NORTH PACIFIC RESEARCH BOARD PROJECT FINAL REPORT

Assessment of female reproductive effort and maternal effects in Pacific Ocean Perch *Sebastes alutus*: do big old females matter?

NPRB Project 629 Final Report

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Abstract

Research on live-bearing fishes of the genus *Sebastes* has shown positive relationships between the age of females and the quality of their offspring, where "quality" is measured as size, oil globule volume, growth rate, days to starvation, and/or swimming speed. Females of different age classes may also spawn at different times, with younger females generally releasing their larvae later in the parturition season. These studies have reintroduced an important concept in life history evolution that ties to fisheries management: the potential need to preserve age structure of the spawning stock, not simply biomass. We are investigating the age-specific characteristics of spawning Pacific Ocean perch (POP) *Sebastes alutus* from the Gulf of Alaska to see if the patterns observed in nearshore rockfishes also occur in this deep water species. In general, we have found support for age-related differences in reproductive characteristics among females although these signals do not appear as strong as that seen for shallow-water species. Our attempt to approximate the timing of parturition for females collected through trawl sampling may have been confounded by an interesting phenomenon – approximately 3% of females examined show evidence of differential development between the two ovarian lobes, suggesting that some fish may release their larvae one ovary at a time. Our research has not found a strong relationship between mother's age and offspring quality in POP, but has revealed differential timing of release that correlates with age, as well as other important aspects of reproductive physiology in this species. Modeling results indicate that maternal effects are not as important as other impacts to population demographics.

Key Words

Pacific Ocean perch, *Sebastes alutus*, Gulf of Alaska, Maternal effects, reproduction, spawning, age structure, management, modeling

Citation recommendation

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Table of Contents

Study chronology

Work related to Project 629 has not been previously supported by the North Pacific Research Board, but initial work was supported by a grant from the NOAA Fisheries Alaska Fisheries Science Center to SS and SA Heppell. This initial support allowed us to conduct field collection of specimens over three years; 2006, 2007, and 2008. We conducted field sampling of Pacific Ocean perch *Sebastes alutus* (POP) during late April and early May in each of the three years aboard the F/V Gold Rush, captained by Mr. Bert Ashley. Sample and data analysis proceeded each field season, and full data analysis and manuscript preparation has been ongoing since the end of the 2008 field season. Project progress reports, upon which some of this final report is based, were filed in January and July 2007, January and July 2008, and January 2009.

Introduction

Pacific Ocean perch *Sebastes alutus* (POP) have been exploited since the early 1960s, when foreign fleets targeted the fish in the Gulf of Alaska. Landings peaked in 1965 then slowly declined for many years until a rebuilding plan for Pacific ocean perch in the Gulf of Alaska brought catch levels back to ~10,000 metric tons in 2000 (DiCosimo and Kimball, 2001). The slow-growing nature and extreme longevity of Pacific Ocean perch may increase the susceptibility of this species to overfishing (Chilton and Beamish, 1982; Leaman and Beamish, 1984), as might the potential influence of maternal effects on offspring survival (Berkeley et al., 2004b).

Research on the reproductive biology of rockfish suggests that the reproductive capacity of the stock may be a function of the age structure, in particular the proportion of old fish in the population. While adult growth rates slow considerably once rockfish mature, rockfish exhibit increases in both relative and absolute fecundity with age (Boehlert et al., 1982). Leaman and Melteff (1987) and Leaman (1991) noted that older fish allocate a large proportion of available energy to reproduction. The removal of older females thus disproportionately reduces spawning output such that reproductive value (the expected lifetime number of offspring from a female of a particular age in a stable age distribution) is highly sensitive to increases in fishing mortality. Maternal effects, such as egg size, yolk provisioning, or parental care may also increase with female age, size or condition, thereby increasing egg quality and subsequent larval survival (reviews in Chambers and Trippel 1997).

Older female black rockfish *Sebates melanops* produce more fit and viable larvae due to greater contribution of lipids to their eggs, manifest as a larger oil globule (Berkeley et al., 2004a; Bobko and Berkeley 2004). Larvae from the oldest females grew more than three times faster and survived starvation more than twice as long as larvae from younger females (Berkeley et al. 2004a); thus, exploitation can be expected to have a disproportionate effect by removing the most effective spawners.

Incorporation of increased fecundity and larval fitness with maternal age in stock assessment models suggests that a failure to consider demographic effects on productivity can lead to an overestimation of appropriate assessment reference points (Murawski et al. 1999). The implication from these studies is that simply conserving spawning biomass is not sufficient, and managers should aim to preserve spawning biomass with a desirable age structure.

Similar relationships have been found in cod *Gadus morhua* (Kjesbu et al. 1996, Marteinsdottir and Steinarsson 1998, Vallin and Nissling 2000, Begg and Mareinsdottir 2000), and striped bass *Morone saxatilis* (Monteleone and Houde 1990). Fecundity-per-age is a common feature of age-specific fisheries models, but it is assumed that there is no change in egg quality through the life of a female. Larval survival may also be dependent on the timing of reproduction; in most studied fish species, older females spawn earlier than younger ones in temperate latitudes, which may directly affect the spatial and temporal overlap of the larvae with their prey (Marteinsdottir and Begg 2002). Compelling evidence from Berkeley et al. (2004a) suggests a disproportionate contribution of early spawners (=older females) to year-class strength, shown by back-calculated birthdates from surviving juveniles. If maternal effects have a substantial impact on offspring production from particular age- or size-classes, population dynamics and resilience to environmental variability may be strongly dependent on age structure (Secor 2000; Secor 2007). In these cases, fisheries managers may need to alter recommended harvest strategies to enhance reproductive potential (Marteinsdottir and Begg 2002).

Given the collapse of several West Coast rockfish species, considerable interest exists in determining whether management policies for Alaska rockfish are sufficiently conservative. In 2002, a panel charged with evaluating a policy that established a fishing mortality rate of 40% ($F_{40\%}$) for Alaska groundfish (Goodman et al. 2002) suggested that this level of removal may not provide sufficient conservation for Alaska rockfish. Dorn's (2002) meta-analysis is the only study that simultaneously considered the productivity of both West Coast and Alaska rockfish, evaluating eight West Coast stocks, one British Columbia POP stock, and three Alaska POP stocks (at that time, Bering Sea and Aleutian Islands POP were assessed as separate stocks). The Alaska POP stocks show greater resiliency than the West Coast stocks, with maximum sustainable yield (MSY) occurring at spawner potential ratio (SPR) rates of approximately $F_{30\%}$. Observed greater productivity in the Bering Sea/Aleutian Islands and Gulf of Alaska POP has been repeated in recent stock-recruitment analyses, which have found that estimated Fmsy reference points are greater than the proxies of $F_{40\%}$ (Spencer and Dorn 2003, Hanselman et al. 2004). However, these studies have not fully considered how changes in age structure may affect estimates of stock productivity and estimation of harvest reference points such as F_{msy}.

In the coastal North Pacific, primary productivity is dependent on inter-annual and inter-decadal variance in the location and timing of upwelling; fishes that evolved in this dynamic environment must have life history traits allowing maximum fitness under a range of conditions. Effects may manifest themselves as among female differences in the allocation of energy to individual offspring (size/number trade-offs), which can then be measured by comparing the size, growth and survival of offspring. At least some species of rockfish appear to initiate the maturation process at the beginning of the reproductive season but fail to complete spawning and show signs of egg resorption (atresia) (Steve Parker, Oregon Department of Fish and Wildlife, personal communication). We hypothesize that there is a physiological "decision" process that controls whether reproduction continues past a certain point or is arrested and the developing oocytes absorbed. This switch is most likely related to body condition and available energy reserves (Kjesbu et al. 1991, 1998), particularly because viviparous rockfish require additional energy reserves for spawning due to provisioning of the larvae (Boehlert and Yoklavich 1984). Therefore, fish in poor condition are less likely to spawn and contribute to subsequent years' recruitment. If younger females are more likely to forego reproduction under adverse environmental conditions, age truncation could have a substantial influence on recruitment in some years. Although general population models that incorporate maternal effects can be evaluated heuristically, there are basic research needs to document reproduction in POP before our "what if" scenarios can be realistically assessed. With a better understanding of the reproductive biology (including maternal effects) and body condition of commercially important marine species in the Northeast Pacific, management efforts can be refined to better reflect changes in exploitable biomass of fish related to the dynamic cycles of productivity that occur in these ecosystems.

Overall our goal with this work was to determine whether older female POP demonstrated maternal effects either through the production of better quality offspring (i.e. larger, better provisioned), or by producing offspring at different times

Objectives

Our original objectives were to expand work initiated under funding by the Alaska Fisheries Science Center in order to:

1. Expand our collection activities of adult POP in both space and time by adding 5-6 additional springtime collecting trips in each of two years,
2. Conduct ichthyoplankton sampling for larval POP to examine relationships between offspring survival, birth date, and reproductive status of adult female POP, specifically timing of parturition, and
3. Expand laboratory analysis to include assessment of energetic stores of both adult and larval POP through proximate analysis

These additional data were to be used in conjunction with planned efforts through the current AFSC project to develop population models that examine

1. Whether maternal effects are actually important at the population level, and
2. The role of the environmental variance component (sea surface temperatures, timing of spring transition, upwelling indices, etc.) in both overall and age-structured success of POP reproduction.

Based on the results of our first (AFSC) field season, we refined our objectives to:

1. Determine the influence of age and energy stores on larval size, quality, and survival,
2. Evaluate whether there were differences in parturition timing across age classes, and
3. Conduct the modeling work to assess the influence that maternal effects might have on the population dynamics of POP

This report separates our objectives and results into two parts: field data collection and laboratory analyses of spawn timing and larval quality by POP from the Gulf of Alaska, and modeling efforts to explore the potential importance of maternal effects on population processes and stock assessments.

PART 1: Analysis of spawn timing, maternal condition, and larval quality in Pacific Ocean Perch from the Gulf of Alaska

Methods

Sample collection

Sampling took place aboard the chartered F/V Gold Rush in slope waters of the Gulf of Alaska south of Kodiak Island, Alaska (Figure 1). We collected adult mature Pacific Ocean perch using the commercial groundfish trawl provided by the Gold Rush, with the locations and depths of all tows based on the knowledge of the captain and the crew of the charter vessel. Sampling was focused in areas for which the captain's fishing records indicated high concentrations of Pacific Ocean perch. The general habitat for this species is described as submarine canyons. Male and females tend to separate by depth during parturition and the depth at which pregnant Pacific Ocean perch are estimated to extrude larvae is 500-700 meters (Love et al., 2002).

Duration of haul time varied, but was typically 20-25 minutes bottom contact time. A third-wire sonar monitoring system was used to estimate the amount of fish entering the net during the tow. The net was pulled on board once the cod end appeared to be full, as determined by the captain based on interpretation of third-wire sonar data.

Once haulback of the net was finished, the contents of the net were emptied onto the deck, and the catch was sorted. Female Pacific Ocean perch were separated into an on-deck bin for sampling, while the remainder of the catch was retained by the vessel. Weight and length were recorded and otoliths, gonad tissues, and muscle tissue samples were extracted. Otoliths were cleaned and stored dry in 24-well tissue culture plates. Gonad tissues were preserved in 10% neutral buffered formalin. Muscle samples were wrapped in aluminum foil and frozen in plastic bags for energy content analysis.

Age determination

Otoliths were used to determine age using the break-and-burn method for ageing Pacific Ocean perch (Westrheim 1973). All ageing was conducted by ageing experts at the NOAA Fisheries Alaska Fisheries Science Center facility in Seattle, Washington. All adult fish were aged in 2006. Due to the large sample size obtained in 2007 and 2008, and time constraints at the ageing center, a subsample of ages were estimated for those years. Samples were binned into 1 cm size classes and a maximum of 10 adult fish per cm length were aged.

Lipid analysis (maternal condition)

Muscle lipid content for each fish was determined following the methods described in Anthony et al. (2000) and Reynolds and Kunz (2001). Tissues were thawed and weighed, dried to a constant mass (i.e., ± 0.01 g of previous 24 hr mass) in a convection oven set at 60ºC Fish, then thoroughly homogenized with mortar and pestle. Lipids were extracted from dried samples with a Soxhlet apparatus and a 7:2 (v/v) hexane/isopropyl alcohol solvent system. Fat mass was determined by subtracting the mass of dried homogenized muscle before Soxhlet extraction from the mass of lean dry mass after lipid extraction.

Larval survival experiments

Female Pacific Ocean perch observed releasing larvae were used for collection of larvae for larval performance trials. Larvae were manually extruded from the female with careful application of pressure to the ventral surface adjacent to the anal opening and external papillae. The larvae from each adult were assigned to a single larval transport container (2-liter polyethylene terephthalate (PET) soft drink bottle). Each container was immediately sealed following larval extraction and placed in a 1.22 meters x 1.07 meters x 0.71 meters tote. A wooden rack, capable of holding 35 larval transport containers was constructed to fit into the tote to securely hold the larval transport containers in place. A seawater bath was used to maintain a cold environment during transport. Larvae collected at sea were transported to the

Alaska Department of Fish and Game/ Alaska Fisheries Science Center Kodiak Laboratory Seawater Facilities rearing laboratories in Kodiak, Alaska.

Larvae were transferred from larval transport containers to individual aquaria, where they were acclimated for five days. A random subsample of 20 larvae from each adult female was photographed with a stereomicroscope. Oil globule diameter for each larva was measured and oil globule volume calculated. The average larval oil globule volume (calculated for each adult female) was used as a proxy for larval condition. Of the larvae that remained at the end of the 5-day acclimation period, 50 actively swimming larvae were used for the survival trials. If sufficient actively swimming larvae from a given female survived the initial five day acclimation period, replicate tanks were stocked with those larvae to enhance statistical comparison.

Two holding tanks, each with 32 aquaria, were utilized for larval rearing experiments. Each tank was 2.0m in diameter and 1.5m tall. A centrally located 0.5m tall standpipe maintained a water depth of 0.43m at the tank edge and 0.55m at the tank center. Inlet pipes were placed in identical locations in each holding tank and monitored daily to ensure identical flow.

For each aquarium, screened inlet and outlet holes were cut through the ends of the aquarium in order to increase water circulation. The size of each inlet and outlet hole was 7.0 cm in diameter and the holes were covered with 0.05mm mesh. A VWR Digital Thermometer and a YSI Model 85-10 multi-meter were used to monitor temperature, salinity, conductivity, and dissolved oxygen in each holding tank on a daily basis. Laboratory photoperiod was regulated to mimic diurnal day-length patterns.

Each larval survival/starvation trial lasted 30 days or until all larvae had died and during which time no food was provided. Larval mortality for each aquarium was monitored at the same time each day, and dead larvae were counted and extracted with a pipette.

Histological preparation and analysis

The total amount of gonad tissue collected varied among fish, depending on the size of the gonad. Smaller gonads were preserved whole; larger gonads were sectioned laterally and sufficient portions from the mid-gonad region preserved. During surveys conducted in 2008, gonads from all specimens were collected and preserved whole. An attempt was made during 2008 to collect both gonads whenever possible.

Histological sections of gonads were prepared using standard histological techniques. Tissue samples were removed from 10% formalin and dehydrated in a graded ethanol series, followed by xylene (to remove the alcohol), and embedded in paraffin wax. Sections were sectioned at 5-7 µm on a Leica RM2155 rotary microtome, affixed to clear glass slides, and stained with Gill-3 hematoxylin and counter-stained with eosin.

Each histological slide was viewed under light microscopy at 4x to 40x magnification, and stage of development was determined using criteria adapted from Wyllie Echeverria (1987), Bowers (1992), and Chilton (2007).

Larval staging for developmental evaluation

Developmental stages of Pacific Ocean perch larvae follow Yamada and Kusakari (1991; table 2). Larvae were photographed with a Leica SP8 APO integral dissecting camera scope interfaced with Leica proprietary imagery software. For samples collected in 2006 and 2007, all larvae preserved from each aged female were transferred to polystyrene Petri dishes, 100 x 15 mm, with clear lids. The lids contained the formalin vapors while allowing the capture of clear digital images. For whole ovary samples collected in 2008, a subset of each aged female's larvae was transferred to Petri dishes so that one layer of larvae covered the bottom of the dish. Preliminary work showed larvae collected from inside the ovary were not as well preserved as larvae closer to the ovarian surface. To randomize the sample from whole ovaries, larvae were squeezed from the ovary and mixed before transfer to the Petri dish. Transfer of all samples was accomplished using a plastic pipette with the end cut to increase mouth diameter and minimize damage to specimens. All specimen transfer occurred inside a ventilation hood in accordance with standard safety practices.

Table 1: Criteria applied for assessing the reproductive condition of female Pacific Ocean Perch (Sebastes alutus) based on macroscopic field and microscopic laboratory assessments. Criteria were modified from Wyllie Echeverria (1987), Bowers (1992), and Chilton (2007

Stage	Macroscopic Description	Histological Description	Oocyte Stages
1. Immature	Thin, thread-like ovaries, pink or light red in color; oocytes not visible	Oogonial nests and unyolked oocytes, oocyte diameter is ? 150 µm, ovarian wall thin, ? 125 µm	Oogonia densely nested with some oocytes at early perinucleus development, with one or two large nucleoli in nucleus
2. Maturing or Intermediate	Ovaries cream to light yellow in color with thin ovarian wall, oocytes visible	Ovary dominated by large oocytes with numerous small red-staining yolk globules, initial yok accumulation evident but yolk globules small	Oogonia nests and early perinucleus oocytes visible, but dominated by larger oocytes with clear vacuoles evident in oocytes
3. Vitellogenesis	Individual bright yellow eggs are visible; ovarian wall thickening darkly pigmented	Yolk globules and oil vesicles present, oocyte diameter up to 500 µm, ovarain wall 300-400 µm thick	Initial oil vacuoles coalescing in oocytes, tertiary yolk stage
4. Fertilized	Large translucent eggs with pink to yellow tint, ovaries enlarged	Large oocytes and embryo diameters to > 1000 µm	Migratory nucleus through early embryonic development may be present
5. Eyed larvae	Ovary enlarged with eyed larvae, ovarian wall thin and easily torn/damaged	Embryos with dark pigmented eyes	Eyed larvae present
6. Post-parturition	Ovary flaccid and dark red, some eyed larvae may be visible	Postovulatory follicles and atretic oocytes, and residual larvae may be present, early stage oocytes loosely associated	Oocytes in several stages present but loosely organized; atretic oocytes, possibly residual eyed larvae or embryos present, network of blood vessels may be evident
7. Resting or non-functional	Ovary red, occassionally flaccid but no visible eyed larvae or oocytes, ovary often enlarged and blood clots present	Red staining, ovary wall may be thick or thin as observed among immature specimens, scattered oogonia may be present	No evidence of post-ovulatory follicles or atretic oocytes, but large amount of tissue associated with histological sample

Table 2: Reproductive stages used for microscopic evaluation of larval development in Pacific Ocean perch. Letters reference photomicrographs in Figure 7, and stages follow Yamada and Kusakari (1991)

		Stage	Description
Early	A	1	Unfertilized eggs
	B	2	Fertilized eggs
	C	11	Late blastula
	D	15	Embryonic shield
	E	16	Head fold, early neurula
	F	17	Optic vesicles, late neurula
Mid	G	18	Beginning of somite formation
	H	20	Optic cups
	I	22	Lens formation
	J	25	Pigmentation of retina begins
	K	29	Pigmentation of peritoneal wall, retina continues to darken
	L	29	Pigmentation of retina complete
Late	M	-	Depicting difference between mid (i) and late (ii) development
	N	30	Depletion of yolk begins
	O	30	Depletion of yolk continues
	P	31	Pre-hatching, more than 50% of yolk depleted
	Q	31	Detail of gut formation with yolk depletion
	R	32	Hatching, gut formation continues with much reduced oil globule

Results

Sample collection

Sampling for female POP was initiated in May, 2006. Two trawls were conducted daily on the 2nd, 5th, and 16th, one trawl on the 4th, and three trawls on the 28th of the month at depths of 95-119 m (Figure 1). A total of 415 specimens were collected, ranging in size from 260-440 mm TL. The mean size of females was 367.0 mm TL (27.9 SD).

In 2007, surveys were completed on April 28th, and May 5th, 13th, 18th, and 30th. A single trawl was made on each date except on the 5th when two trawls were conducted. The 2007 trawls were at depths of 97-120 m. Larvae were collected from up to 24 near-term females during each trip and transported to Kodiak for laboratory experimental studies. Additionally, a total of 608 specimens were examined from these trawls for other maternal effect features. Fish ranged in size from 220-460 mm TL. Mean TL was 363.5 mm (38.5 SD).

The surveys conducted in 2008 were developed with the intention of targeting larger, potentially older female POP. One trawl was completed each day on May 18th and 19th at depths of 188-191 m. A total of 332 specimens were examined. Females ranged from 262-494 mm TL, averaging 406 mm TL (35.3 SD).

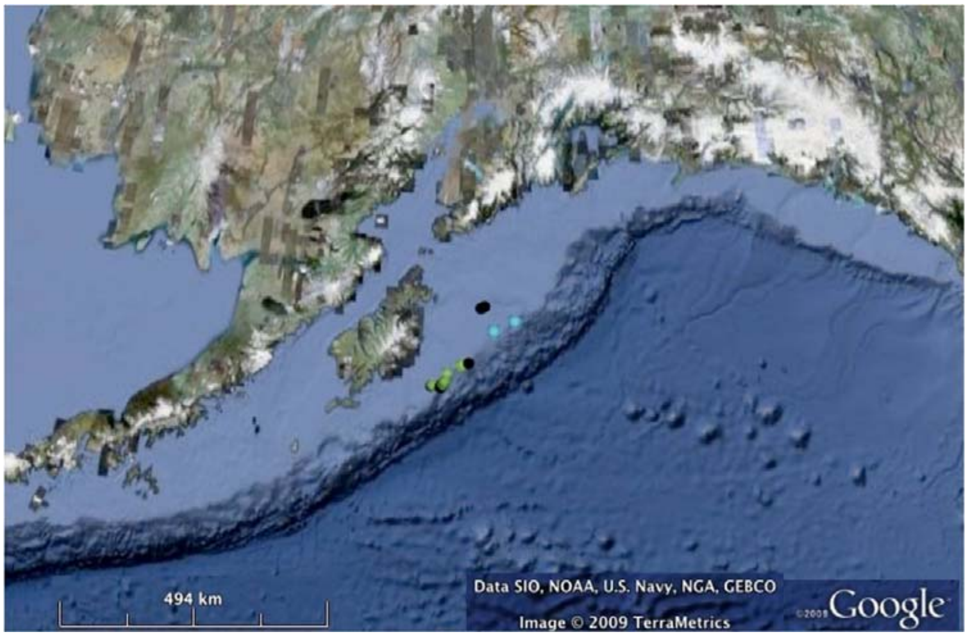


Figure 1: Trawl locations of POP sampling in 2006, (black circles), 2007 (green circles), and 2008 (blue circles)

Table 3: Catch summary for the three years of POP sampling

Year	Tows	Specimens	Aged Specimens	Age **Mean (s.d., range)**	Mean (s.d.) **Length(mm)**	 **Weight(kg)**
2006	10	415	412	10 (3, 4-31)	367 (28)	0.40 (0.17)
2007	6	608	174	12 (6, 4-32)	363 (38)	0.45 (0.22)
2008	2	332	140	17 (6, 8-31)	406 (35)	0.99 (0.26)

Larval provisioning and survival

We found no support for a relationship between maternal condition and larval oil globule volume (Figure 2a; $p = 0.29$, $r^2 = 0.271$), maternal age and condition (Figure 2b; $p = 0.45$, $r^2 = 0.196$), or maternal age and larval oil globule volume (Figure 2c; $p = 0.602$, $r^2 = 0.136$).

We encountered difficulties with the larval survival trials, and as such results are not reported here because we lack confidence in their veracity. Difficulties included larval barotrauma during capture, stocked larvae from different females being at different developmental stages at the onset of the experiment (which confounds the relevant comparisons to maternal age and body condition) and substantial changes in laboratory sea water temperature over the course of the study, which may have altered mortality rates. This change in temperature likely did not bias the results, rather it would have increased starvation rate evenly for all individuals because of an increase in metabolic rate with the increase in temperature.

Histological analysis of maturational status

A total of 706 ovarian histological preparations were examined (2006 n = 322, 2007 n = 203, 2008 n = 181). In calendar weeks 16 and 17, 50% or less of fish aged 4-9 had eyed larvae, the most advanced stage of development prior to spawning, while 100% of fish aged 10+ had eyed larvae (Figure 3). Starting in week 18 post-parturition ovaries were observed first in the oldest fish, although these never comprised more than 50% of all ovaries evaluated during the monitoring period. Through week 22 eyed larvae and post-parturition status were observed in all age classes, although the youngest age group generally lagged behind the older age groups in development, during most weeks. Similar results are seen for size-based interpretation of the data (Figure 4). Stage 2 oocytes, the least developed oocytes observed, are seen primarily in the youngest and smallest fish.

One interesting feature that should be noted for this and future studies is evidence for asynchronous development between the two lobes of the ovary in POP (Figure 5). We observed the presence of this phenomenon in 2007, and this was the motivation for the 2008 change in collection procedure to collect both lobes of the ovary. Although this condition was only recorded from 3.2% of the observed specimens for which reproductive condition was assessed from both ovaries, when encountered this variation between ovaries was evident both macro- and microscopically. Additionally, a single hermaphroditic specimen was recorded. These differences were most evident among specimens which possessed one apparently spent, resting, or non-functional ovary while the other contained eyed larvae.

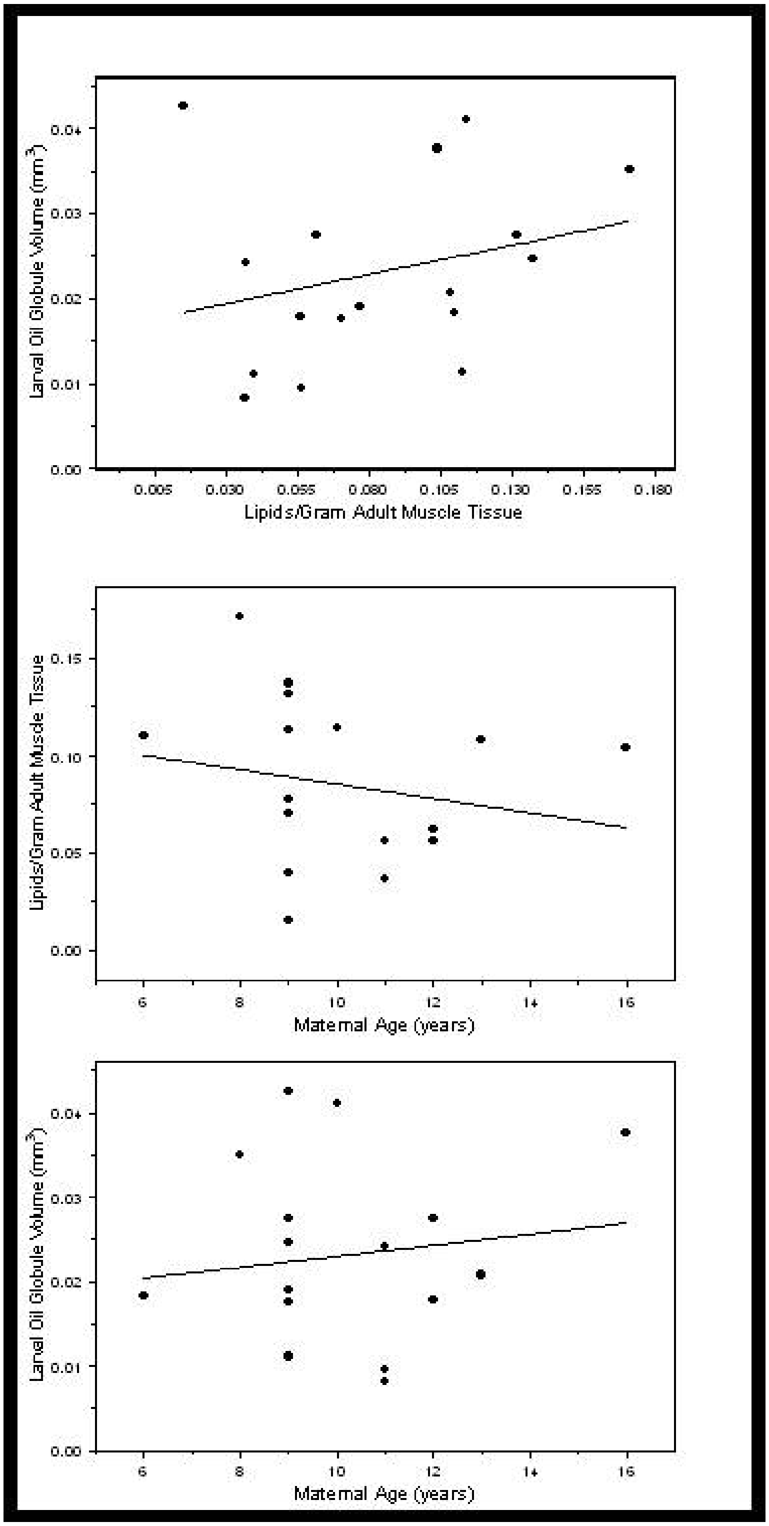


Figure 2: Pacific Ocean perch (A) Larval oil globule volume as function of adult condition, (B) Adult condition as a function of maternal age, and (C) Larval oil globule volume as a function of maternal age.

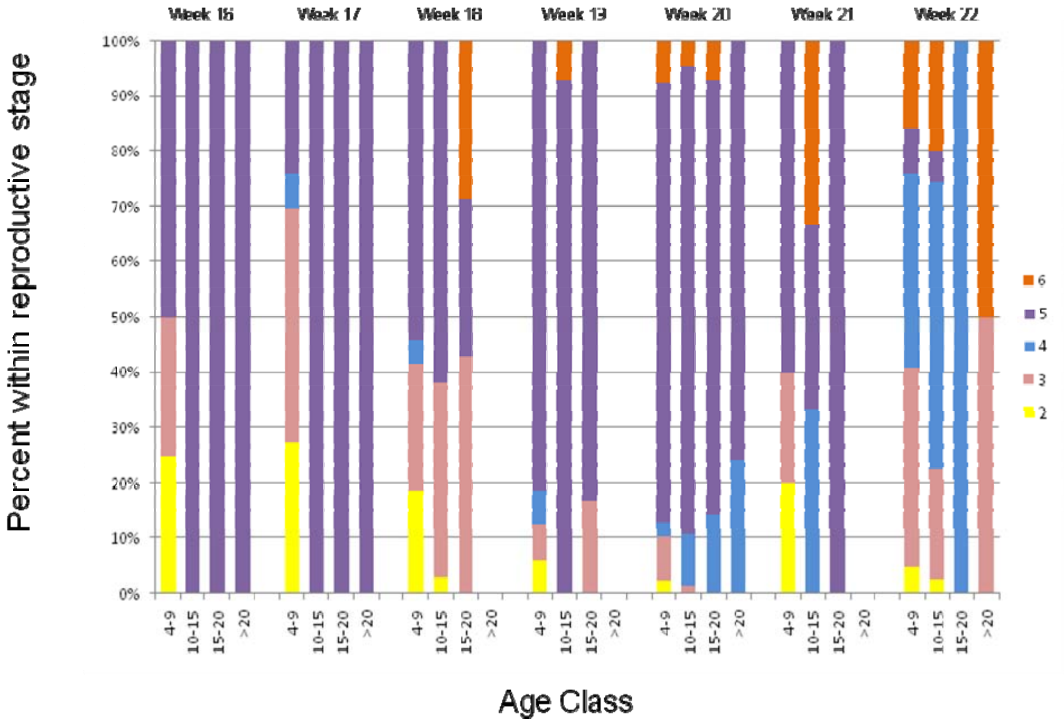


Figure 3: The reproductive status of Kodiak Island Pacific Ocean perch by age class and week of year, as evaluated by gonad histology, for all years combined (n = 543). Stages are as per table 1.

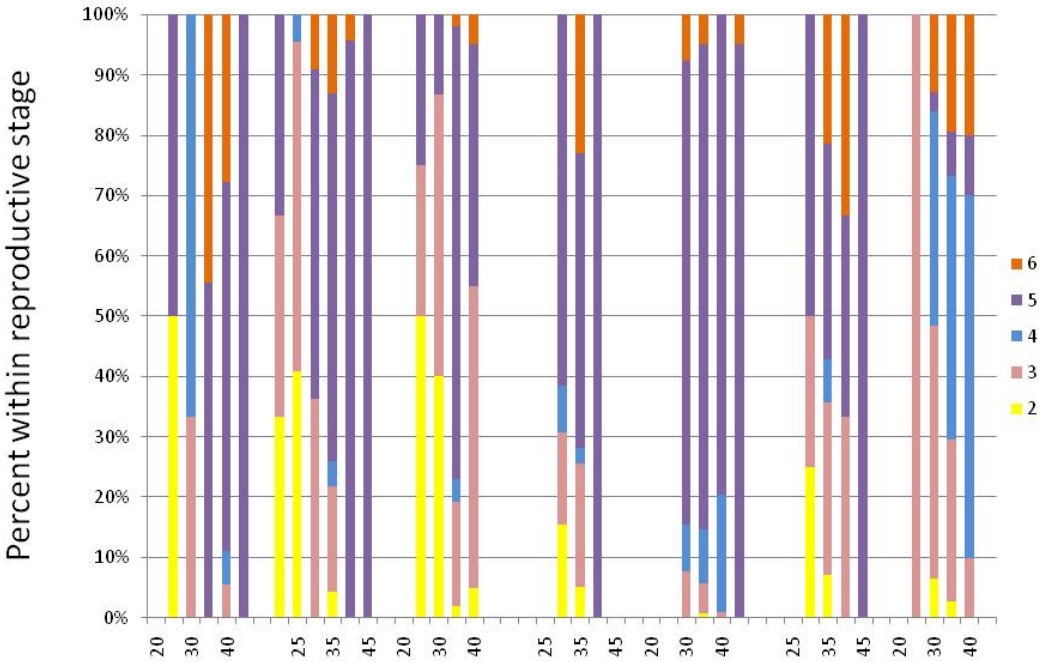


Figure 4: The reproductive status of Kodiak Island Pacific Ocean perch by size class (5 cm bins) and week of year, as evaluated by gonad histology, for all years combined (n = 706). Stages are as per table 1.

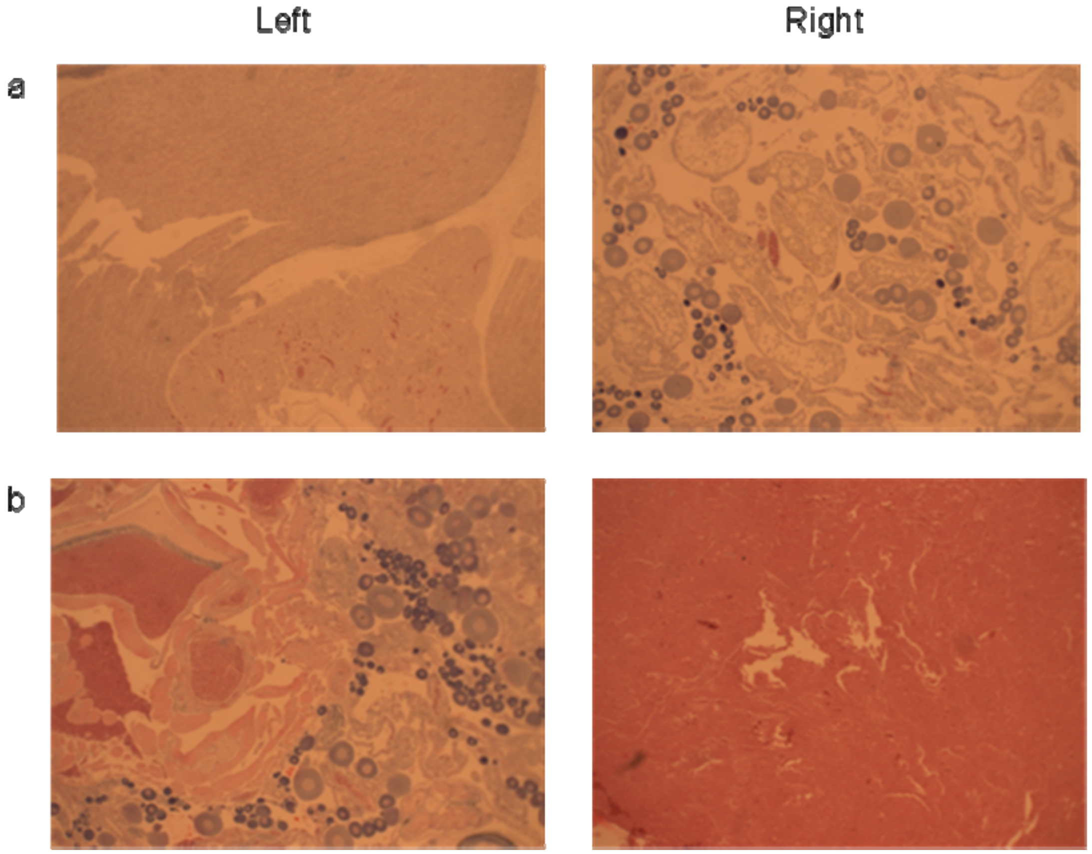


Figure 5: Representative histological preparations documenting asynchronous development between ovarian hemispheres in Pacific Ocean perch. Left and right refer to the left and right lobes of the ovary, respectively. Magnification = 80x in all photographs.

Larval development

Larvae were staged from a total of 355 females (2006 n = 115, 2007 n = 113, 2008 n = 127; Figure 6). Fish in all age classes had eyed larvae at stage 30 during the first week of sampling (calendar week 16). Development to stage 31 (attained immediately prior to spawning) occurred between week 19 and 20, but occurred primarily in the oldest age classes. At calendar weeks 20 and 21 the vast majority of fish (80%) in the oldest age classes were at stage 31, while only 15% of the youngest fish had reached this stage. By week 22 60% of the youngest fish were close to the parturition stage. Interpretation of the results for week 22 are somewhat confounded by the lack of older fish.

It should be noted that we found existing visual guides of developmental stage insufficient to conduct our work, with low-resolution, black-and white images the only published work available. Therefore, we created our own photographic guide (Figure 7), in order to facilitate this work. In addition to facilitating our own work, such a guide should prove useful for future research into the reproductive ecology of POP.

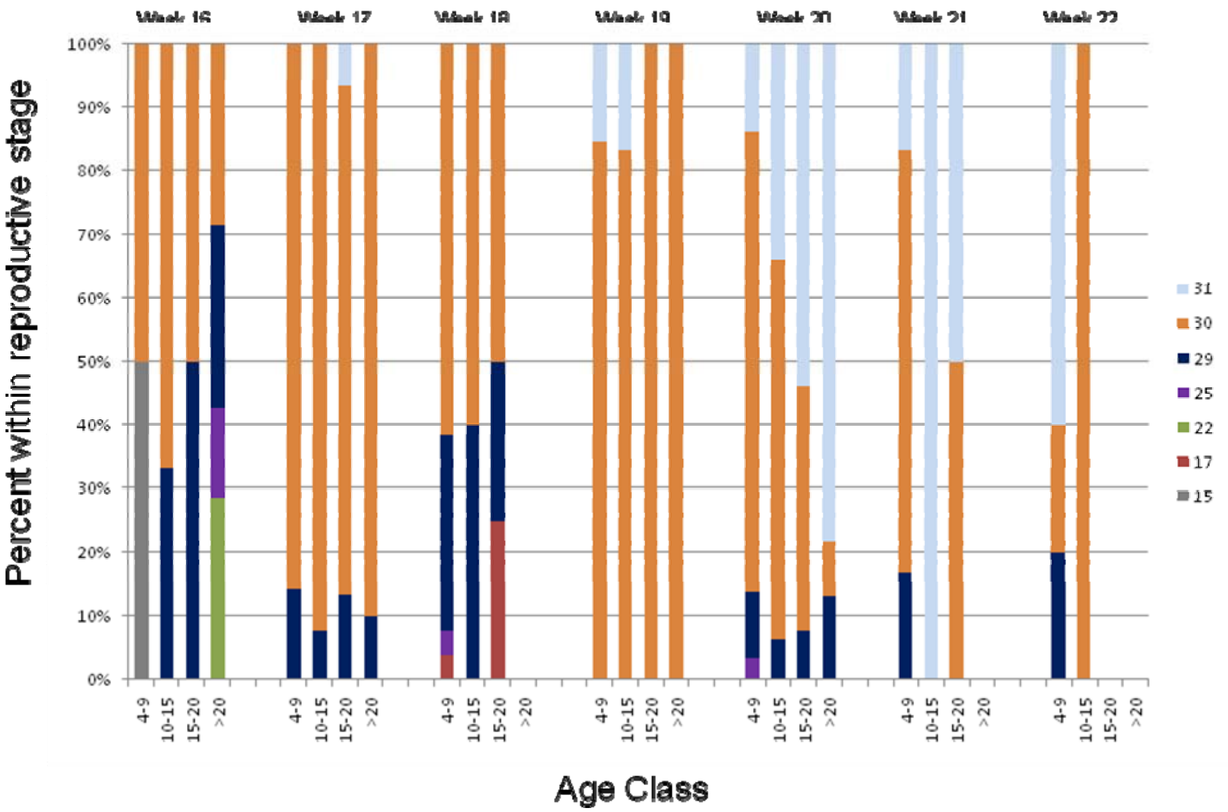


Figure 6: The reproductive status of Kodiak Island Pacific Ocean perch by age class and week of year, as evaluated by microscopic staging of viable larvae, for all years combined (n = 271). Stages are as per table 2.

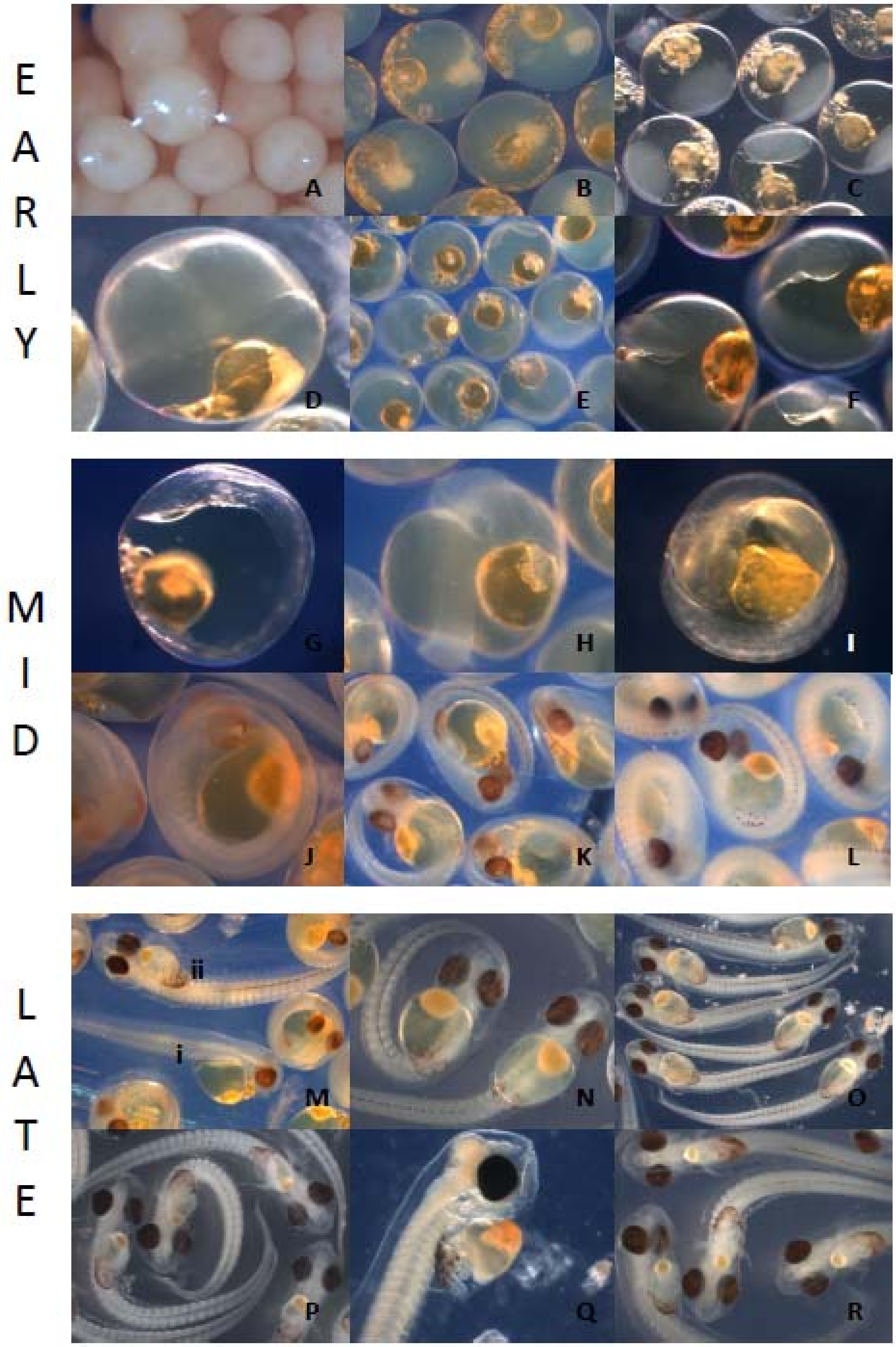


Figure 7: Developmental stages of POP larvae. Letters correspond to the developmental stages listed in table 2.

Discussion

There was no statistically significant relationship between maternal age or condition and offspring provisioning, as measured by the size of the larval oil globule, which we used as a proxy for energy allocation. We also found no support for a relationship between maternal age and condition nor maternal age and larval survival in the larval performance trials conducted in 2007. While this could be a true biological effect, it is also possible the lack of response is entirely an artifact of the sampling technique. From our samples we could not obtain competent larvae from multiple age groups at the same time, the larvae experienced some level of barotrauma during capture, and there were problems with seawater temperatures in the laboratory. Due to these complications, the results are not particularly informative.

Reproductive development and timing of parturition are the primary variables showing a response to maternal age. Older adults tended to have larvae that matured earlier in the parturition season, potentially allowing females to release their larvae over an extended period of time. Similar findings of longer spawning period were reported for black rockfish by Berkeley and co-workers in which (Berkeley and Bobko 2004; Berkeley et al 2004). In a dynamic ocean, producing larvae over an extended period of time increases the probability that larvae will enter the ocean during favorable environmental conditions.

As mentioned in the results, one interesting aspect of POP biology that we have discovered is the asynchronous development between the two ovarian lobes. Because the less developed ovary could be either the left or right lobe, care in the future must be taken to sample from both ovaries or at least the most advanced ovary when conducting reproductive assessments on POP. More importantly, the asynchronous development between lobes might allow a fish to extend the parturition season, perhaps by double depending on the timing of maturation of larvae in the second (later) ovarian lobe. If there is a limited amount of time that a POP can hold larvae in her gonad, maturing early in the parturition season as older female do would not necessarily extend the spawning period, but this strategy combined with asynchronous development of the ovaries would allow such an event to take place. This result requires further investigation.

Overall, our work demonstrates some level of maternal effect, but not to the same degree as that seen in shallow-water species (Bobko and Berkeley 2004a, Sogard et al 2008). This could be a true result, perhaps related to the deeper ocean water into which POP larvae are released relative to that of some of the other species which have been more often studied. Given the current age structure that we were able to sample, it would seem that unless parturition date is the driver for offspring survival (which it may very well be), then at this time maternal effects may not be as big a management concern as maintaining overall healthy population size. It is also possible that our results are an artifact of the "ghost of fishing past", because of the continuing age truncation of POP, limiting our ability to sample the oldest ages possible in this species. Only by sampling populations of POP with substantially older fish could we hope to conclusively resolve this particular speculation.

PART 2: Do age structure and maternal effects matter at the population level? Heuristic model explorations.

A variety of researchers studying the early life history of fishes have noted a relationship between egg size or larval characteristics and maternal age, size or condition (reviewed by Chambers and Leggett 1996). Recent interest in this phenomenon has focused on the effects of age truncation on population dynamics and the potential importance of maintaining age structure as a tool for population conservation and sustainable fisheries (Berkeley 2006). An increase in total mortality naturally reduces the proportion of older, larger fish in the population, with an overall effect of a decrease in per capita productivity even if the biomass of the population is maintained. If age-related maternal effects play a predictable role in egg and larval survival, the productivity of a fished population may become more variable or depressed than would be predicted from a spawning stock biomass-based model. These ideas are relatively straightforward to explore with age-structured models.

Because of a delay in analysis of the data, we did not incorporate results from the field study directly into our models. Also, our intent was to explore the relative influence of maternal effects on population productivity and common status measures used in stock assessment, rather than to produce a predictive model for POP. Here we provide methods and preliminary results for three modeling approaches to examine the population-level implications of age truncation and maternal effects.

Effects of Age Truncation on POP productivity

We used a simple "population fecundity" (examples used in Boreman 1997, Tereshchenko 2002) calculation to explore changes in productivity expected from age distributions for POP from the Gulf of Alaska:

$$N * \text{proportion in age class} * \% \text{ mature} * \text{wt-specific fecundity} * \text{egg survival} \qquad (1)$$

Population size estimates, age distributions, maturation and weight-specific fecundity parameters were taken from the Heifitz et al. 1999 slope rockfish assessment. There were noticeably different cumulative age distributions in the early 1980s relative to the mid 1990s (Figure M1). We examined the change in young-of-the-year (YOY) production that would be expected from age distributions in 1980 and 1996 assuming a constant N of 100,000 female fish and a range of different maternal effect functions driving larval survival (Figure M2). Hypothetical larval survival was held constant in the “no maternal effects” scenario.

YOY production per age class, based on Equation 1, was dramatically lower under all maternal effect scenarios due to the loss of older age classes in the 1996 age distribution (Figure M3a and b). Projections of annual YOY *S. alutus* production based on the age structure recorded from NMFS surveys conducted in 1980 ranged range from a minimum of 2,520 YOY produced in each of the three maternal effect scenarios to a maximum of 7,774,247 YOY when considering a step-wise maternal effect relationship (Fig. M3a). Cumulative minimum and maximum YOY production of all age classes combined were generated by the exponential and step maternal effect models, respectively. Peak production was

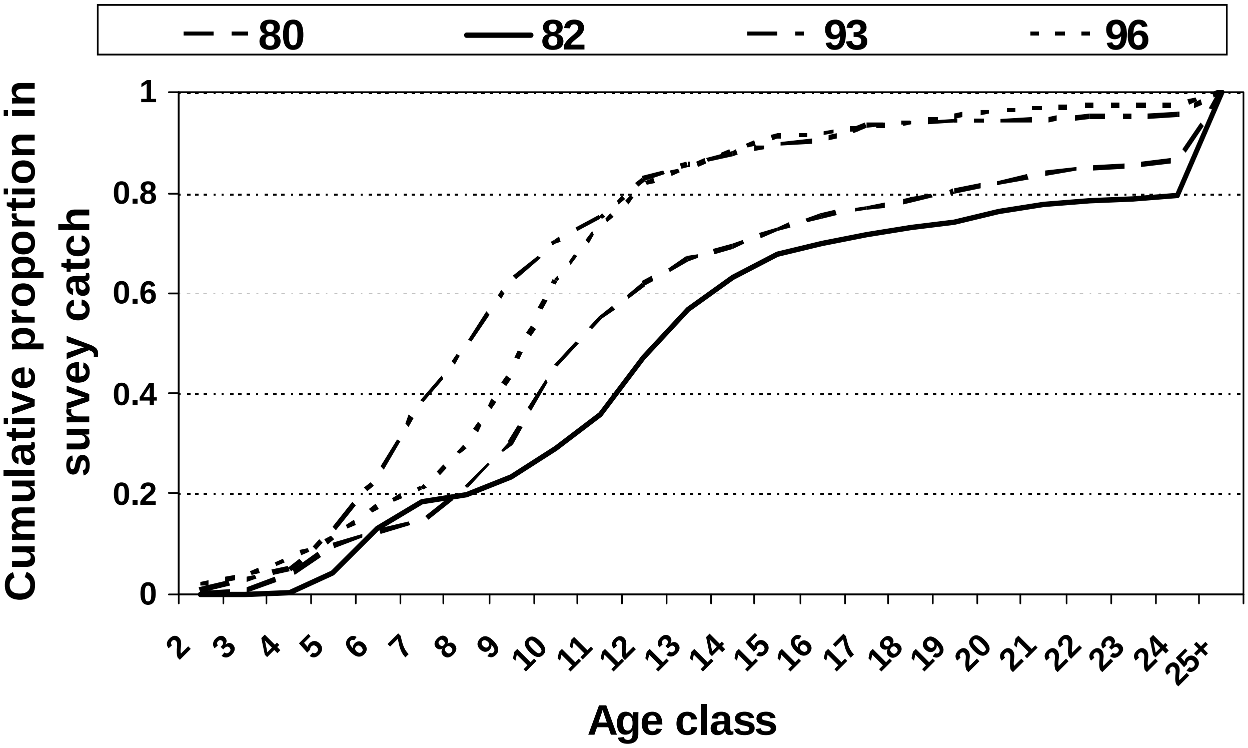


Figure M1. Cumulative proportion of catch-at-age for POP reported in the Slope Survey in four different survey years, showing a shift towards younger (and smaller) fish. The population fecundity calculations in this report are based on the pooled age distributions for 1980 and 1982 vs. the 1996 age distribution.

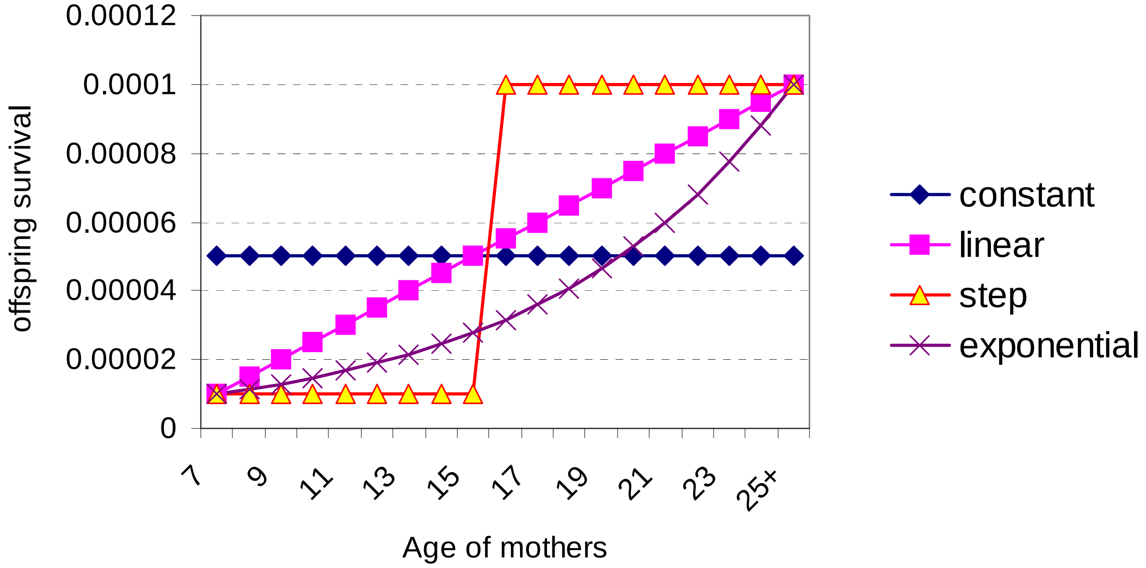
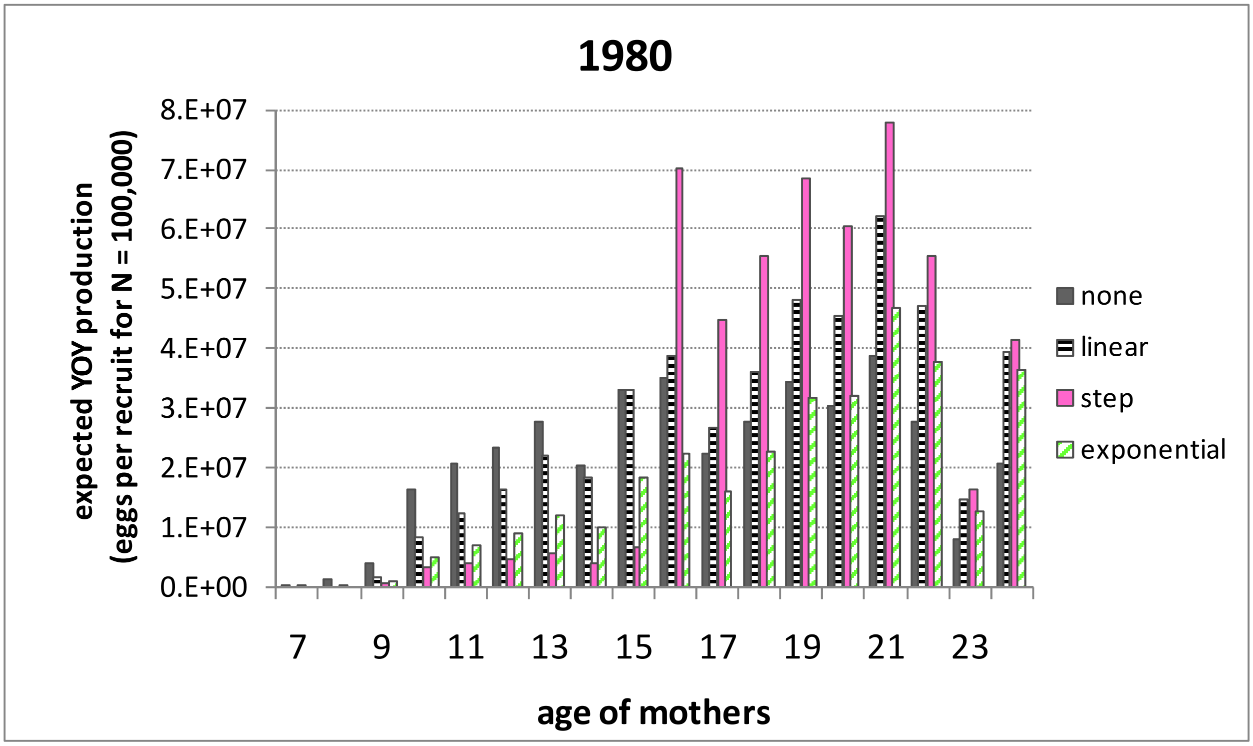


Figure M2. Hypothetical relationships between maternal age and larval survival applied to examine changes in POP population fecundity (Equation 1) with age distributions observed in the slope survey.

A.



B.

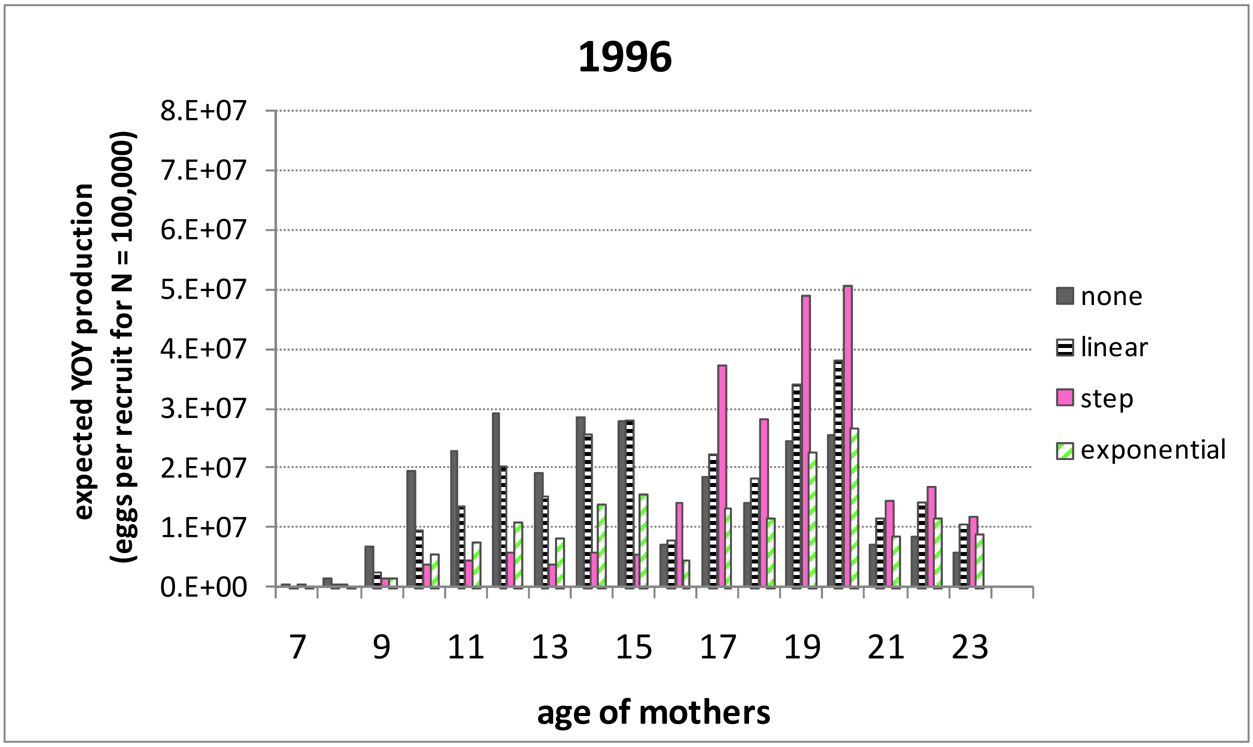
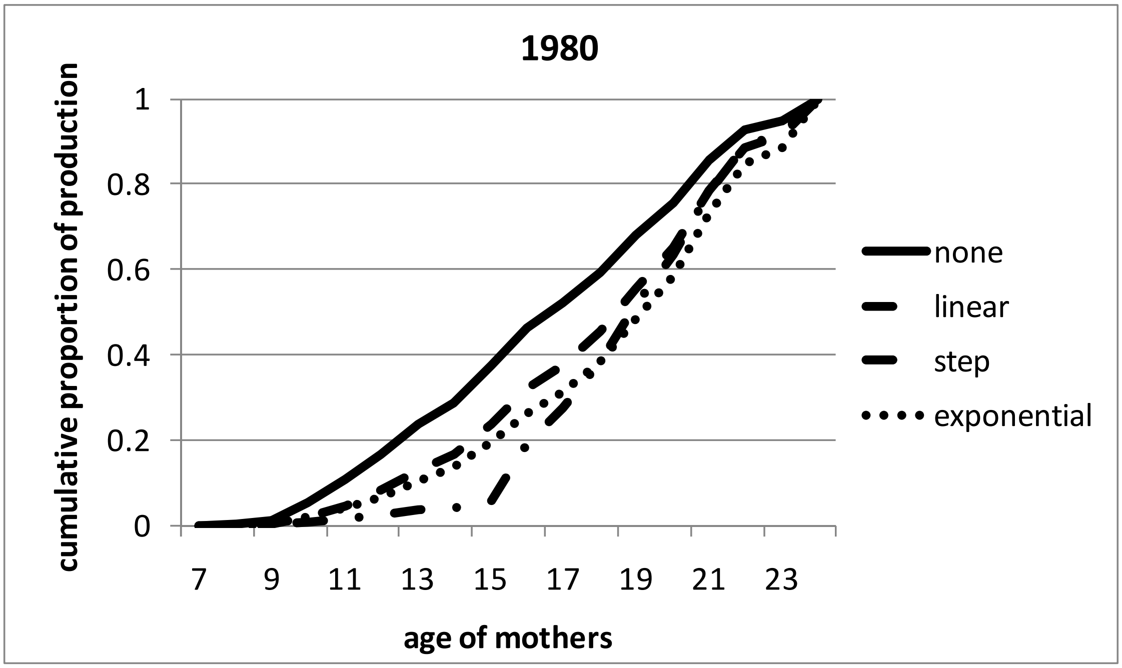


Figure M3. Young of the year (YOY) production by age class for hypothetical populations of POP with observed age distributions in 1980 (A) and 1996 (B), generated by Equation 1 and the maternal effect functions shown in Figure M2. N = 100,000 female fish for both graphs.

A.



B.

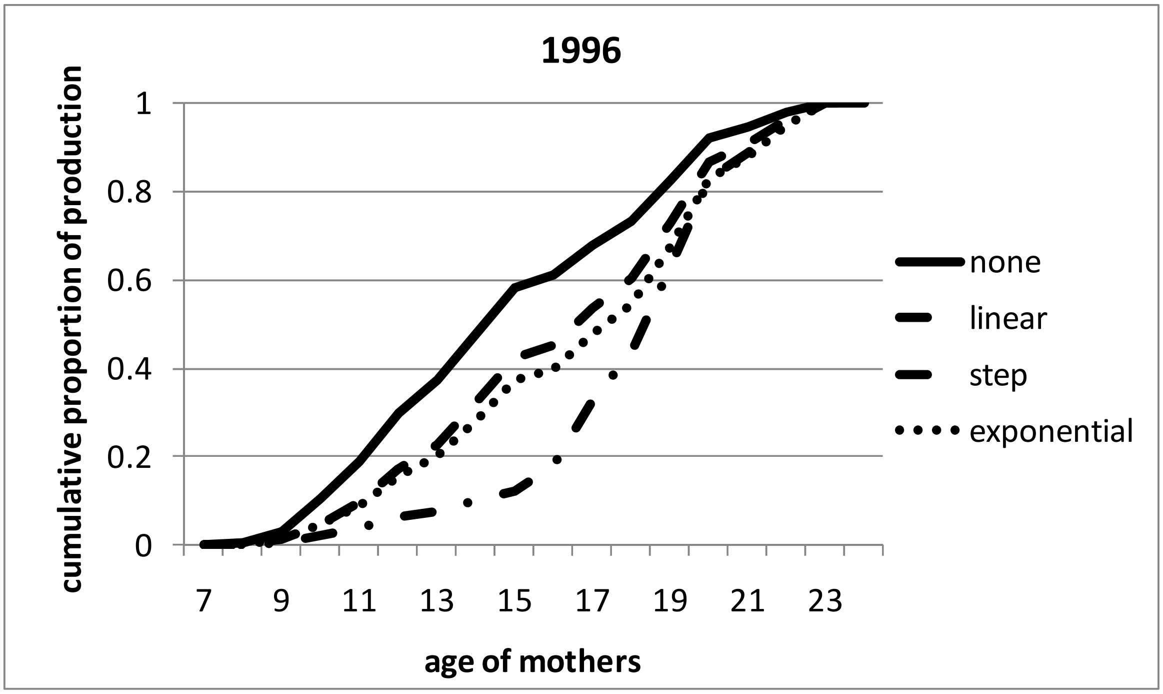


Figure M4. Expected cumulative proportion of young-of-the-year production by female age class in a population of Pacific ocean perch with observed age distributions from surveys in 1980 (a) and 1996 (b). Lines denote different maternal effects on larval survival (Fig. M2).

observed at age 21 in all four models. Models based on 1996 NMFS age structure data reflected a substantial proportional decrease among age classes of 20 years or more (Fig. M3b). The lowest level of age-specific fecundity (4,476 YOY) was contributed by the first reproductive age class and was equivalent in each of the maternal effect scenarios. Maximum age-specific YOY production (5,072,798) was estimated from the step step-wise maternal effect scenario. Cumulative minimum and maximum YOY production of all age classes combined were generated by the exponential and linear maternal effect models, respectively. Age 25+ was the largest producer of YOY for both distributions; in 1980, YOY production by the oldest age class would have been 34-70 million YOY, while in 1996 the age 25+ group would have been expected to produce 6.7-13.5 million YOY.

Projected differences in population productivity between 1980-82 and 1996 age distributions indicated reductions in YOY production among all models of 60-73% (Fig. M4). The effect of an increase in larval survival with maternal age on total expected YOY production for a population of 100,000 fish was much less than the loss due to reduced fecundity; this can be seen by comparing the percent change in YOY expected for the two age distributions with and without maternal effects included.

The primary loss is caused by the reduction in per capita fecundity, but a correlation between maternal age and larval survival can magnify the potential loss by 10-15%.

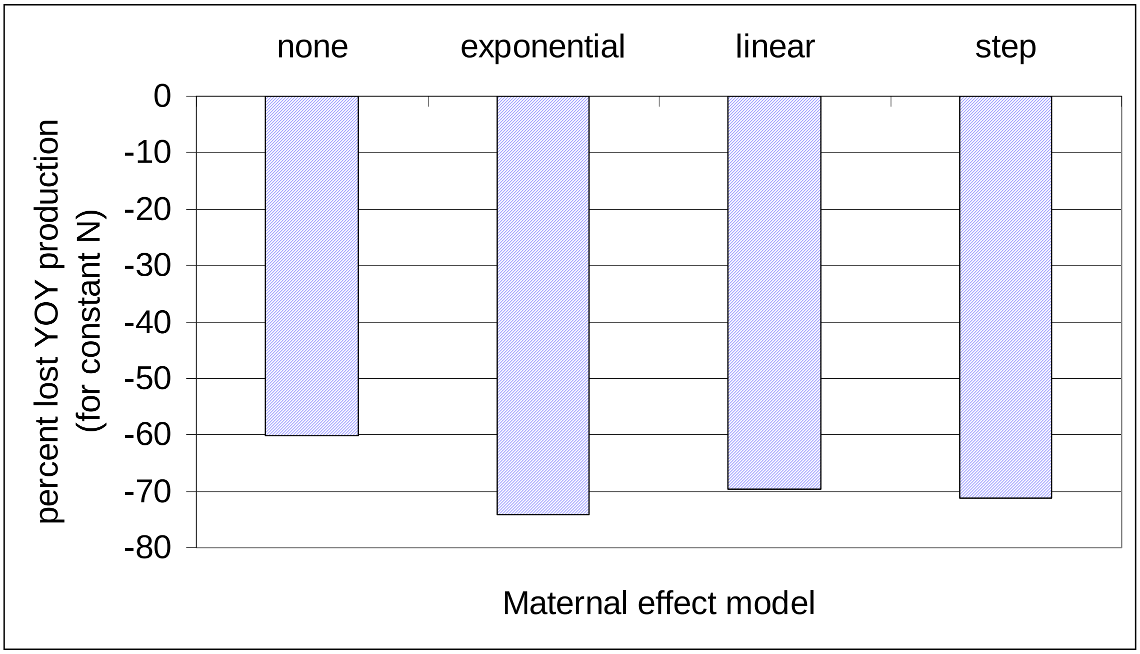


Figure M5. Calculated loss in per capita you-of-the-year production through age truncation, based on Equation 1 and maternal effects models shown in Figure M2.

It is not surprising that the per capita YOY production decreases when the age distribution is biased toward younger, smaller females. What this analysis shows is the *relative* magnitude of maternal effect induced changes in productivity when a population becomes age trunctated, as compared to a truncated population without maternal effects. We chose a set of maternal age – larval survival functions that were loosely based on the magnitude of larval survival rates that might be expected from changes in oil globule volume or swimming competency (an order of magnitude from lowest to highest survival, Figure M2); additional empirical investigation is needed to determine the actual expected range of survival rates. However, these results suggest that even if the maternal effect is relatively strong, the proportional loss in per capita productivity is largely a function of reduced fecundity (as a function of body size) because of a loss of large, highly fecund older fish. We did not examine the change in population fecundity when biomass is held constant, but this would be an important follow-up exercise, as the expectation for density compensation would be an increase in the number of young females in a population undergoing harvest (in other words, we might not expect N to remain constant as it was in these calculations).

Maternal effects and assessment metrics

Estimates of stock productivity can depend upon many factors that affect the stock-recruitment data, including stochastic variability in recruitment, the degree of autocorrelation in recruitment residuals, and the exploitation history. Because studies examining how maternal affects may affect fishing mortality reference points consist of relatively few case-specific studies (Spencer et al. 2007, Murawski et al 2001), a generalized understanding of how the maternal effects may influence fishing mortality reference points in a wide variety of situations has not emerged. For example, both the Alaska POP (Spencer et al. 2007) and the Georges Bank cod (Murawski et al. 2001) have experienced large fishing mortality rates in their past. Would the influence of maternal effects upon estimated productivity be similar with a more moderate exploitation history? Another issue is the life-history characteristics of the stock, as maternal effects have been suggested for long-lived, relatively low productivity rockfish stocks as well as short-lived Atlantic cod stocks. The recruitment pattern for a stock is related to its longevity (Longhurst 2002), and it is plausible that the influence of maternal effects upon estimated stock productivity is affected by its life-history characteristics.

Appendix 1 shows the results of simulation modeling designed to gain a more generalized understanding of how maternal effects can influence the productivity of marine fish populations. We use deterministic simulation models to characterize some general patterns of how maternal effects affect both the actual and estimated productivity of fish populations. Next, we use simulation modeling to determine how the influence of maternal effects upon estimated productivity is affected by exploitation history and autocorrelation in recruitment residuals for two types of life histories based upon Bering Sea/Aleutian Islands POP and Pacific cod. One of the key questions from these simulations is to examine the extent of bias in F_{msy} that may occur if maternal effects exists but is not recognized in the estimation of stock-recruitment parameters.

In summary, the mean of fishery reference point ratios $F_{msy(TL)}/ F_{msy(VL)}$ for POP indicate that $F_{msy(TL)}$ is generally larger than $F_{msy\ (VL)}$ for most harvest rates and levels of recruitment autocorrelation, with the mean of ratios ranging from 1.01 to 1.13 (Appendix Figure A6) . At the heavy fishing mortality rates of $F_{20\%}$ the degree of bias becomes reduced. The mean of ratios of $F_{crash(TL)}/ F_{crash(VL)}$ is larger than the mean of ratios observed for $F_{msy(TL)}/ F_{msy(VL)}$ for all combination of harvest rate and autocorrelation pattern, ranging from 1.10 to 1.30. Although there is on average some bias in F_{msy} of approximately 10%, the bias observed in F_{crash} is larger and exceeds 20% for most combinations of harvest rate and autocorrelation pattern.

The bias in F_{msy} and F_{crash} is reduced with the high fishing mortality rates of $F_{20\%}$. This effect results from the increased amount of data that occurs at small stock sizes for heavily-fished stocks, which result in improved estimates of the steepness parameter that determines the F_{msy} and F_{crash} reference points. This is revealed in the median yield obtained for each level of fishing mortality from the 200 POP simulations with an autocorrelation coefficient of 0.0 and $F_{40\%}$, which is a fishing rate close to F_{msy}. (Figure 8). The peak of the median estimated yields is close to the peak of the true yield curve for this stock, but the median estimated yields for higher fishing mortality rates are larger than the true yield due in part to the limited observations at these higher levels of fishing mortality. Additionally, the bias in estimated mortality at high fishing mortality rates is increased when maternal effects are not incorporated in the estimation of stock-recruitment parameters. As the fishing rate increases to $F_{20\%}$, the degree of bias at the larger fishing mortality rates is reduced.

A necessary part of adjusting fisheries management procedures to account for maternal effects is analyzing the extent to which management procedures do not account for maternal effects may be in error in meeting conservation goals. An age-specific maternal effect in larval survival clearly reduces the productivity of the stock simply due to increased levels of mortality. Bias in estimated yield and fishing mortality reference points that occurs when estimation of stock-recruitment parameters incorrectly neglects maternal effects can be affected by several factors, including the life-history characteristics and the levels of exploitation. Based on simulations of possible maternal effects in POP, the bias in F_{msy} observed when maternal effects were incorrectly neglected was less than approximately 10% in many situations. It is intuitive that the bias in estimated stock productivity is increased at high fishing mortality rates, as these are situations characterized by a relatively large proportion of young spawners that would likely be subject to maternal effects.

Because fishing rate reference points are largely influenced by the steepness of the stock-recruitment curve, any factor that influences the proportion of a given data set that occurs at small stock sizes can influence estimated fishing mortality reference points, including autocorrelated errors in recruitment residuals, the exploitation history, and the life-history of the species. The results obtained in the evaluation of fishery reference points as they relate to possible maternal effects in POP indicated that biases in estimated fishing mortality reference points may result from a lack of recognition of maternal effects. However, it is not clear how managing with potentially biased fishing reference points over a period of time affect risk of overfishing the stock. For example, what is the significance of any bias resulting from maternal effect relative to implementation errors in achieving target fishing rates, or observation errors on abundance surveys? An additional step for future research is to conduct management strategy evaluations to assess the impact of managing stocks with potentially biased reference points.

Effects of age-specific larval release timing in a variable environment

Our field data, like some other studies of rockfishes (e.g., Sogard et al. 2008) and gadids (e.g., Begg and Martiensdottier 2000), shows that the earliest spawners are primarily larger and/or older females. There have been a number of explanations posed for this pattern of maternal effects on spawn timing, mostly centered around the expected greater efficiency of larger or older females to allocate excess energy into reproduction (Marshall et al. 2008). This may enable older females to start physiological processes, such as vitellogenesis, and reproductive behaviors, such as migration, earlier in the year. The advantages of this to the older females would be most apparent if settling juveniles must compete for food or space (Lucero 2009). However, it is not a simple rule of older females spawning first; in black rockfish, the earliest spawners do tend to be older, but older females as a group spawn over the entire season (Bobko and Berkeley 2004). Thus, the net effect of a diverse age structure may simply be that the spawning or parturition season is more protracted. Under highly stochastic environmental conditions for larvae, a longer reproductive season may increase the probability that some of the year's cohort will be in the right place at the right time for optimum survival; this could lead to a decrease in year-to-year variance in cohort strength for populations with a broad age structure, relative to a truncated one.

We have constructed an individual-based model based on the distribution of timing of parturition calculated by Bobko and Berkeley (2004) to examine the population-level effects of age truncation when spawn timing affects larval survival probability. The model follows individual females over time, with stochastic survival dependent on natural and fishing mortality and stochastic reproductive success dependent on the "match" of spawn timing and optimal environmental conditions (based on timing of spring transition). The initial results are striking; annual variability in cohort strength can be strongly dependent on age structure when larval survival is strongly dependent on a tight matching of parturition and environmental conditions. We hope to adapt the modeling approach for POP to incorporate our data on age and parturition timing, then compare the resulting year class strength variability to observations in Alaska, British Columbia, and southern populations in Oregon and Washington.

Conclusions from models

Although preliminary, all of our modeling efforts suggest that the population-level effects of an increase in larval survival with maternal age is relatively minor unless the survival rate differences are very large. This does not necessarily mean that maternal effects are inconsequential; arguably, they can't be if they have evolved as a regular pattern in fish life histories. However, it may be that the effects are more complex, subtle or less predictable than we expected, or even multi-generational (Sogard, *personal* *communication*). Our initial results from the timing of reproduction analysis are intriguing, although there is not an obvious selection mechanism for this phenomenon.

Overall conclusions

Our study reveals that there are maternal effects in POP, but this is primarily through an expansion of spawning timing in older fish as opposed to an increase in reproductive investment per offspring. In large part work such as this suffers from the ghost of harvest past. The oldest POP we caught was 32 years old. Given that the maximum lifespan of POP is somewhere on the order of 100 years, this lack of contrast in the age data is a confounding factor around which we must perform our analyses. There was massive harvest of Gulf of Alaska POP in the 1960's, with peak landings somewhere around 350,000 metric tons in 1965. Had that substantial harvest not occurred, many of those fish would in all likelihood be alive today, contributing to a much broader age range than is currently observed. Therefore, while our work finds evidence for a maternal effect in the form of timing of parturition, had we sampled across a broader age range it is certainly possible that we would have found other aspects of maternal effects as well. As discussed in the modeling section, larval survival would have to substantially increase in order for there to be a strong effect. This does not mean that maternal effects are unimportant; rather it indicates that the effect may be more nuanced than we have been able to detect at this time.

Publications

Three publications are currently in progress from this work, and work on these publications is moving forward. We anticipate that at least two of these publications will be submitted for peer review before August 2009.

Outreach Presentations

- Heppell, SA. Fish assemblages, the value of big old fecund female fish (BOFFFs) and rebuilding plans for depleted species in the California Current System (CCS). Public Interest Environmental Law Conference, Eugene, OR 2010. Invited talk and panelist

Peer Presentations

- Heppell, SS and WD Smith. "Maternal effects, age structure and population resiliency: managing for diversity in the face of uncertainty" American Fisheries Society Annual Meeting, Ottawa. 2008. Invited talk.
- Heppell, SS and WD Smith. "Long-lived marine species and resiliency to overfishing" International Marine Conservation Congress, Washington DC 2009. Contributed Talk.

- Heppell, SA, SS Heppell, WD Smith, L Arnold and S Piovano Maternal effects in Pacific ocean perch (*Sebastes alutus*) from the Gulf of Alaska. Oregon Chapter of the American Fisheries Society annual meeting. Bend, OR 2009. Contributed paper.
- Heppell, SA, SS Heppell, WD Smith, L Arnold and S Piovano. Maternal effects in Pacific ocean perch (*Sebastes alutus*) from the Gulf of Alaska. American Society of Ichthyologists and Herpetologists Annual Meeting, Portland, OR. 2009. Contributed Poster.
- Spencer, P.D. 2009. What are the management implications of maternal effects: A review and progress report from the North Pacific. Fish Reproduction and Fisheries Working Group 3 Meeting. Vigo, Spain.
- Spencer, P.D. 2008. The influences of maternal age of spawning, recruitment variability, and life-history pattern upon harvest reference points and fishery management. Symposium on Parental Effects and their Consequences for Recruitment Dynamics and the Sustainability of Harvested Stocks. American Fisheries Society 138th Annual Meeting, Ottawa, Canada.
- Spencer, P.D. 2007. The effect of spawner age on stock productivity: influences of life-history pattern and recruitment variability. National Marine Protected Area Science Center Institute Working Group on Maternal Age Effects and Marine Reserves, Santa Cruz, CA.
- Spencer, P.D., D. H. Hanselman and M. Dorn. 2006. The effect of maternal age of spawning on estimation of F_{msy} for Alaskan Pacific ocean perch. 14th Western Groundfish Conference, Newport, Oregon.

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Literature Cited

Anthony, JA, DD Roby & KR Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Exp. Marine Biol. Ecol. 248: 53-78.

Begg, G.A., Marteinsdóttir, G., 2000. Spawning origins of pelagic juvenile cod (Gadus morhua) inferred from spatially explicit age distributions: potential influences on year-class strength and recruitment. Mar. Ecol.Prog. Ser. 202:193–217.

Berkeley, SA, C Chapman, and SM Sogard. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology 85:1258-1264.

Berkeley, SA, MA Hixon, RJ Larson, and MS Love. 2004b. Fisheries Sustainability via Protection of Age Structure and Spatial Distribution of Fish Populations. Fisheries 23: 23-32.

Bobko, SJ, and SA Berkeley. 2004. Maturity, ovarian cycle, fecundity and age-specific parturition of black rockfish (*Sebastes melanops*). Fishery Bulletin 102:418-429.

Boehlert, GW, WH Barss, and PB Lamberson. 1982. Fecundity of the widow rockfish, *Sebastes entomelas*, off the coast of Oregon Fish. Bull. 80: 881-884

Boehlert, GW and MM Yoklavich. 1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. 167:354-370.

Bowers, MJ 1992. Annual reproductive cycle of oocytes and embryos of yellowtail rockfish *Sebastes flavidus* (Family Scorpaenidae). Fishery Bulletin 90: 231-242.

Burden, R.L. and J.D. Faires. 2001. Numerical Analysis, 7th ed. Brooks-Cole, Pacific Grove, CA. 864 pp.

Chambers RC, and Trippel EA (eds) 1997. Early life history and recruitment in fish populations. Fish and Fisheries Series 21. Chapman & Hall, London, p 63–102

Chilton, E. 2007. Maturity of female northern rockfish *Sebastes polyspinis* in the central Gulf of Alaska. Alaska Fishery Research Bulletin 12(2): 264-269.

Chilton, DE and RJ Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci 60: 102 pp.

DiCosimo J and N Kimball. 2001. Groundfish of the Gulf of Alaska: A Species Profile. North Pacific Fishery Management Council, Anchorage, AK

Dorn, MW 2002. Advice on west coast rockfish harvest rates from Bayesian meta-analysis of stock-recruitment relationships. N. Am. J. Fish. Man. 22:280-300.

Goodman, DG, M Mangel, G Parkes, T Quinn, V Restrepo, T Smith, and K Stokes. 2002. Scientific review of the harvest strategy currently used in the BSAI and GOA groundfish fishery management plans. North Pacific Fishery Management Council, 605 W. 4th Ave, suite 306, Anchorage, AK

Hanselman, D, J Heifetz, JT Fujioka, and JN Ianelli. 2004. Pacific ocean perch. In: Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska for 2005. North Pacific Fishery Management Council, 605 W. 4th Ave, suite 306, Anchorage, AK, pp. 385-410.

Kjesbu OS, Klungsoyr J, Kryvi H, Witthames PR, Greer Walker M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can J Fish Aquat Sci 48:2333–2343.

Kjesbu, OS, P Solemdal, P Bratland, and M Fonn. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J Fish and Aquat Sci 53: 610-620.

Kjesbu, OS, PR Witthames, P Solemdal, and M Greer Walker. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. J Sea Res 40:303–321

Leaman, BM and BR Melteff. 1987. Incorporating reproductive value into Pacific ocean perch management. Lowell Wakefield Fisheries Symposium: Proceedings of the International Rockfish Symposium Anchorage, AK. Alaska SeaGrant Report 87-2: 355-368.

Leaman, BM. 1991. Reproductive styles and life history variables relative to exploitation and management of Sebastes stocks. Environmental biology of fishes. 30:253-271.

Leaman, BM, and RJ Beamish. 1984. Ecological and management implications of longevity in some northeast Pacific groundfishes. Int. North Pac. Fish. Comm. Bull. 42:85–97.

Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. Fisheries Research 56:125-131.

Love, MS, M Yoklavich, and S Thorsteinson 2002. The Rockfishes of the Northeast Pacific. University of California Press. 404pp

Lucero, Y. 2008. Maternal effects and time to recovery. Bulletin of Marine Science 83:217-234.

Marteinsdottir, G. and A. Steinarsson. 1998. Maternal influence on the size and viability of Iceland cod (*Gadus morhua* L.) eggs and larvae. Journal of Fish Biology 52: 1241-1258.

Marteinsdottir, G. and G.A. Begg. 2002 Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod, *Gadus morhua*. Mar. Ecol. Prog. Series 235:235-256.

Monteleone, D M, and ED Houde. 1990. Influence of maternal size on survival and growth of striped bass *Morone saxatilis* Walbaum eggs and larvae. J. Exp. Mar. Biol. Ecol. 140:1-11.

Murawski, S.A. P.J. Rago, and E.A. Trippel. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES J. Mar. Sci. 58:1002-1014.

Murawski, SA, PJ Rago, and EA Trippel. 1999. Impacts of demographic variation in spawning success on reference points for fishery management. p 77–85 In: Restrepo VR (ed) Proc 5th Nat NMFS Stock Assessment Workshop: providing scientific advice to implement the precautionary approach under the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Tech Memo NMFS-F/SPO-40.

Myers, R.A., K.G. Bowen, and N.J. Barrowman. 1999. Maximum reproductive rate of fish at low population size. Can J. Fish. Aquat. Sci. 56:2404:2419.

Reynolds, S. & T. Kunz. 2001. Standard methods for destructive composition analysis. p. 242. In: J.R. Speakman (ed.) Body composition analysis of animals: a handbook of non-destructive methods, Cambridge University Press, Cambridge ; New York.

Secor, DH 2000. Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment in Chesapeake Bay striped bass. ICES J. Mar. Sci. 57: 403-411.

Secor DH 2007. The year-class phenomenon and the storage effect in marine fishes. Journal of Sea Research 57:91-103.

Sogard, SM, SA Berkeley, and R Fisher. 2008. Maternal effects in rockfishes Sebastes spp.: a comparison among species. Mar. Ecol. Prog. Ser. 360: 227-236.

Spencer, P and M Dorn. 2003. Evaluation of Bering Sea/Aleutian Islands Pacific ocean perch management parameters using Bayesian stock-recruit analysis. Report prepared for the North Pacific Fishery Management Council, Anchorage, AK

Spencer, P., D. Hanselman, and M. Dorn. 2007. The effect of maternal age of spawning on estimation of Fmsy for Alaskan Pacific ocean perch. pp. 513-534 In J. Heifetz, J. DiCosimo, A.J. Gharrett, M.S. Love, V.M. O'Connell, and R.D. Stanley [eds.]. Biology, assessment, and management of north Pacific rockfishes. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Spencer, P.D. and J.N. Ianelli. 2008. Pacific ocean perch. In Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 2009, pp. 917-972. North Pacific Fishery Management Council, 605 W. 4th Ave, suite 306. Anchorage, AK 99501

Thompson, G, J. Ianelli, R. Lauth, S. Gaichas, and K. Aydin. 2008. Assessment of the Pacific Cod Stock in the Eastern Bering Sea and Aleutian Islands Area. In Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 2009, pp. 221-401. North Pacific Fishery Management Council, 605 W. 4th Ave, suite 306. Anchorage, AK 99501

Vallin L, and A Nissling. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*: implications for stock structure effects on recruitment. Fish Res 49:21–37.

Westrheim, S.J. 1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.

Wyllie Echeverria, T. 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. Fishery Bulletin 85: 229--250.

Yamada, J, and M Kusakari. 1991. Staging and the time course of embryonic development in kurosoi, *Sebastes schegeli*. Env. Biol. Fish. 30: 103-110

Appendix I

The influences of maternal age of spawning, recruitment variability, and life-history pattern upon harvest reference points and fishery management.

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Introduction

Maternal effects, defined here as the reduction in larval viability with reduced spawner age, have been proposed as one feature of marine fish populations that motivate the conservation of age and size structure. For example, Berkeley et al. (2004b) suggested marine protected areas as a potential management tool for conserving a sufficient amount of age and size structure such that larval viability remains relatively high. However, relatively little work has been conducted to examine how maternal effects can influence traditionally used fishery management reference points, and how current harvest strategies may need to be modified to account for maternal effects in larval survival.

Maternal effects can be viewed as affecting both the actual productivity of a stock and the estimated productivity obtained from empirical data. Maternal effects clearly results in reduced recruitment relative to an unaffected population, as the production of recruits from a given number of eggs is reduced due to increased larval mortality. Estimated productivity, however, is obtained from comparing a given empirical recruitment time series to a measure of reproductive potential that represents our available knowledge of maternal effects, and generally involve transforming the units of reproductive potential from eggs to viable larvae. Because this transformation affects both the estimated parameters for the stock-recruitment curve and the expected lifetime production of reproduction output, the estimated yield curves can change in complex ways. In particular, the comparison of an empirical recruitment time series against a diminished measure of reproductive output obtained with maternal effects results in a stock-recruitment curve appearing steeper at low stock sizes, although it is critical to remember that units of measurement for reproductive output have changed (Spencer et al. 2007).

Few studies have evaluated the influence of maternal effects on estimated productivity, but the available information suggests that maternal effects have more influence on estimated productivity at high fishing mortality rates. Spencer et al. (2007) found that hypothesized maternal effects reduced the estimated F_{msy} (the fishing rate that maximizes sustainable yield) for Bering Sea/Aleutian Islands (BSAI) and Gulf of Alaska (GOA) Pacific ocean perch (POP) by 3% and 9%, respectively. In contrast, the reductions in F_{crash} (the maximum fishing rate a stock could sustainably support) for these two stocks were 17% and 22%. Similarly, Murawski et al. (2001) found that estimates of F_{med} (the fishing rate corresponding to the median level of recruits/spawner) for Georges Bank Atlantic cod declined from 0.61 to 0.57 when maternal effects were considered, whereas estimated F_{crash} declined from 1.4 to 0.88.

Estimates of stock productivity can depend upon many factors that affect the stock-recruitment data, including stochastic variability in recruitment, the degree of autocorrelation in recruitment residuals, and the exploitation history. Because studies examining how maternal affects may affect fishing mortality reference points consist of relatively few case-specific studies (Spencer et al. 2007, Murawski et al 2001), a generalized understanding of how the maternal effects may influence fishing mortality reference points in a wide variety of situations has not emerged. For example, both the Alaska POP (Spencer et al. 2007) and the Georges Bank cod (Murawski et al. 2001) have experienced large fishing mortality rates in their past. Would the influence of maternal effects upon estimated productivity be similar with a more moderate exploitation history? Another issue is the life-history characteristics of the stock, as maternal effects have been suggested for long-lived, relatively low productivity rockfish stocks as well as short-lived Atlantic cod stocks. The recruitment pattern for a stock is related to its longevity (Longhurst 2002), and it is plausible that the influence of maternal effects upon estimated stock productivity is affected by its life-history characteristics.

The purpose of this appendix is to use simulation modeling to gain a more generalized understanding of how maternal effects can influence the productivity of marine fish populations. We use deterministic simulation models to characterize some general patterns of how maternal effects affect both the actual and estimated productivity of fish populations. Next, we use simulation modeling to determine how the influence of maternal effects upon estimated productivity is affected by exploitation history and autocorrelation in recruitment residuals for two types of life histories based upon Bering Sea/Aleutian Islands POP and Pacific cod. One of the key questions from these simulations is to examine the extent of bias in F_{msy} that may occur if maternal effects exists but is not recognized in the estimation of stock-recruitment parameters.

Methods

A two-stage recruitment model was used to relate age-dependent larval survival to stock productivity (Figure 1). The “viable larvae” stage represents the period from eggs to 14-day viable larvae, and is followed by a “pre-recruit” phase representing the period from 14 days to age of recruitment, defined as age 1 for Pacific cod and age 3 for POP. For each stage, the Beverton-Holt recruitment model was used to model the survivors remaining at the end of the stage. The differential equation describing Beverton-Holt mortality is

$$\frac{dN}{dt} = -(a + bN)N \qquad \text{Eq. 1}$$

and the discrete-time solution is

$$N_{t+\Delta t} = \frac{N_t}{\alpha + \beta N_t} \qquad \text{Eq. 2}$$

where α and β are density-independent and density-dependent parameters, respectively, and are defined as

$$\beta = \frac{b}{a}(e^{a\Delta t} - 1) \qquad \text{and} \qquad \alpha = e^{a\Delta t} \qquad \text{Eq. 3}$$

Maternal effects in survival occur when the mortality rate terms *a* and *b* are a function of spawner age, which can be expressed by expanding Eq. 1 to a system of differential equations

$$\begin{array}{ccc} \frac{dN_1}{dt} & = & -\left(a_1 + b_{1\bullet} \sum_{i=1}^{m} N_i \right) N_1 \\ \vdots & \ddots & \vdots \\ \frac{dN_m}{dt} & = & -\left(a_m + b_{m\bullet} \sum_{i=1}^{m} N_i \right) N_m \end{array} \qquad \text{Eq. 4}$$

where *m* is the total number of ages and $b_{i\bullet}$ is the density-dependent effect of each individual upon the mortality rate for another individual of age *i*.

For simplicity, it is assumed that any maternal effects in survival occur in the viable larvae stage, and the survival during the pre-recruit phase is not dependent upon spawner age and can be modeled with Eq. 2. Values of α and β for the pre-recruit phase were obtained from traditional stock-recruitment analyses applied to estimates of eggs and recruits obtained from recent stock assessments of BSAI POP and Pacific cod. Note that this is an approximation for this stage, as more precise estimation of α and β would require information on production of viable larvae, which currently does not exist; thus, the parameters used for this simulation should be considered as illustrative. Fitting the Beverton-Holt curve was facilitated by reparameterizing Eq. 2 in terms of R_0 (the predicted recruitment for an unfished stock) and steepness (*z*; the predicted recruitment divided by R_0 when the stock is at 20% of its unfished size) with the following equations

$$\beta = \frac{z - 0.2}{0.8 R_0 z} \qquad \alpha = \frac{\phi(1 - z)}{4z} \qquad \text{Eq. 5}$$

where φ is the expected lifetime egg production per recruit in an unfished stock.

Bayesian lognormal prior distributions were used to estimate *z* and R_0 for BSAI POP and Pacific cod. The mean values of the prior distributions for *z* were set to 0.79 and 0.39 for Pacific cod and POP, respectively, and are representative values obtained from a meta-analysis by Myers et al. (1999) for the Gadidae and Scorpaenidae families. The mean values of R_0 were taken as the recruitments associated with the largest observed stock sizes. For POP, estimates of *z* and R_0 of 0.76 and 75.51, respectively, were obtained, which corresponds to estimates of α and β of 36,320 and 1.20174e-2, respectively.

Three cases were considered for production of viable larvae: 1) no maternal effects (NOME) in which *a* is constant over spawner age and *b*=0; 2) density-independent maternal effects (DIVL) in which *a* decreases with spawner age and *b* = 0; and 3) density-dependent maternal effects (DDVL) in which both *a* and *b* decrease with spawner age.

Estimates of *a* for the viable larvae stage were obtained from modifications to the larval survival relationships found in the laboratory by Berkeley et al. (2004a), in which the days to 50% mortality ($d_{50\%}$) for larval black rockfish can be modeled as an exponential function of maternal age with the following form

$$d_{50\%} = c_1 + c_2(1 - e^{c_3 * age}) \qquad \text{Eq. 7}$$

where c_1, c_2, and c_3 are constants and *age* is maternal age (Figure 2). The original c_1, c_2, and c_3 parameters derived by Berkeley et al. (2004a) were modified to account for differences in longevity between black rockfish and Pacific cod and Pacific ocean perch. Specifically, black rockfish have an estimated natural mortality rate of 0.20 for older females, which differs substantially from that estimated for Pacific cod (0.34; Thompson 2008) and Pacific ocean perch (0.06; Spencer and Ianelli 2008). It is plausible that the range of maternal ages where larval survival is diminished is greater for longer-lived fish than shorter-lived fish. Thus, the parameters of Eq. 7 were modified such that the survival of larvae from younger spawners was decreased for POP and increased for Pacific cod relative to black rockfish. The daily instantaneous mortality rate (*a*) was computed from $d_{50\%}$ as

$$a = \ln(0.5) / d_{50\%} \qquad \text{Eq. 8}$$

As spawner age increases the larval survival to 14 days, computed as exp(-*a**14), approaches its asymptote more gradually for POP than either black rockfish or Pacific cod, reflecting its increased longevity (Figure 2).

When no maternal effects in larval survival occur, the *a* parameter for all spawner ages is set to the daily mortality rate associated with the maximum age. When density-independent maternal effects in larval survival occur, the *a* parameter is derived from Eq. 7 and 8 for each spawner age. Finally, density-dependent maternal effects are modeled by multiplying the *a* parameter from Eq. 7 and 8 by a constant *b*/*a* ratio. Because density-dependence in the viable larvae stage is expected to be small, the *b*/*a* ratio was set to one-tenth that estimated from the pre-recruit phase.

In the NOME and DIVL cases, system (4) reduces to either a single differential equation or a series of independent differential equations, respectively, and could thus be solved analytically. In the DDVL case, the Adams-Bashforth-Moulton numerical method (Burden and Faires 2001) was used solve the system of differential equations. This method uses four previous function evaluations to obtain a numerical solution at a particular point, and Runge-Kutta methods were used to obtain the initial function evaluations.

Stochastic simulation modeling was conducted to estimate any biases in estimated stock productivity and fishing rate reference points for the two life-history types in the presence of maternal effects under a range of conditions. An operational model that incorporates maternal effects in larval survival, autocorrelated recruitment variability, and level of harvesting was used to simulate recruitment. Each simulation begins with the stock abundance and age structure in equilibrium with no fishing, and is then harvested for 100 years. The harvest rates modeled were expressed in terms of spawning potential ratio (SPR), in which a harvest rate of $F_{xx\%}$, produces a value of eggs produced per spawner that is *xx%* of the value for an unfished population. The five harvest rated modeled were $F_{100\%}$ (an unfished population), $F_{80\%}$, $F_{xx\%}$, $F_{xx\%}$, and $F_{xx\%}$. Two hundred simulations were conducted for each of the 25 combinations of harvest rate and recruitment pattern for each life-history pattern, and time series of recruits, total larvae (which is proportional to eggs, and ignores the maternal effect in larval survival), and viable larvae were obtained for each simulation. For each of the two measures of reproductive output (total larvae and viable larvae), an estimation model was used to estimate stock recruitment parameters, equilibrium yield as a function of fishing mortality, and the F_{msy} and F_{crash}. For each of these two reference points, the ratio of the value obtained when total larvae are used as reproductive output to the value obtained when viable larvae are used as reproductive output provides a measure of any potential bias associated with ignoring maternal effects when they, in fact, occur.

Results and Discussion

The general pattern of the influence of maternal effects upon actual and estimated stock productivity can be illustrated with deterministic runs using the recruitment model above. Pacific cod life-history parameters are used for these deterministic runs, although the general patterns would apply to any stock with maternal effects in larval survival.

General implications of maternal effects in larval survival upon equilibrium recruitment and yield

Maternal effects in larval survival add additional age-dependent mortality that reduces recruitment and equilibrium yield, and the degree of reduction is related to the spawner age structure. To illustrate this, consider the recruitment produced from a population without maternal effects relative to an otherwise equal population with density-independent maternal effects (Figure 3). Because a stock in equilibrium with no fishing will have a relatively small proportion of young spawners that would be affected by maternal effects, the reduction in recruitment with the additional larval mortality from maternal effects is relatively small. As the stock size and egg production is further reduced due to fishing pressure, the relative reduction in recruitment increases due to the increased proportion of young spawners. The equilibrium recruitment occurs where the recruits produced are replaced by the lifetime egg production per recruit, and the replacement lines corresponding to F=0 and F=0.25 are shown in Figure 4a. In this example, the recruitment equilibrium at F=0 is not substantially affected by maternal effects, whereas some reduction in equilibrium recruitment due to maternal effects is observed at F=0.25.

The reduction in equilibrium recruitment with increased fishing is more pronounced when maternal effects in larval survival occur, and the F rate that corresponds results in an equilibrium recruitment of zero (F_{crash}) is lowered with maternal effects (Fig 4b). The more rapid reduction in equilibrium recruitment with increasing fishing mortality results directly in changes to both the scale and shape of the equilibrium yield curve, which is computed as the product of equilibrium recruitment and yield-per-recruit (which is unaffected by maternal effects). In the example shown in Figure 4c, the maximum equilibrium yield is reduced when maternal effects occur. Additionally, the shape of the yield curve is altered because of the disproportionate influence of maternal effects at high fishing mortalities with truncated age structures, as the relative difference in equilibrium yield increases with fishing mortality.

Incorporation of maternal effects in the density-independent a parameter affects both the asymptote and slope at the origin of the Beverton-Holt curve, and thus affects the scale of the equilibrium yield curve as well as the fishing rate reference points F_{msy} and F_{crash}. This is illustrated in Figures 4a-b, in which stock recruitment and yield curves with a baseline level of the a parameter (and $b = 0$) are compared to curves obtained when the baseline level of a is doubled and tripled. In contrast, incorporation of maternal effects in the b parameter affects essentially the scale of the equilibrium yield curve; this is illustrated in Figures 4c-d which show the effect of doubling and tripling a baseline level of b. This is consistent with the traditional theory for the Beverton-Holt curve without maternal effects, in which the b parameter only affects the scale of the curve and does not influence the fishing rate reference points. For example, equilibrium recruitment for the Beverton-Holt model can be expressed as

$$R_{eq} = \frac{\phi - \alpha}{\phi\beta} \qquad \text{Eq. 9}$$

where φ is the reproductive output produced per recruit. Thus, a change in β (or b) scales the equilibrium recruitment by a constant factor. Maternal effects in the b parameter does result in slight differences in the shape of the yield curve and the value of F_{msy} because b varies by age and the degree of larval mortality is determined by the amount of age truncation. However, the extent of this effect is less than that observed with the a parameter and is not observable in the plot in Figure 4d. Because fishing rate reference points are a critical component of fisheries management, this result indicates much of the management concern are maternal effects that affect density-independent mortality, or the slope at the origin of the stock-recruitment curve, rather than the scale parameters.

General implications of maternal effects in larval survival upon estimated recruitment

Consideration of maternal effects in the estimation of stock-recruitment parameters typically involves relating an observed time series of recruits to an improved estimate of reproductive potential that reflects maternal effects. A key point for this type of analysis is that while maternal effects does alter the definition of reproductive potential (typically transforming the units from eggs or spawning stock biomass to viable larvae), it does not alter the available recruitment data. Instead, recruits are defined as the number of young fish entering the population, and are often estimated from field data from juvenile surveys or population models that rely upon information on age and size structure. Maternal effects generally diminish the reproductive potential produced by a fished stock, relative to an unfished stock, because of the age-dependent larvae survival and the reduction of older ages associated with fished stocks (Spencer et al 2007, Murawski et al. 2001). Thus, estimation of stock-recruitment parameters typically involves comparing a given time-series of recruits to a diminished measure of reproductive output, which results in an increase in steepness in the stock recruitment curve. This is illustrated in Figure 5, in which the stock-recruitment curve obtained from using viable larvae for reproductive output is shifted to the left of the estimated curve obtained from using total larvae as reproductive output.

The diminished reproductive potential associated with maternal effects also affects the replacement lines, which have a slope of the inverse of the expected lifetime production of reproductive output per recruit. Thus, the diminished production of reproductive output per recruit associated with maternal effects implies a larger number of recruits required to produced a given level of reproductive output (relative to an unfished population), which also shifts the replacement lines obtained with maternal effects to the left of those obtained without maternal effects, as shown in Figure 5. Because the equilibrium recruitment is the intersection of the replacement line and the stock recruitment curve, these two effects can potentially moderate any change in estimated equilibrium recruitment when the units of reproductive output are altered to reflect maternal effects. In the example in Figure 5, two sets of estimated stock-recruitment curves and replacement lines are shown, one with density-independent maternal effects and one with no maternal effects. Despite the change in the estimated recruitment curves, the equilibrium recruitment for this level of fishing mortality is nearly identical.

Simulation modeling of the influence of maternal effects upon fishing mortality reference points in stochastic environments

Apart from the general influences of maternal effects illustrated above, marine populations are subject to many factors that can affect the productivity estimated from stock-recruitment relationships. Because fishing rate reference points are largely influenced by the steepness of the stock-recruitment curve, any factor that influences the proportion of a given data set that occurs at small stock sizes can influence estimated fishing mortality reference points, including autocorrelated errors in recruitment residuals, the exploitation history, and the life-history of the species. One key question to be addressed for stochastic environments is the degree to which fishing mortality reference points are biased for stocks in which a true maternal effect in larval survival is not recognized in the estimation of stock-recruitment parameters. This question is addressed with simulation modeling that computes the ratio of the fishing rate reference point estimated from using total larvae as reproductive potential (i.e. $F_{msy(TL)}$) to that obtained using viable larvae as reproductive potential (i.e. $F_{msy(VL)}$) for five harvest rates and 5 levels of autocorrelation in the stock-recruitment residuals.

The mean of ratios of $F_{msy(TL)}/ F_{msy(VL)}$ for POP indicates that the $F_{msy(TL)}$ is generally larger than $F_{msy\ (VL)}$ for most harvest rates and levels of recruitment autocorrelation, with the mean of ratios ranging from 1.01 to 1.13 (Figure 6) . At the heavy fishing mortality rates of $F_{20\%}$ the degree of bias becomes reduced. The mean of ratios of $F_{crash(TL)}/ F_{crash(VL)}$ is larger than the mean of ratios observed for $F_{msy(TL)}/ F_{msy(VL)}$ for all combination of harvest rate and autocorrelation pattern, ranging from 1.10 to 1.30. These results indicate that while there is on average some bias in F_{msy} of approximately 10%, the bias observed in F_{crash} is larger and exceeds 20% for most combinations of harvest rate and autocorrelation pattern.

The general patterns observed for POP were also observed for Pacific cod, but the overall bias was reduced (Figure 7). The mean of the ratios $F_{msy(TL)}/ F_{msy(VL)}$ ranged from 0.98 to 1.04, whereas the mean of the ratios $F_{crash(TL)}/ F_{crash(VL)}$ ranged from 1.02 to 1.12. Additonally, the bias in the reference points was reduced at high levels of recruitment autocorrelation. These results reflect the reduced longevity of Pacific cod relative to POP, as a 100 year simulation essentially encompasses more generations of Pacific cod than POP. Thus, a series of poor recruitments will more quickly result in reduced biomass for Pacifc cod than for POP and increase the likelihood of observing low stock sizes that allow more accurate estimation of the steepness of the stock-recruitment curve. Additionally, the potential for a series of poor recruitments is enhanced with autocorrelated recruitment variability. These results indicate how the stock life-history characteristics can be a factor in the determining how estimated stock productivity can be influenced by maternal effects.

For both life-history types, the bias in F_{msy} and F_{crash} is reduced with the high fishing mortality rates of $F_{20\%}$. This effect results from the increased amount of data that occurs at small stock sizes for heavily-fished stocks, which result in improved estimates of the steepness parameter that determines the F_{msy} and F_{crash} reference points. This is revealed in the median yield obtained for each level of fishing mortality from the 200 POP simulations with an autocorrelation coefficient of 0.0 and $F_{40\%}$, which is a fishing rate close to F_{msy}. (Figure 8a). The peak of the median estimated yields is close to the peak of the true yield curve for this stock, but the median estimated yields for higher fishing mortality rates are larger than the true yield due in part to the limited observations at these higher levels of fishing mortality. Additionally, the bias in estimated mortality at high fishing mortality rates is increased when maternal effects are not incorporated in the estimation of stock-recruitment parameters. As the fishing rate increases to $F_{20\%}$, the degree of bias at the larger fishing mortality rates is reduced.

Conclusions

A necessary part of adjusting fisheries management procedures to account for maternal effects is analyzing the extent to which management procedures which do not account for maternal effects may be in error in meeting conservation goals. A maternal effect in larval survival clearly reduces the productivity of the stock simply due to increased mortality. However, bias in estimated yield and fishing mortality reference points that occurs when estimation of stock-recruitment parameters incorrectly neglects maternal effects can be affected by several factors, including the life-history characteristics and the levels of exploitation. For the life-history types modeled here, the bias in F_{msy} observed when maternal effects was incorrectly neglected was less than approximately 10% in many situations, suggesting that one approach to minimizing the influence of maternal effects is to avoid harvesting at rates larger than F_{msy}. It is intuitive that the bias in estimated stock productivity is increased at high fishing mortality rates, as these are situations characterize by a relatively large proportion of young spawners that would be subject to maternal effects.

The results obtained in this study indicate that biases in estimated fishing mortality reference points may result from a lack of recognition of maternal effects. However, it is not clear how managing with potentially biased fishing reference points over a period of time affect risk of overfishing the stock. For example, what is the significance of any bias to due maternal effect relative to implementation errors in achieving target fishing rates, or observation errors on abundance surveys? An additional step for future research is to conduct management strategy evaluations to assess the impact of managing stocks with potentially biased reference points.

References

Berkeley, S.A., C. Chapman, and S.M. Sogard. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, Sebastes melanops. Ecology 85: 1258-1264.

Berkeley, S.A., M.A. Hixon, R.J. Larson, and M.S. Love. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29(8):23-32.

Burden, R.L. and J.D. Faires. 2001. Numerical Analysis, 7th ed. Brooks-Cole, Pacific Grove, CA. 864 pp.

Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. Fisheries Research 56:125-131.

Murawski, S.A. P.J. Rago, and E.A. Trippel. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES J. Mar. Sci. 58:1002-1014.

Myers, R.A., K.G. Bowen, and N.J. Barrowman. 1999. Maximum reproductive rate of fish at low population size. Can J. Fish. Aquat. Sci. 56:2404:2419.

Spencer, P., D. Hanselman, and M. Dorn. 2007. The effect of maternal age of spawning on estimation of Fmsy for Alaskan Pacific ocean perch. pp. 513-534 In J. Heifetz, J. DiCosimo, A.J. Gharrett, M.S. Love, V.M. O'Connell, and R.D. Stanley [eds.]. Biology, assessment, and management of north Pacific rockfishes. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Spencer, P.D. and J.N. Ianelli. 2008. Pacific ocean perch. In Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 2009, pp. 917-972. North Pacific Fishery Management Council, 605 W. 4th Ave, suite 306. Anchorage, AK 99501

Thompson, G, J. Ianelli, R. Lauth, S. Gaichas, and K. Aydin. 2008. Assessment of the Pacific Cod Stock in the Eastern Bering Sea and Aleutian Islands Area. In Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 2009, pp. 221-401. North Pacific Fishery Management Council, 605 W. 4th Ave, suite 306. Anchorage, AK 99501

Figure 1. A schematic model of how maternal effects in larval survival may affect recruits. With maternal effects, the mortality between the egg and viable larval stage is a function of spawner age, and may be strictly density-independent mortality or some combination of density-independent and density-dependent mortality.

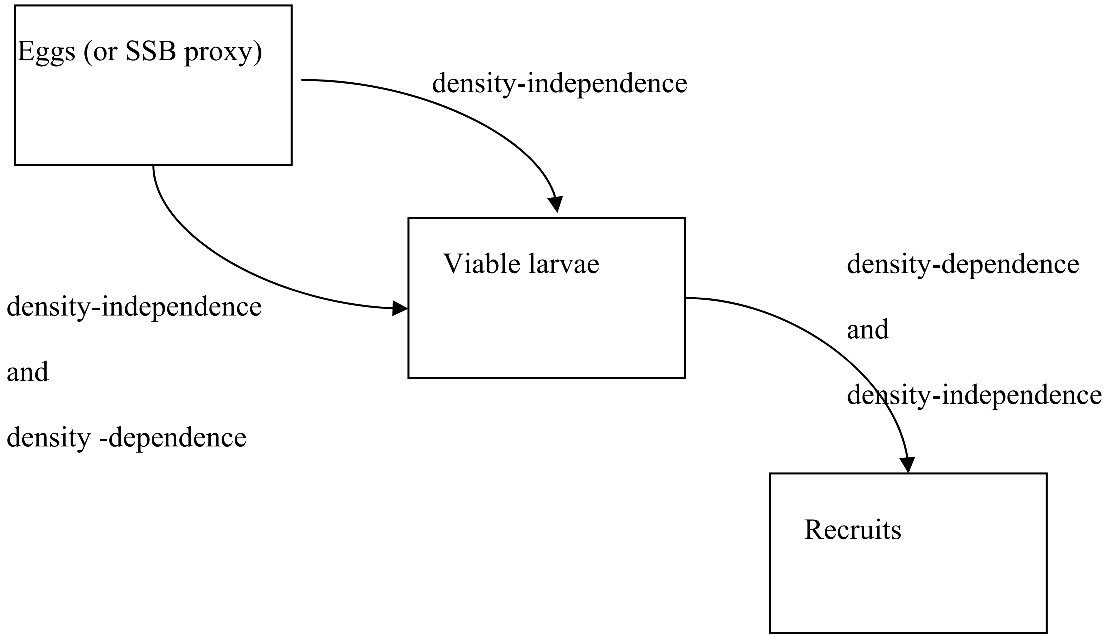

Figure 2. Reduction in larval survival as function of spawner age for black rockfish (solid line) based upon laboratory research from Berkeley et al. (2004) and hypothesized for Bering Sea/Aleutian Islands Pacific ocean perch and Pacific cod.

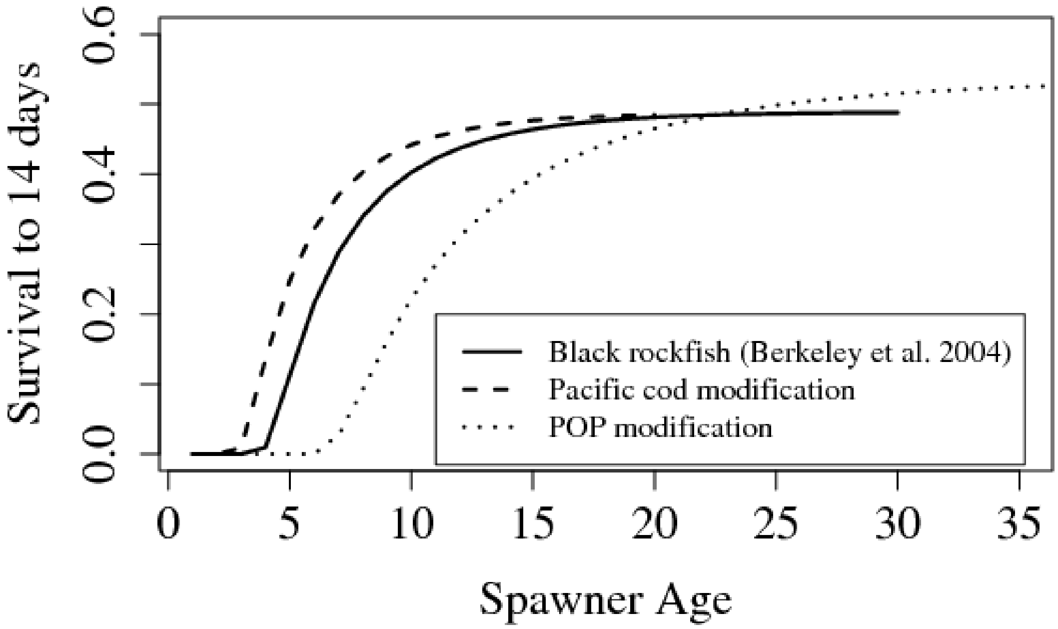

Figure 3. Stock-recruitment curves (a), and equilibrium recruitment (b) and yield (c) as a function of fishing mortality for a stock with (solid line) and without (dashed line) maternal effects in larval survival. Reduced larval survival from maternal effects reduces the recruitment produced from a given level of egg production, and disproportionately lowers equilibrium recruitment and yield at high fishing rates.

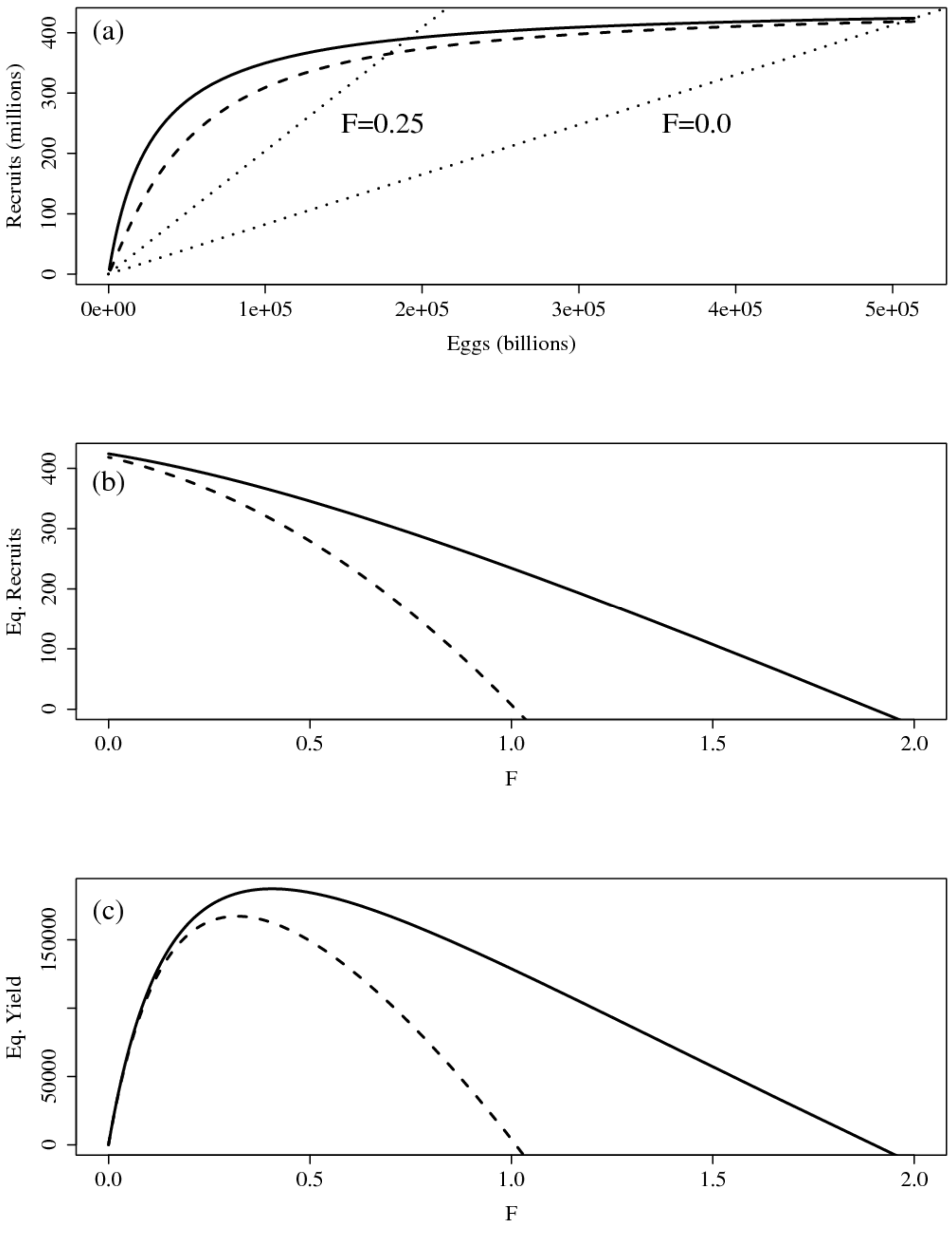

Figure 4. The influence of maternal effects in the Beverton-Holt density-independent mortality parameter *a* (top row) and density-independent parameter *b* (bottom row) upon stock recruitment and yield curves.

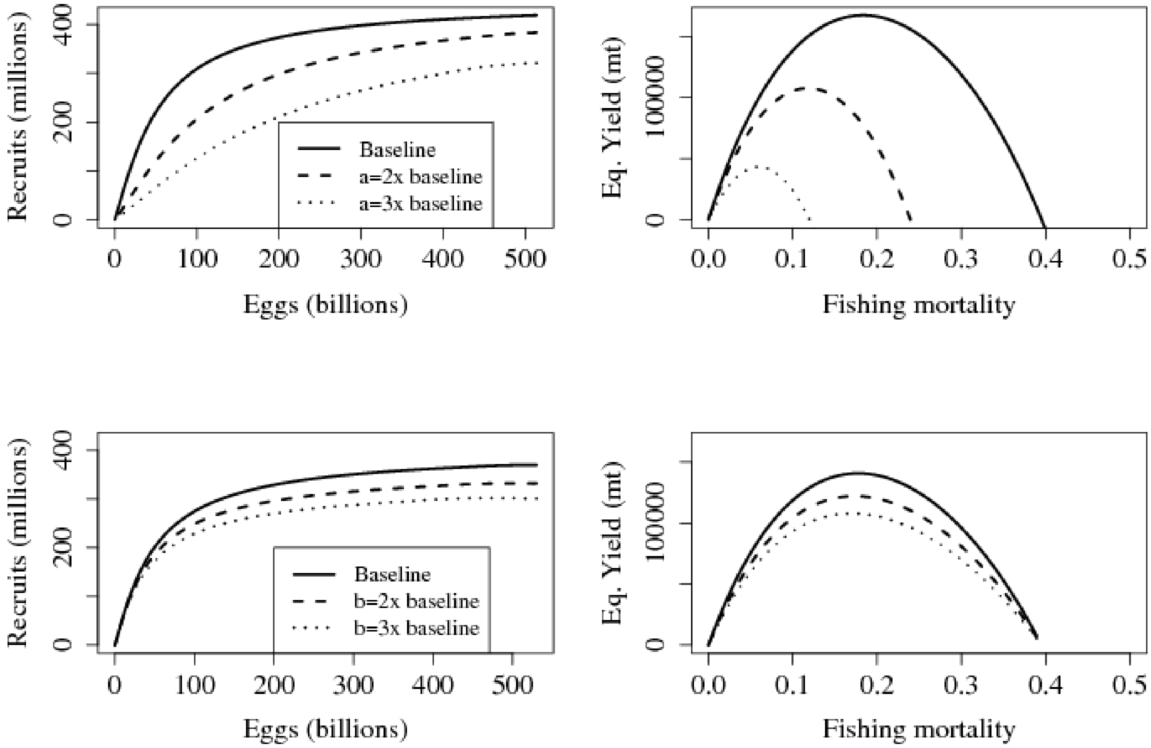

Figure 5. The influence of maternal effects in larval survival upon estimated stock recruitment curves and replacement lines. The estimated stock recruitment curve obtained from a given time series of recruitment and a measure of reproductive potential diminished from maternal effects is located to the left relative to the stock-recruitment curve obtained when the measured reproductive potential does not include maternal effects. Similarly, the replacement line for a given level of fishing mortality is also shifted to the left, as the expected lifetime production of reproductive output is reduced with maternal effects.

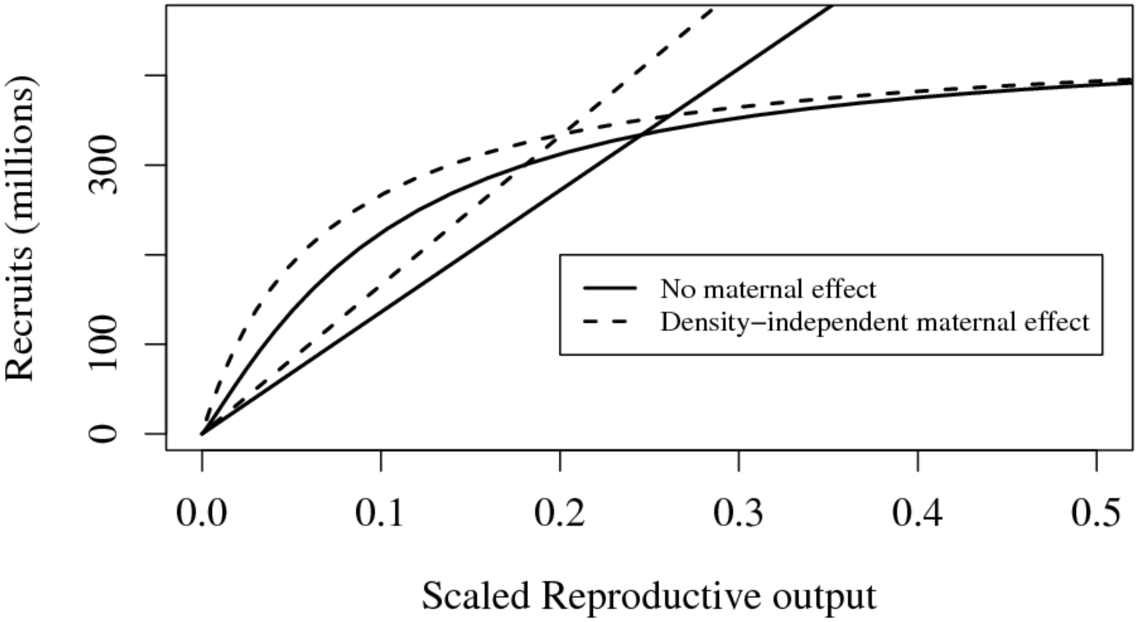

Figure 6. The ratio $F_{msy(TL)}/F_{msy(VL)}$ (a) and $F_{crash(TL)}/F_{crash(VL)}$ (b) for simulated POP populations with maternal effects in larval survival. The mean ratio from 200 simulations is shown for each combination of five levels of recruitment autocorrelation and harvest rate (expressed in terms of spawning potential ratio).

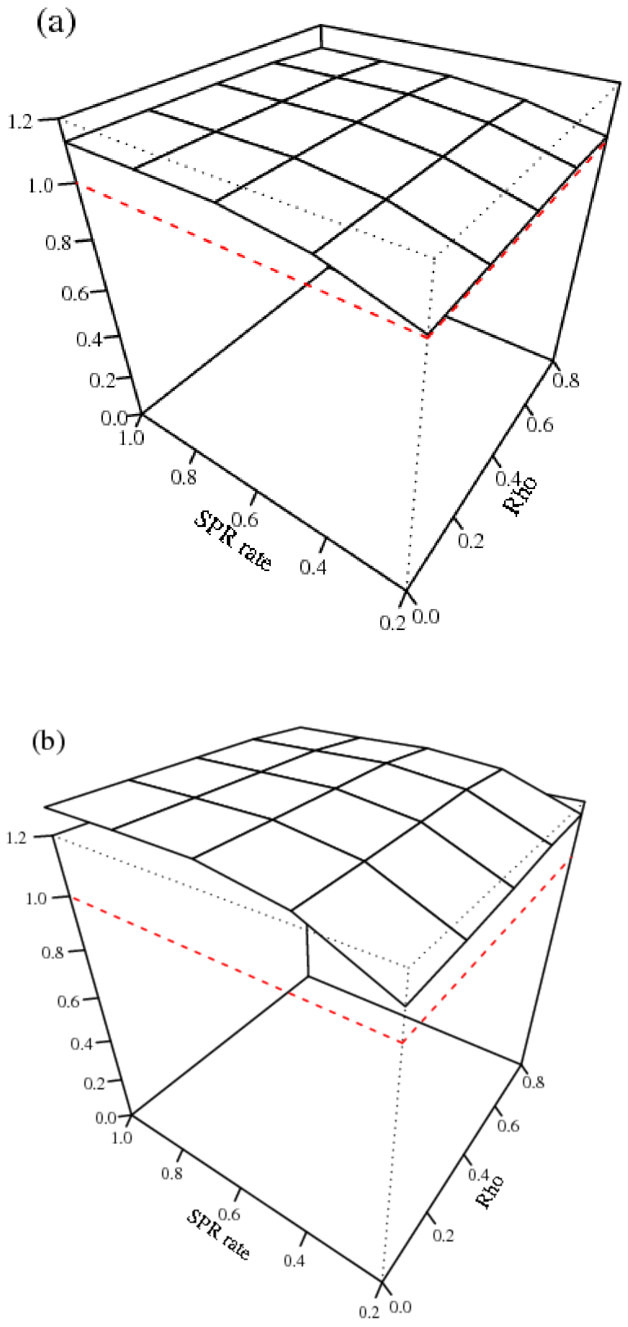

Figure 7. The ratio $F_{msy(TL)}/F_{msy(VL)}$ (a) and $F_{crash(TL)}/F_{crash(VL)}$ (b) for simulated Pacific cod populations with maternal effects in larval survival. The mean ratio from 200 simulations is shown for each combination of five levels of recruitment autocorrelation and harvest rate (expressed in terms of spawning potential ratio).

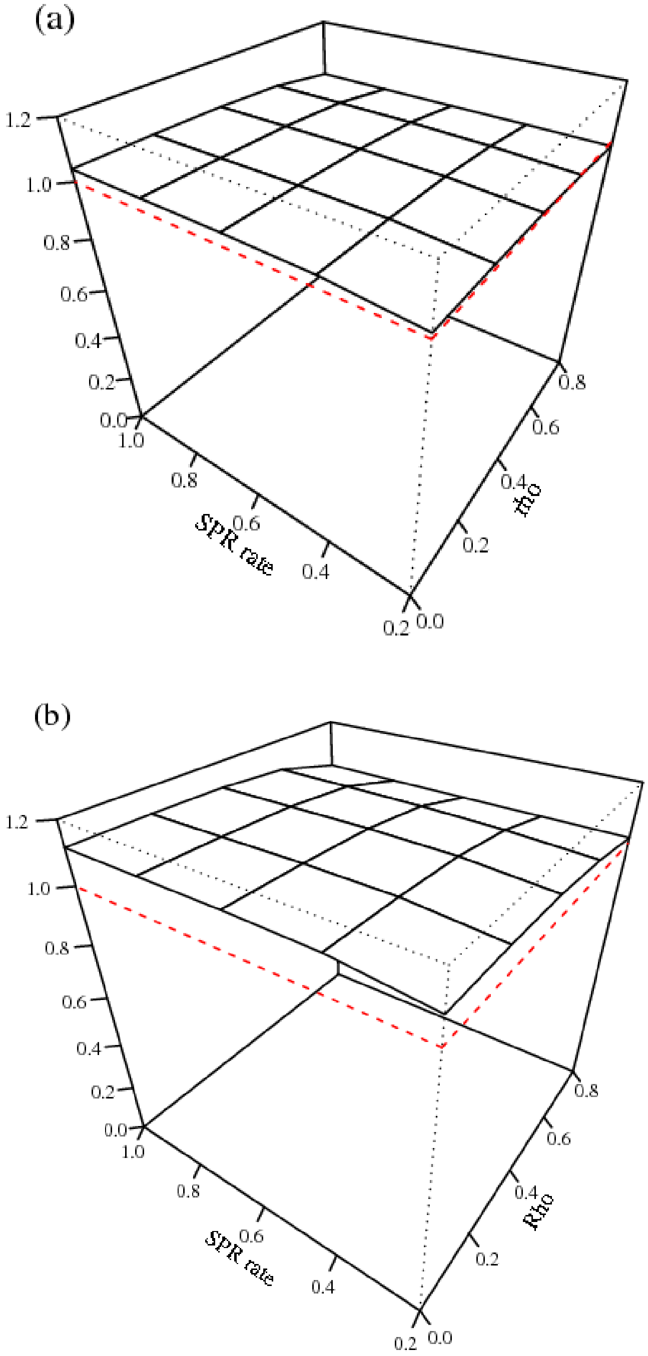

Figure 8) The median estimated yield from 200 simulations for a POP population with maternal effects in larval survival, no recruitment autocorrelation (ρ = 0), and fishing at $F_{40\%}$ (a) and $F_{20\%r}$ (b). The true equilibrium yield curve is shown with the solid line, whereas the estimated yield obtained when maternal effects are either incorporated or not incorporated in the estimation procedure are shown with the dashed and dotted lines, respectively.