and Barnes (2016). We further classified actively spawning fish into subphases based on the two most advanced stages of oocyte development (MAS₁ and MAS₂) and the incidence and relative ages of postovulatory follicles (POFs), which are spawning markers that denote the recent release of an egg. Oocyte developmental stages used to categorize actively spawning

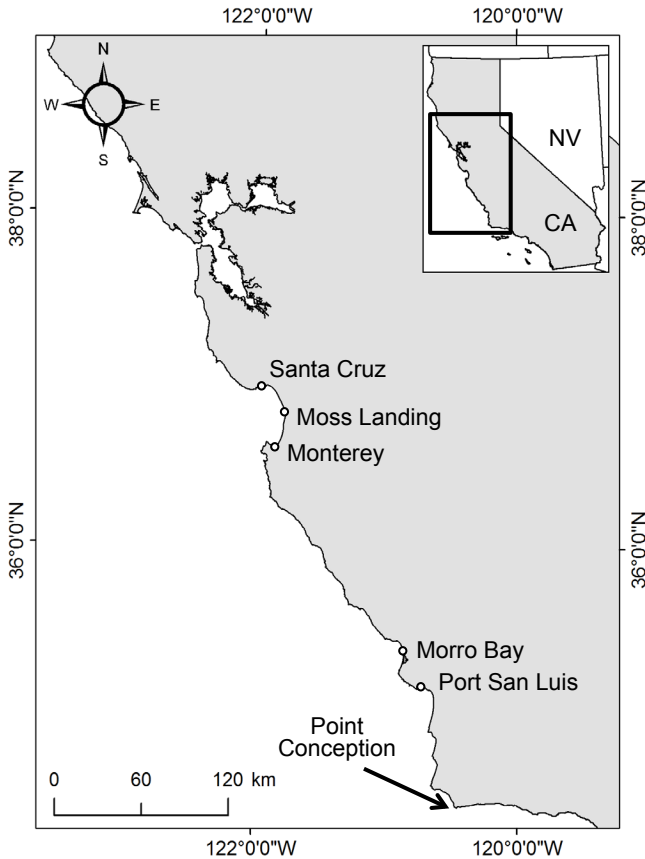


Figure 2. Primary locations used to sample adult California halibut females from commercial and recreational fisheries (2012 and 2013).

subphases (in order from least to most developed) were cortical alveoli (CA), yolk granule (YG; all vitellogenic substages), final maturation (FM; also described as germinal vesicle migration, yolk coalescence, and germinal vesicle breakdown), and hydrated (HD) (fig. 3). Because exact ages of POFs remain unknown for California halibut, we assigned relative POF ages based on descriptions for northern anchovy (*Engraulis mordax*), another batch spawning species that releases pelagic eggs and occupies similar latitudes (Hunter and Goldberg 1980; Hunter and Macewicz 1985; fig. 3). We categorized POFs as “new” and assumed that they indicated spawning activity within 24 hours of capture if they were relatively large, irregularly shaped, and showed little or no signs of degradation (e.g., expansive lumen, clearly recognizable and intact granulosa epithelial layer). We identified POFs as “old”, representing a spawning event that had taken place more than 24 hours prior to capture, if they appeared shrunken with a narrowed lumen and degraded granulosa.

Spawning Season and Daily Spawning Fraction

We defined the duration of the spawning season as the number of consecutive weeks in which two-thirds of our samples were identified as spawning capable (i.e.,

fish possessing tertiary vitellogenic oocytes) or actively spawning (i.e., those possessing hydrated oocytes and/or POFs of any age). We calculated daily spawning fraction (S) based on the proportion of females containing 1) hydrated oocytes and 2) new POFs. Calculating two S estimates allowed us to assess the extent to which this reproductive metric may vary based on the specific spawning marker used. For populations with low spawning synchronicity and/or broad spawning seasons, it is common to apply a correction to daily spawning fractions using the equation: $S = 24 * S/D$, where D is the duration (hr) of the spawning marker (Hunter and Macewicz 1985; Murua et al. 2003; Kurita et al. 2011; Lowerre-Barbieri et al. 2011). Additionally, spawning marker durations are known to vary with temperature (e.g., Ganas et al. 2007a; Kurita et al. 2011). Without information about the duration of spawning markers for California halibut, we assumed temperature-dependent relationships developed for Japanese flounder, *Paralichthys olivaceus* (Kurita et al. 2011). Like California halibut, Japanese flounder are multiple-batch spawners that exhibit indeterminate fecundity. They also experience temperatures similar to central California halibut and display comparable spawning seasons. Thus, we used the following relationships to estimate temperature-dependent durations of spawning markers for California halibut: $D = 59.4 * e^{-0.122T}$ for hydrated oocytes and $D = 62.9 * e^{-0.118T}$ for new POFs (Kurita et al. 2011), where T was mean daily sea surface temperature ($^{\circ}\text{C}$) for each capture date. Sea surface temperatures were obtained from the National Oceanic and Atmospheric Administration’s National Data Buoy Center (Station 46114; <https://www.ndbc.noaa.gov/>). Bottom temperature data were not available for the dates and locations of our samples. Using temperature-dependent durations for each spawning marker, we calculated corrected S for all days in which we collected three or more fish. We estimated interspawning interval (ISI), which represents the number of days between spawning events, by taking the reciprocal of \bar{S} (Wootton et al. 1978; Murua et al. 2003; Lowerre-Barbieri et al. 2011). Finally, we calculated spawning frequency (F), defined as the number of spawning events per female per season, by dividing the duration of the spawning season by ISI . Due to sample size limitations in 2012, spawning season, S , ISI , and F were estimated for 2013 only.

Batch Fecundity

For species with indeterminate fecundity, the number of eggs produced is not fixed prior to the onset of spawning (Hunter et al. 1985, Hunter et al. 1992, and Ganas 2013). Instead, primary growth oocytes continue to be recruited to the supply of secondary growth oocytes throughout the spawning season. Therefore, the

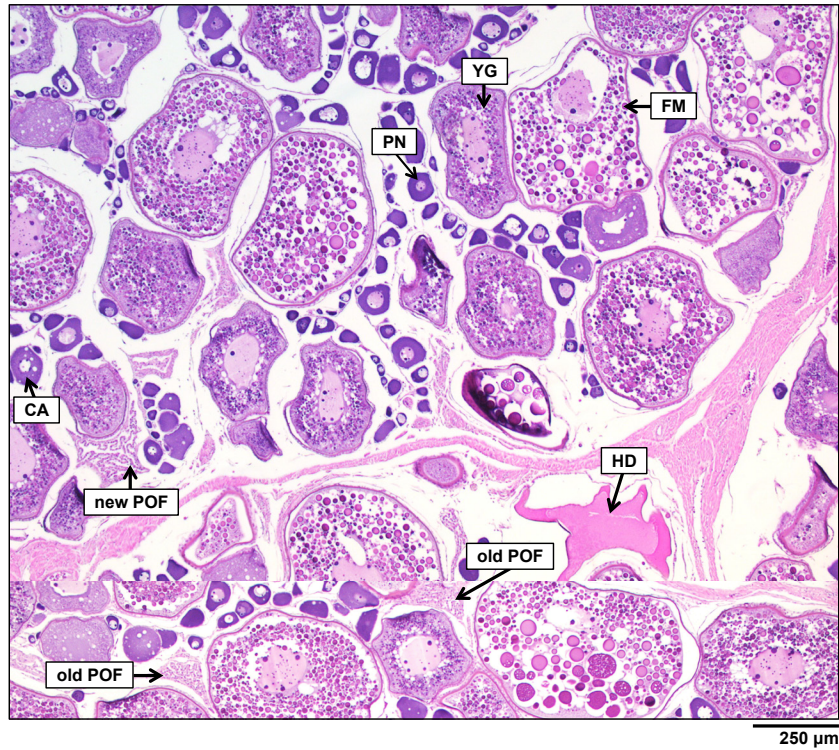


Figure 3. Oocyte developmental stages for an actively spawning California halibut female (PN: perinucleolar; CA: cortical alveoli; YG: yolk granule (includes all substages of vitellogenesis); FM: final maturation (including germinal vesicle migration, yolk coalescence, and germinal vesicle breakdown substages); HD: hydrated). Postovulatory follicles (POFs, new and old) are also indicated.

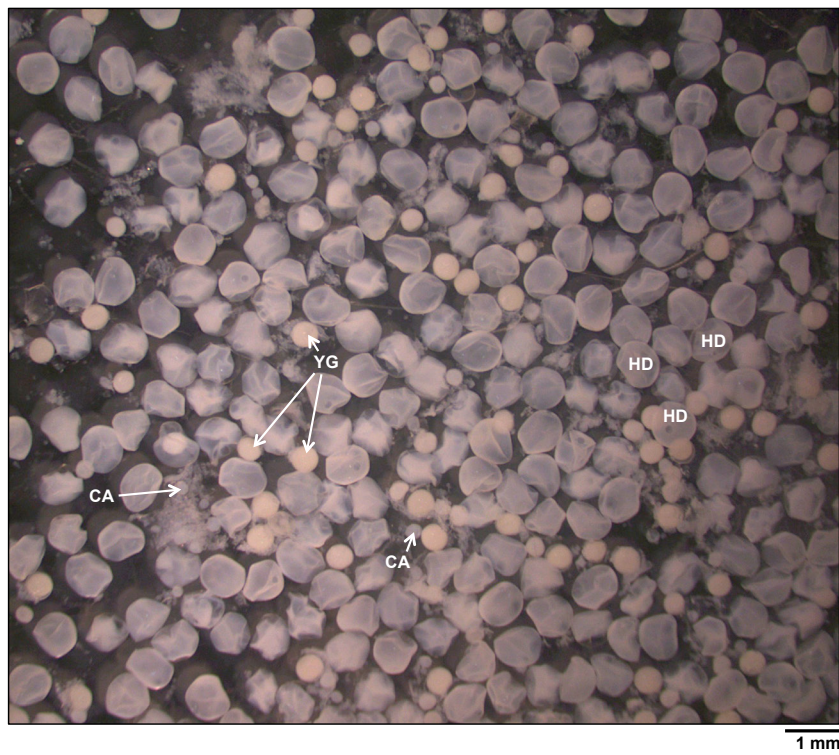


Figure 4. Whole mount image of preserved ovarian tissue from a California halibut female in the late hydration subphase of spawning. Oocyte developmental stages (CA: cortical alveoli; YG: yolk granule (includes all substages of vitellogenesis); HD: hydrated) were identified based on characteristics (e.g., relative size, coloration) observed during histological analyses. There is no final maturation (FM) stage for the late hydration subphase.

TABLE 1
Criteria used to identify subphases of actively spawning California halibut females. The most advanced stage (MAS₁) and second most stage (MAS₂) of oocyte development are listed, along with the incidence and relative age of postovulatory follicles (POFs; NP = not present) and sample sizes (n). Oocyte developmental stages, in order from least to most advanced, are cortical alveoli (CA), yolk granule (YG), final maturation (FM), and hydrated (HD).

Actively Spawning Subphase	MAS ₁	MAS ₂	POF	n
Early Hydration	HD	FM	NP	6
Late Hydration	HD	YG	NP	17
Spawning in Progress	HD	FM or YG	New	16
Recently Spawning	FM or YG	YG or CA	New or Old	1

potential annual fecundity for an individual is a product of the spawning frequency and number of eggs released per spawning event (i.e., batch fecundity). When viewing whole mounts, it can be difficult to differentiate types of secondary growth oocytes that make up distinct batches, especially when there are no clear differences in mean oocyte diameter (Lesyna and Barnes 2016). Thus, we counted only hydrated oocytes from whole mount samples because they were easily distinguishable from earlier stages of oocyte development based upon their large size, translucent color, irregular shape, and obvious presence of an oil globule (fig. 4).

We estimated batch fecundity for actively spawning California halibut using gravimetric and hydrated oocyte methods (Bagenal 1978; Hunter and Goldberg 1980; Hunter et al. 1985). We blotted and weighed ovaries. We then separated ovarian tissue from the ovarian wall, weighed the ovarian wall (0.1 g), and subtracted its mass from that of the preserved ovary. Doing so yielded a more accurate measure of total ovarian tissue (g), from which we removed five subsamples (0.3 to 0.5 g). We counted the number of hydrated oocytes in each subsample and multiplied mean egg density (number of eggs per gram) by the total ovarian tissue mass to estimate absolute batch fecundity (Hunter and Goldberg 1980; Macewicz and Hunter 1993). We then divided absolute batch fecundity by somatic body weight (i.e., total body weight minus ovary mass) to estimate relative batch fecundity. This procedure for estimating batch fecundity was suitable for the ovaries (n = 14) that contained a thorough mixture of all oocyte developmental stages. However, some females (n = 26) exhibited an accumulation of hydrated eggs in the oviduct and/or ovarian lumen. This resulted in at least one section of the ovary that was made up exclusively of hydrated eggs and another that consisted of an assortment of all developmental stages. To appropriately subsample these fish, we separated “hydrated-only” sections from the remaining ovarian tissue. We then subsampled “hydrated-only” and

mixed oocyte sections as previously described. Mean egg densities for each section were multiplied by their respective total masses and then added together to estimate batch fecundity for these fish, which were captured after spawning had already been initiated. Finally, we quantified the log-linear relationship between batch fecundity and fork length and used an analysis of variance (ANOVA) to test for differences in mean batch fecundity by age and year (v3.4.2, R Core Team 2017). We did not have sufficient data to test the relationship between body weight and batch fecundity.

Annual Fecundity

We calculated both absolute and relative annual fecundity for central California halibut. Each estimate involved multiplying batch fecundity by F, which varied based on the spawning marker used to calculate S and ISI (Murua et al. 2003).

RESULTS

We collected a total of 205 California halibut females between 2012 and 2013. Sampling efforts resulted in the collection of 40 fish on 31 different days in 2012 and 165 fish on 57 different days in 2013. Fork lengths measured from 532 to 1110 mm (848 ± 105 SD), ages ranged from 3 to 19 yr (8.2 ± 2.2 SD), and capture depths were all less than 40 m (16 ± 6 SD). Actively spawning females (all subphases) were collected at depths of 18.1 ± 5.6 (SD) m. We conducted histological analyses on all samples, but four fish could not be aged due to missing or unreadable otoliths. We identified four subphases of actively spawning fish: “early hydration”, “late hydration”, “spawning in progress”, and “recently spawned” (table 1). Ovaries with both hydrated eggs and oocytes in the final maturation stage of development (FM or germinal vesicle migration [GVM]) were identified as being in the early hydration subphase at the time of capture. We classified fish as being in the late hydration subphase once all FM oocytes had begun to hydrate, resulting in yolk granule as the second most advanced stage of oocyte development. Ovaries in early and late hydration subphases did not possess POFs. New POFs were only observed in spawning in progress and recently spawned fish. Those with both hydrated oocytes and new POFs were termed spawning in progress. As soon as hydrated oocytes were no longer detected, but new and/or old POFs remained, fish were categorized as having recently spawned.

Spawning Season and Daily Spawning Fraction

We collected three or more adult females on only one sampling day in 2012; therefore, we were unable to calculate reproductive metrics for that year. In 2013, We collected three or more fish on 26 different days. More

TABLE 2
 Numbers of adult California halibut females sampled, by reproductive phase and week (2013 only).
 Sample sizes (n) and weekly portions of spawning fish (i.e., spawning capable and actively spawning phases) are also listed.
 The area in gray represents the supposed duration of the summer spawning season.

Week	Developing	Spawning Capable	Actively Spawning	Regressing	Regenerating	n	Proportion Spawning
23		1				1	
24	1	1			1	3	0.33
25	1		4			5	0.80
26		2	3			5	1.00
27	1	5	3	1		10	0.80
28		11	2			13	1.00
29	1	11	5			17	0.94
30	1	8	5			14	0.93
31	2	13	9			24	0.92
32	2	9	8			19	0.89
33		12	5			17	1.00
34	1	3	2		1	7	0.71
35	1	7	9	2		19	0.84
36	1	3				4	0.75
37							
39							
40							
41	2	1		2		5	0.20
42							
43					1	1	
44							
45							
46							
47			1			1	

than two-thirds of fish sampled every week between June 22 and September 2 were identified as spawning capable or actively spawning (table 2). Thus, we supposed that the spawning season lasted approximately 10 weeks in 2013. However, considerably low catches in both commercial and recreational fisheries restricted our ability to sample prior to mid-June (n = 4) and after the first week of September (n = 7) (fig. 1). Mean *S* based on proportions of fish with hydrated oocytes was 0.78 ± 0.63 , whereas *S* based on proportions of fish with new POFs equaled 0.38 ± 0.37 (n = 25) (Supplementary tables 1 and 2). Thus, *ISI* estimates ($1/S$) were 1.28 d and 2.65 d using hydrated oocytes and new POFs as spawning markers, respectively. When dividing the duration of the spawning season by *ISI*, we estimated mean *F* to be between 26.4 (hydrated oocytes) and 54.9 (new POFs) batches per female per season.

We assessed biweekly proportions of each reproductive phase in 2013 (n = 14 [165 fish]) and found that proportions of actively spawning females were relatively constant (0.36 ± 0.07 SD) throughout the summer (fig 5). Spawning capable (0.53 ± 0.33 SD) and developing (0.11 ± 0.13 SD) fish were present throughout the sampling period, but proportions of these fish displayed greater variation through time. We encountered few regenerating females (i.e., resting) throughout the study period. Females in the regenerating phase were found in mid-June, at the end of August, and in mid-October.

Two-thirds of these occurrences were outside of what we considered to be the summer spawning season. We also observed a relatively large proportion of regressing (i.e., spent) females in early fall (0.40 at the end of September). Although sample sizes were limited, decreased landings of California halibut in nearshore waters, combined with increased proportions of regressing individuals, suggests a cessation of spawning activity in September and October. Small proportions of regressing and regenerating individuals were found within the spawning season identified (mid to late June and mid-August), suggesting some degree of asynchronicity in spawning activity among individual California halibut.

Batch Fecundity

We initially estimated batch fecundity for 40 actively spawning California halibut females (8 from 2012 and 32 from 2013) measuring 680 to 924 mm fork length (table 3). Of all four actively spawning subphases, we found that the late hydration subphase accounted for the greatest minimum (198,608), mean ($597,445 \pm 318,419$ SD; n = 17) and maximum (1,474,584) estimates of batch fecundity. We considered this particular spawning subphase to be the ideal target for assessing reproductive output of California halibut because ovaries in the late hydration subphase would possess a complete batch of eggs that had fully hydrated, but had not yet been released. This was evidenced by the presence of hydrated

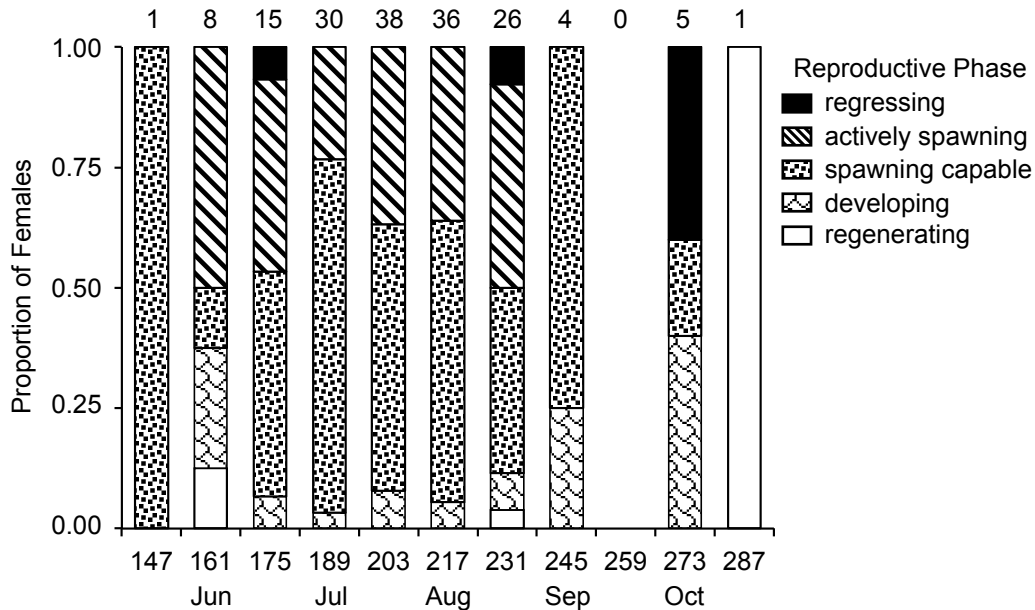


Figure 5. Biweekly proportions of California halibut, by reproductive phase and Julian day (2013 only). Sample sizes are indicated above each bar and the approximate starts of each month are also shown. One additional mature fish was sampled in late November (not shown).

oocytes, absence of the next most advanced stage of oocyte development (i.e., FM), and lack of POFs. Batch fecundity for females in the early hydration subphase would be underestimated because only a portion of the complete spawning batch of eggs would have been hydrated at the time of capture (i.e., FM oocytes would eventually hydrate and be released along with co-occurring HD oocytes). Batch fecundity would also be underestimated for females found to be spawning-in-progress given the prevalence of spawning markers (i.e., new and old POFs), which signify the partial release of HD oocytes—either through spawning or handling. Recently spawned fish would possess POFs, but no hydrated eggs with which to estimate batch fecundity.

We found a log-linear relationship between fork length and batch fecundity ($\log BF = 5.91(\log FL) - 26.63$; $R_{adj} = 0.429$, $F_{0.1(2), 1,15} = 13.03$, $p < 0.01$) for females captured in the late hydration subphase of spawning (fig. 6A). An ANOVA indicated that there were no signifi-

cant differences in batch fecundity by age ($F_{0.1(6), 1,14} = 0.86$, $p = 0.37$). This was due to substantial variability in batch fecundity and because all females in the late hydration subphase were between 6 and 9 yr of age (fig. 6B). There was no difference in batch fecundity between 2012 and 2013 ($F_{0.1(2), 14} = 0.92$, $p = 0.36$). Thus, we pooled year-specific batch fecundity data for California halibut. Relative batch fecundity for fish in the late hydration subphase was 84 ± 46 (SD) eggs per gram ($n = 8$).

Annual Fecundity

We estimated absolute annual fecundity for central California halibut to be between 5.2×10^6 and 3.8×10^7 eggs per female per season (mean = $32,798,772 \pm 18,085,548$ SD) using new POFs as the spawning marker to calculate *S*, *ISI*, and *F*. Using hydrated oocytes as the designated spawning marker, the range for absolute annual fecundity was 1.1×10^7 to 8.1×10^7 eggs per female per season (mean = $15,504,874 \pm 8,549,532$ SD). Mean relative annual fecundity ranged from 867 to 4,226 eggs per gram ($2,036 \pm 1,125$ SD) using the new POF spawning marker and 1,835 to 8,940 eggs per gram ($4,307 \pm 2,380$ SD) using the hydrated oocyte spawning marker.

DISCUSSION

This study represents an initial investigation into various reproductive tactics of California halibut. Previous studies involved estimating length- and age-at-maturity (Love and Brooks 1990; Lesyna and Barnes 2016), dis-

TABLE 3
 Estimates of batch fecundity (number of eggs)
 for California halibut, by actively spawning subphase.
 Sample sizes (n) are also shown.

Actively Spawning Subphase	Min	Mean (\pm SD)	Max	n
Early Hydration	93,394	505,058 \pm 222,273	722,791	6
Late Hydration	198,608	597,445 \pm 318,419	1,474,584	17
Spawning in Progress	39,681	400,533 \pm 231,748	908,587	17
Recently Spawned	N/A	N/A	N/A	0
All Subphases	39,681	499,899 \pm 280,035	1,474,584	40

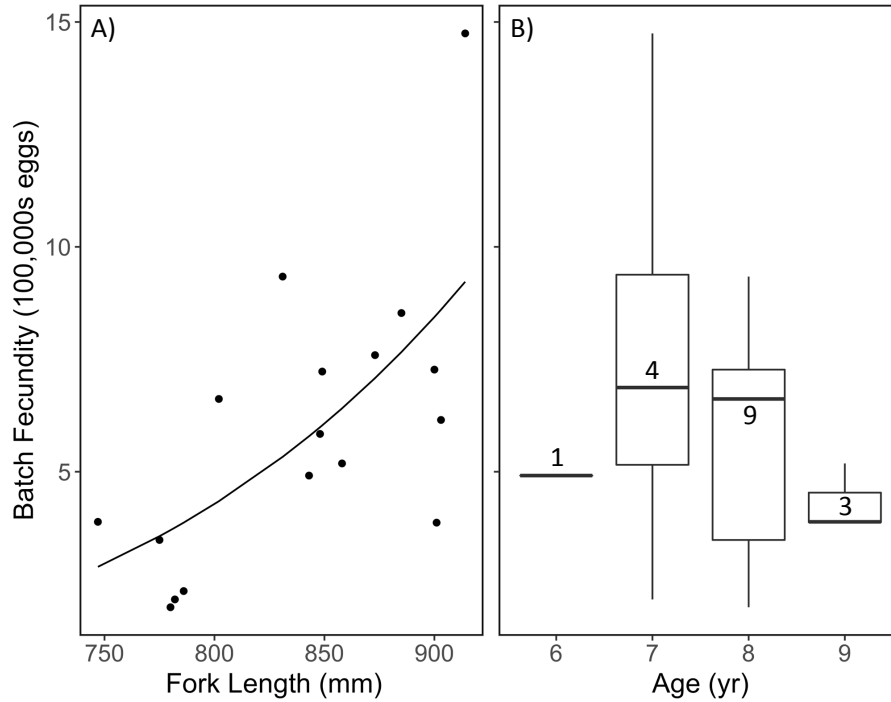


Figure 6. Estimates of batch fecundity (100,000s hydrated eggs) for California halibut captured in the late hydration subphase of spawning, by A) fork length (mm) and B) age (yr). The predicted log-linear relationship between fork length and batch fecundity is shown. Numbers indicate sample sizes for each age (yr).

cussions of spawning seasonality (Barnes et al. 2016), and measures of reproductive output from fish held in captivity. We combined estimates of spawning duration, S , ISI , F , and batch fecundity to assess annual reproductive output for this multiple-batch spawning species. Here, we have proposed an approximate spawning season of 10 weeks (June to September) for central California halibut. Mean S ranged from 0.38 to 0.78, depending upon the specific spawning marker (i.e., hydrated oocytes or new POFs). This resulted in variable estimates of ISI and F , which ranged from 1.3 to 2.7 d and 26 to 55 spawning batches per female per season, respectively. Even though we assessed a narrow range of sizes, we found that batch fecundity for California halibut in the late hydration subphase of spawning significantly increased with fork length. Mean batch fecundity was $597,445 \pm 318,419$ eggs per female (relative batch fecundity = 84 ± 46 eggs per gram). When we scaled batch fecundity by F , we found that annual fecundity for central California halibut ranged from 5.2×10^6 to 8.1×10^7 eggs per female per season. Each of these reproductive metrics are similar to those reported for other batch spawning species with indeterminate fecundity (e.g., spawning duration, Minami and Tanaka 1992; ISI , Lefebvre et al. 2016; relative batch fecundity, Almatar et al. 2004).

We postulated that the spawning season for central California halibut was relatively short and restricted to the summer months. We observed spawning capable and

actively spawning females from the end of June to the beginning of September. A study of captive fish from southern California showed spawning activity between February and mid-May and mid-May through September, depending upon water temperatures and photoperiod (Caddell et al. 1990). Love and Brooks (1990) also observed spring and summer spawning from analyzing fish catches in southern California, though the incidence of California halibut larvae during CalCOFI ichthyoplankton surveys suggests that spawning activity may occur year-round south of Point Conception (Barnes et al. 2015). We were unable to assess spawning activity for central California halibut in winter or spring because of considerably reduced or non-existent landings during this time. The apparent regional differences in spawning seasons may be due to the limited timeframe of our sampling. However, given that spawning seasons for other paralicthyid flatfishes become more protracted as latitude decreases (e.g., Minami and Tanaka 1992; Ganas et al. 2015), we believe it is plausible that central California halibut undergo shorter spawning durations relative to southern California conspecifics.

In addition to a potentially brief spawning season, we found fairly short $ISIs$. We estimated that, on average, wild-caught fish from central California spawned once every 1.3 to 2.7 d. Captive fish held under “natural conditions” in southern California were reported to spawn once every 7.0 to 14.0 d (Caddell et al. 1990; excluding

data from 1986 to 1987, when severe bacterial infections were found). We acknowledge that using proxies such as stage descriptions for POFs of northern anchovy (Hunter et al. 1985) and temperature-dependent spawning marker durations obtained from Japanese flounder (Kurita et al. 2011) may be inappropriate for California halibut due to different life history strategies, metabolic rates, and other unidentified factors that may lead to variable degradation rates. For instance, incorrectly assuming that oocyte hydration was completed within 24 hr or that “new” POFs were generated less than one day prior to capture would lead to artificially high estimates of S , deceptively short ISI , and overestimated F . We also do not yet understand which spawning marker is most appropriate for use in calculations of various reproductive metrics for California halibut. Finally, the use of sea surface temperature may impact our estimates of spawning marker duration for California halibut, which is generally considered a bottom-associated species. S , ISI , and F values reported here could be improved upon by detailed stage descriptions and temperature-dependent spawning marker durations that are specific to California halibut.

Although our ISI estimates were assumed to be constant throughout the proposed spawning season, this is unrealistic given the temporal changes in spawning activity reported for California halibut held in captivity. Caddell et al. (1990) found sporadic spawning at the start of each season, increased frequencies (i.e., to daily or once every other day) with increasing temperature and photoperiod, and noticeable decreases toward the end of the season (Caddell et al. 1990). In addition to assuming constant ISI through time, we necessarily made the assumption that spawning duration was equal among all fish. Yet individual spawning periods are often much shorter than the timeframe over which spawning activity is observed at the population level (Rijnsdorp et al. 2015). Given the temporal overlap among developing, spawning capable, and regressing females, we assert that there is some degree of asynchronicity in spawning duration for California halibut. While some fish may spawn from beginning to end, it is probable that a number of fish do not spawn until well into the season. A portion of the population may also enter the regressing phase before a particular season comes to a close (Kjesbu et al. 1996; Wright and Trippel 2009). Variations in spawning frequency and duration can be due to size, age, or local environmental conditions (Lambert 1990; Hutchings and Myers 1993; Trippel et al. 1997). For example, smaller (younger) individuals tend to exhibit shorter, more delayed spawning periods and less frequent spawning than larger (older) conspecifics (Ganias et al. 2007b; Klibansky and Scharf 2013; Lefebvre et al. 2016). These demographic effects on various reproductive metrics can substantially alter estimates of reproductive output

for individual fish, especially if population means (e.g., spawning duration, S , ISI , F) are extrapolated outside the range of sizes or ages sampled.

Another important consideration when assessing S , ISI , and F for central California halibut is the possibility that this population feeds and spawns nearshore during the summer and moves offshore or southward for the remainder of the year. We believe that these seasonal migrations are plausible based on limited commercial and recreational catches north of Point Conception in late fall, winter, and early spring. If central California halibut remain nearshore only to feed and spawn in summer, samples may have been obtained from spawning aggregations rather than mixed populations of spawning and non-spawning fish, which would inflate estimates of spawning activity. A year-round movement study would allow for an evaluation of our hypothesis that central California halibut undergo seasonal migrations. If paired with reproductive analyses, movement data could elucidate whether or not there is spatial separation between spawning and non-spawning fish and support or refute our assertion that spawning is restricted to the summer months off central California. Despite these caveats, however, our estimates of ISI fall well within the range of those reported for other flatfish species (typically 1 to 4 days; Rijnsdorp et al. 2015). Many paralichthyids, including Japanese flounder (*Paralichthys olivaceus*; Kurita et al. 2011), Pacific sanddab (*Citharichthys sordidus*; Lefebvre et al. 2016), and longfin sanddab (*Citharichthys xanthostigma*; Goldberg 1982) spawn on daily time steps in temperate regions. If California halibut spawn as we have described, the combination of brief spawning seasons and short $ISIs$ would suggest a unique reproductive tactic north of Point Conception. This would involve decreasing the time between spawning events when favorable conditions (e.g., warmer temperatures, longer photoperiods, and increased food availability) are constrained to a few months, as opposed to southern California and Mexico, when conditions for spawning are favorable nearly year-round (Caddell et al. 1990; Barnes et al. 2015).

As with many of the more detailed aspects of their reproductive biology, diel patterns in spawning behavior (e.g., the exact time of day that eggs are released) remain unknown for California halibut. When this is the case for other multiple-batch spawners that exhibit indeterminate fecundity, we recommend the use of histological analyses to identify subphases of actively spawning females. Doing so will enable the selection of the late hydration subphase, which is most appropriate for estimating batch fecundity using the hydrated oocyte method (Hunter et al. 1985). Any other subphase to estimate batch fecundity based on hydrated oocytes would result in underestimations due to incomplete hydration

or partial spawning. However, focusing on a small subset of adult fish, such as those in the late hydration sub-phase, leads to a considerable reduction in sample sizes.

Because of small sample sizes from a narrow range of fork lengths (747 to 914 mm), we consider our fecundity estimates to be preliminary. Although these estimates pertain to the sizes of California halibut most commonly caught in commercial and recreational fisheries north of Point Conception, they do not embody the full extent of fish that are considered sexually mature (i.e., ≥ 466 mm; Lesyna and Barnes 2016). Because spawning duration, S , ISI , F , and batch fecundity are known to vary among size classes of individuals within the same species (e.g., *Citharichthys sordidus*, Lefebvre et al. 2016), our estimates would benefit from additional sampling of both smaller and larger adults.

Batch fecundities were similar between our study ($597,445 \pm 318,419$; $n = 17$) and the only other estimate for the species (approximately 522,000; $n = 7$, Caddell et al. 1990). However, differences in F led to a substantial disparity in annual fecundity. We found that spawning occurred 26 to 55 times per female per season, north of Point Conception. Estimates of F for captive fish from Southern California were reported to be between 5 and 13 (Caddell et al. 1990). Contrasting F values resulted in annual fecundities that were substantially greater for central California halibut (5.2×10^6 to 8.1×10^7 eggs per female per season) when compared to captive females from Southern California (6.6×10^6 eggs per female per season). Notably, reproductive estimates obtained from fish held in captivity may be conservative due to physiological limitations within an artificial environment. However, the fish we sampled were also larger (863 ± 67 mm) than those from the captive study (means ranged from 505 to 589 mm). Because we observed a significant log-linear relationship between fork length and batch fecundity even within a narrow range of sizes, additional fecundity estimates from smaller central California halibut would aid in regional comparisons of fecundity.

We have provided baseline information that improves our understanding about the reproduction tactics of California halibut: a prolific, multiple-batch spawner with indeterminate fecundity. However, there is still much to learn about the spawning activities of this commercially and recreationally important species. Because our analyses were restricted to the narrow range of sizes and ages commonly caught in recreational and commercial fisheries, we were unable to effectively quantify relationships among spawning season, S , ISI , F , or batch fecundity and length, weight, or age. This would be a worthwhile area of study in the future. Continued data collection on the spawning activities of California halibut with similar demographic characteristics would also be valu-

able because of the small sample sizes that were available during this study and because each of the reproductive metrics we have presented may change under different environmental or ecological conditions (Armstrong and Witthames 2012). Finally, a thorough investigation into the relationships between reproductive output and environmental variation would aid in our understanding about drivers of California halibut recruitment, thereby improving data inputs for stock assessment models pertaining to this species.

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SUPPLEMENTARY TABLE 1

Numbers of California halibut females sampled (n), proportions of individuals with hydrated oocytes, mean daily sea surface temperatures (T, °C), temperature-dependent durations of hydrated oocytes, and corrected spawning fractions (S) by sampling date (2013 only). Temperature data were obtained from the National Oceanic and Atmospheric Administration's National Data Buoy Center (Stn 46114). Temperature-dependent durations (D, hr) of hydrated oocytes were calculated using the equation $D = 59.4 * e^{-0.122T}$ (*Paralichthys olivaceus*, Kurita et al. 2011).

Date	n	Proportion with Hydrated Oocytes	T (°C)	Estimated Duration of Hydrated Oocytes (hr)	Corrected S
6/22/13	3	0.33	13.15	11.9	0.67
6/23/13	2		13.33	11.7	
6/25/13	3	0.33	13.63	11.3	0.71
6/26/13	1		14.13	10.6	
6/28/13	1		13.07	12.1	
7/1/13	2		13.45	11.5	
7/2/13	2		13.90	10.9	
7/5/13	1		14.01	10.8	
7/6/13	4	0.50	13.15	11.9	1.00
7/7/13	1		13.99	10.8	
7/10/13	1		13.72	11.1	
7/12/13	3	0.67	13.52	11.4	1.40
7/13/13	8	0.00	13.52	11.4	0.00
7/14/13	1		13.41	11.6	
7/15/13	3	0.33	13.45	11.5	0.69
7/16/13	5	0.40	14.26	10.4	0.92
7/17/13	1		14.59	10.0	
7/19/13	6	0.17	13.24	11.8	0.34
7/20/13	1		13.30	11.7	
7/21/13	1		13.47	11.5	
7/23/13	1		14.21	10.5	
7/24/13	1		14.38	10.3	
7/25/13	5	0.20	14.39	10.3	0.47
7/27/13	2		14.31	10.4	
7/28/13	5	0.40	14.49	10.1	0.95
7/29/13	1		14.60	10.0	
7/30/13	1		14.89	9.7	
7/31/13	1		14.76	9.8	
8/1/13	4	0.25	14.22	10.5	0.57
8/2/13	2		13.55	11.4	
8/3/13	7	0.14	13.58	11.3	0.30
8/4/13	8	0.25	13.09	12.0	0.50
8/6/13	1		13.64	11.2	
8/7/13	5	0.00	14.46	10.2	0.00
8/8/13	3	1.00	14.99	9.5	2.52
8/9/13	7	0.43	14.97	9.6	1.08
8/11/13	3	0.33	14.11	10.6	0.75
8/13/13	5	0.60	13.97	10.8	1.33
8/14/13	1		14.07	10.7	
8/15/13	2		13.45	11.5	
8/17/13	2		14.05	10.7	
8/18/13	7	0.14	12.81	12.4	0.28
8/20/13	1		15.25	9.2	
8/24/13	3	0.33	14.55	10.1	0.79
8/25/13	3	0.33	14.75	9.8	0.81
8/26/13	6	0.83	15.34	9.1	2.19
8/28/13	5	0.00	14.72	9.9	0.00
8/30/13	5	0.60	13.91	10.9	1.32
9/1/13	2			10.7	
9/2/13	4	0.00	14.33	10.0	0.00
2013	147	0.34	14.01	10.8	0.78

SUPPLEMENTARY TABLE 2

Numbers of California halibut females sampled (n), proportions of individuals with new postovulatory follicles (POFs), mean daily sea surface temperatures (T, °C), temperature-dependent durations of new POFs, and corrected spawning fractions (S) by sampling date (2013 only). Temperature data were obtained from the National Oceanic and Atmospheric Administration's National Data Buoy Center (Stn 46114). Temperature-dependent durations (D, hr) of new POFs were calculated using the equation $D = 62.9 * e^{-0.118T}$ (*Paralichthys olivaceus*, Kurita et al. 2011).

Date	n	Proportion with New POFs	T (°C)	Estimated Duration of New POFs (hr)	Corrected S
6/22/13	3	0.33	13.15	13.3	0.60
6/23/13	2		13.33	13.0	
6/25/13	3	0.00	13.63	12.6	0.00
6/26/13	1		14.13	11.9	
6/28/13	1		13.07	13.5	
7/1/13	2		13.45	12.9	
7/2/13	2		13.90	12.2	
7/5/13	1		14.01	12.0	
7/6/13	4	0.00	13.15	13.3	0.00
7/7/13	1		13.99	12.1	
7/10/13	1		13.72	12.5	
7/12/13	3	0.33	13.52	12.8	0.63
7/13/13	8	0.00	13.52	12.8	0.00
7/14/13	1		13.41	12.9	
7/15/13	3	0.00	13.45	12.9	0.00
7/16/13	5	0.20	14.26	11.7	0.41
7/17/13	1		14.59	11.2	
7/19/13	6	0.00	13.24	13.2	0.00
7/20/13	1		13.30	13.1	
7/21/13	1		13.47	12.8	
7/23/13	1		14.21	11.8	
7/24/13	1		14.38	11.5	
7/25/13	5	0.20	14.39	11.5	0.42
7/27/13	2		14.31	11.6	
7/28/13	5	0.20	14.49	11.4	0.42
7/29/13	1		14.60	11.2	
7/30/13	1		14.89	10.9	
7/31/13	1		14.76	11.0	
8/1/13	4	0.50	14.22	11.7	1.02
8/2/13	2		13.55	12.7	
8/3/13	7	0.14	13.58	12.7	0.27
8/4/13	8	0.25	13.09	13.4	0.45
8/6/13	1		13.64	12.6	
8/7/13	5	0.00	14.46	11.4	0.00
8/8/13	3	0.33	14.99	10.7	0.75
8/9/13	7	0.00	14.97	10.8	0.00
8/11/13	3	0.33	14.11	11.9	0.67
8/13/13	5	0.20	13.97	12.1	0.40
8/14/13	1		14.07	12.0	
8/15/13	2		13.45	12.9	
8/17/13	2		14.05	12.0	
8/18/13	7	0.00	12.81	13.9	0.00
8/20/13	1		15.25	10.4	
8/24/13	3	0.33	14.55	11.3	0.71
8/25/13	3	0.33	14.75	11.0	0.73
8/26/13	6	0.33	15.34	10.3	0.78
8/28/13	5	0.00	14.72	11.1	0.00
8/30/13	5	0.60	13.91	12.2	1.18
9/1/13	2			10.7	
9/2/13	4	0.00	14.33	10.0	0.00
2013	147	0.18	14.01	12.1	0.38