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Environment, krill and squid in the Monterey Bay: from fisheries to life histories and back again

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Abstract

The fishery for market squid in California is extremely valuable and only recently subject to regulations (in that sense, it is one of the last great open-access fisheries on the western coast of North America). We briefly review the history of the fishery for *Loligo opalescens*, on an annual time scale. Within-season analyses suggest that cohorts of squid persist offshore and move inshore for reproduction throughout the season. In order to predict the timing of inshore movement of squid, we develop a life history model using stochastic dynamic programming. This model allows us to link squid growth and reproduction with environmental factors, particularly, upwelling, temperature, and food abundance, in a consistent Darwinian framework. Using the model, we predict the timing of squid movement inshore in cold and warm environments, and the amount of biomass inshore in weekly intervals. We compare the model predictions with unpublished fishery-dependent data subsampled from landings and discuss the implications of our work for management of the squid fishery.

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1. Introduction

The California market squid, *Loligo opalescens* Berry, has had an active fishery for over 150 years, yet remains almost completely unregulated (Vojkovich, 1998). The most recent management

recommendation by the California Department of Fish and Game (CDFG) includes (1) a yearly quota of 125,000 tons, (2) a reduction in the number of permits issued by 45% of current levels, (3) an expansion of the weekend fishing ban, and (4) the possible adoption of no-take spawning areas (Mangel et al., 2002). Currently in California, the fishery for market squid is the largest in both value and tonnage, with 2000–2001 landings in Southern California reaching 115,670 mt and Central California landings at 7730 mt, a total of

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123,401 mt, down slightly from a total high of 126,722 mt in 1999–2000 (CDFG, 2003). However, catch rates fluctuate dramatically in response to variable environmental conditions, such as El Niño–Southern Oscillation Events (ENSO) (Vojkovich, 1998; Rodhouse, 2001) (Fig. 1). For example, the highest landings that have occurred during an ENSO event is up to ten times less than the established yearly quota of 125,000 tons (CDFG, 2003).

In 1984, 1993, and 1997 statewide landings plummeted during El Niño conditions (Fig. 1; to 1996 only), despite an overall increasing trend in catches. In both the Southern California and Monterey Bay fisheries, catches recovered after the declines; however, squid landings have recovered more slowly in Monterey (Vojkovich, 1998; Mangel et al., 2002). Beginning in the early 1980s, important technological, capacity, and regulatory changes that contribute to increase in catch per unit effort (CPUE), measuring in tons per successful landing, have occurred. The increase in CPUE may reflect these changes more than an increase in the availability of squid (Mangel et al., 2002); alternatively, the increase may reflect a nonlinear relationship between squid abundance and catch, due to schooling behavior of squid and non-random distribution of fishing effort.

Fishing occurs primarily at night with purse seines, which surpassed lampara nets as the most common harvest method in 1989 following the removal of their ban in the Monterey Bay (Mangel

et al., 2002; CDFG, 2003). Spawning squid are attracted to high-powered lights hung over the edges of special light vessels, which also actively search for spawning aggregations (CDFG, 2003). When many squids have aggregated, the seines encircle the squid, catching large quantities in a single netting (Vojkovich, 1998). In California, the fishery for adult squid occurs in the spawning grounds near shore (CDFG, 2003). Peak catches occur during the fall and winter off southern California, and during late spring and summer in central California. From port samples collected, the average age of harvested market squid was 188 days (CDFG, 2003).

L. opalescens also plays a crucial role in the California Current ecosystem, acting as a major prey item for a number of marine mammals and birds, and a variety of commercially important fish species, such as rockfish, salmon, and sanddabs. All of these species feed on “market sized” squid, up to 180 mm mantle length (ML), and these squid often comprise a large percentage of the fishes’ diets. In addition, krill (euphausiids) compose up to 65% of a market squid’s diet (Karpov and Cailliet, 1979), a potential California fishery (although it is currently illegal to land or fish krill in state waters), and squid are in direct competition with numerous species of commercial interest for krill (Morejohn et al., 1978). Thus, squid form the penultimate link of a relatively simple, trophic system consisting of upwelling-induced nutrient enrichment, phytoplankton, krill, squid, and the various predators of squid (Fig. 2) (Mangel et al., 2002).

The productivity of this linked system is strongly affected by inter-annual events such as El Niño (McGowan et al., 1998). Large-scale declines in zooplankton (and especially krill) abundance occurred in the central California upwelling system during the 1997/98 El Niño (Marinovic et al., 2002), and similar observations were made off southern California during both the 1982/83 and 1997/98 El Niño events (McGowan et al., 1998). As described above, market squid landings in California declined dramatically following both these events. The abundance and spatial distribution of krill is also connected to environmental conditions within a year (Fig. 3; see

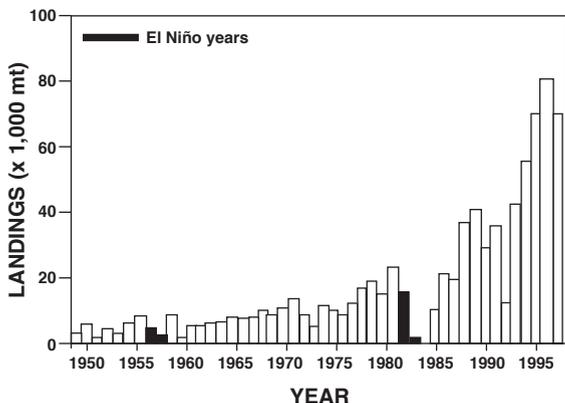


Fig. 1. Statewide landings of squid 1950–1995 (from Vojkovich, 1998).

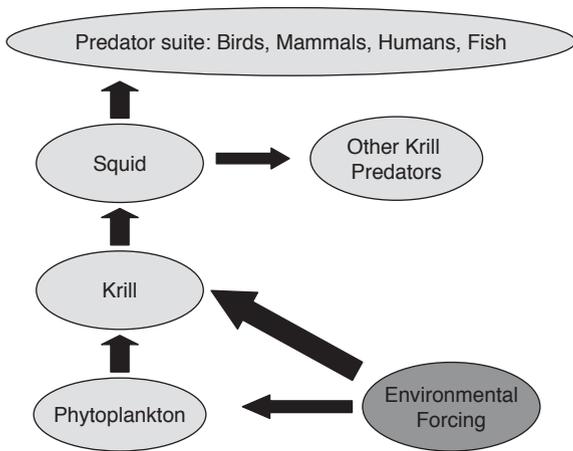


Fig. 2. Simple, conceptual foodweb connecting environment, krill and squid.

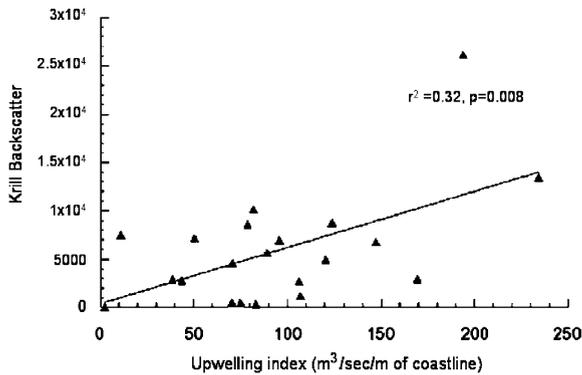


Fig. 3. Relationship between krill abundance (as measured by acoustic backscatter) and an upwelling index in Monterey Bay, measured on a monthly basis May–November 1997, 1998, 1999, showing that krill abundance correlates with the index of upwelling, $r^2 = 0.32, p = 0.008$ (from Mangel et al., 2002).

Mangel et al., 2002 for further details on calculation of the upwelling index). We are thus led to consider the relationship between environmental forcing, krill availability and squid (Mangel et al., 2002) in the context of the fishery.

1.1. Life history of *Loligo opalescens* (Berry)

The California market squid is an annual, semelparous species living a maximum of 1 year (Jackson, 1998; Butler et al., 1999; CDFG, 2003; Jackson and Domeier, 2003). Semelparity makes

squid more prone to environmental fluctuations (Rodhouse, 2001), and makes management very difficult because of large interannual population fluctuations (Brodziak and Rosenberg, 1993; Anderson and Rodhouse, 2001). In addition, if there is poor or no recruitment in a particular year, the local population may crash, and with most mature individuals available to the fishery, there is no “safety” stock that can reproduce the following year.

L. opalescens ranges from Baja California in Mexico to Alaska (Fields, 1965; Wing and Mercer, 1990), with large spawning grounds located off of central and southern California (CDFG, 2003). Squid spend most of their life offshore, until reproduction, when they move onto spawning grounds with depths of 3–180 m (Hixon, 1983). Egg capsules are found year around in Monterey Bay, with the greatest concentrations inshore during the spring and summer (Fields, 1965). Females lay a cluster of capsules, each containing 180–300 eggs (Fields, 1965; Okutani and McGowan, 1969), which hatch in 3–5 weeks into larvae with a length of 2.5–3 mm, resembling adults (Yang et al., 1986). Larvae grow exponentially from hatching to about 50 days then grow linearly (Yang et al., 1986), reaching a maximum size of 305 mm total length (TL) (Vojkovich, 1998) and a weight of 56–84 g (Fields, 1965) in 365 days. A number of other growth trajectories have been proposed for squid including: linear (Butler et al., 1999), exponential (Jackson and Domeier, 2003), and asymptotic (Spratt, 1979).

Females mature at sizes ranging from 81–140 mm mantle length (ML) (Hixon, 1983). Twenty-five to fifty percent of the total body weight in fully mature females constitutes reproductive organs (Fields, 1965). Yang et al. (1986) reared *L. opalescens* in captivity from eggs to an age of 250 days, and spawning began on day 173.

2. Within-season analyses

Squid collected from surveys on the fishing grounds of the Channel Islands and Monterey Bay by our colleagues, Baldo Marinovic and Nancy Gong, (Fig. 4) show a wide range of sizes at which

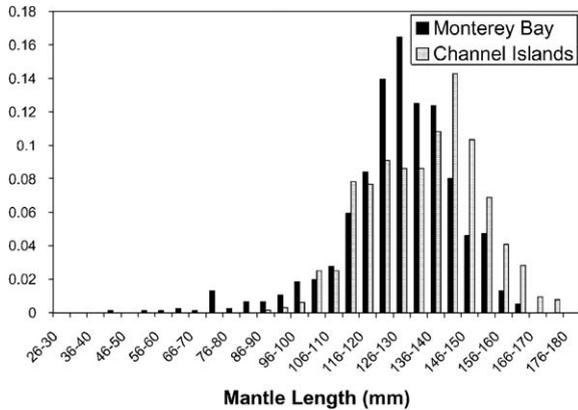


Fig. 4. Size distribution of squid collected on the fishing grounds of the Channel Islands and Monterey Bay by our colleagues Baldo Marinovic and Nancy Gong (1999–2001).

squid enter the fishery (and implicitly, a wide range of size of maturity). These samples were collected from April to October of 2000, with additional Channel Island samples occurring in January and February 1999, as well as November and December 2000 from subsamples collected from fishery landings. One possibility is that squid move inshore simultaneously but are captured across the entire calendar year. An alternative view is that squid are moving inshore throughout the calendar year, according to a life history rule. For example, it might be that squids use a time-based rule for moving inshore in which, after a certain length of time offshore, inshore movement occurs. They might use a size-based rule, in which movement inshore occurs once a size threshold is crossed. Finally, they might use a size- and time-based rule, in which the threshold for inshore movement varies according to time of year.

We analyzed catch data from the Pacific States Marine Fisheries Commission. The unit of effort was in trips per week; we calculated CPUE by dividing the total weekly catch (in pounds) of purse seine trips by the number of purse seine trips in that week. (This gear type accounts for 92% of the total catch landed at Monterey and Moss Landing from 1981–2000). In order to explore these views, we analyzed the within-season dynamics of catch and effort using a DeLury–Leslie depletion method (Quinn and Deriso, 1999). This

is a linear model

$$\text{CPUE}(t) = \frac{C(t)}{E(t)} = qB_0 - qK(t) + Z_\sigma(t), \quad (1)$$

where B_0 is initial biomass, $C(t)$ is catch during period t , $E(t)$ is effort during period t , $K(t)$ is cumulative catch to period t , q is catchability, and $Z_\sigma(t)$ is a normally distributed random variable with mean 0 and standard deviation σ . The y -intercept of the regression line for CPUE vs. cumulative catch can be used as an estimate for initial biomass, B_0 and the slope of the regression provides an estimate of q . Our DeLury estimates produced very few values of catchability q that were positive and many that were negative and most were statistically insignificant at the 5% level. The analysis is consistent with the view that there is no single inshore stock that is fished down; rather the inshore biomass available to the fishery changes throughout the fishing season, due to recruitment from offshore.

Understanding the life history of *L. opalescens*, and describing the mechanisms that drive squid behavior, is crucial, if reasonable and effective management policy is to be made. There are already data that show the availability of squid to the fishery year round, with peaks in April and November. However, there has been little explanation of this phenomenon. We seek to provide insight into the life cycle of squid and the importance of that life cycle for the fishery, through analysis of environmental variation, prey variation, and life history variation.

3. A life history model for squid

In order to explain the mechanism behind the varying sizes, shown by Marinovic and Gong's data (Fig. 4), and times at which squid enter the spawning grounds and recruit to the fishery, we developed a life history model (Clark and Mangel, 2000) for the squid, in which a genetic program of development and maturation is cued to environmental factors. We use the model to determine the pattern of growth and maturation that maximizes a squid's reproductive fitness, and by doing this, provide a possible explanation for the size and age

Table 1
Parameters for the life history model

Parameter	Interpretation
$E(y)$	Environment in year y
A	Model fit for exponential growth = 2.73, from Yang et al. (1986)
$B(t, E)$	Growth rate at day t when environment is E ($= 1, 2$)
a	Model fit for linear growth = 0.034, from Yang et al. (1986)
b	Exponential for linear growth = 1.477, from Yang et al. (1986)
$L(t)$	Length at week t within the year
m	Daily mortality rate ($= 0.01$) from assumption that monthly mortality is 0.3 from (Butler et al., 2001)
g	Gonadal weight ($= 25$ – 50% of body weight) (Hixon, 1983)
W_0	Egg weight ($= 0.001$ g) assumed to be larval hatching weight from Yang et al. (1986)
r	Estimated allometric exponent in fecundity-length relationship ($= 2.15$)
$L_{bi}(t)$	Size of offspring laid in week t at the start of next year's fishery if the next year environment is normal ($i=1$) or El Niño ($i=2$)
$S_{bi}(t)$	Survival of offspring laid in week t to the start of next year's fishery if the next year environment is the same ($i=1$) or different ($i=2$) from the current environment
m_b	Size-dependent mortality for juveniles which is a function of m and the maximum size of 230 mm

ranges observed within the squid fishery, as well as the continuous movement of squid inshore. Our model is a general description, not precisely cued to either the Monterey Bay or Channel Islands fishery.

The model includes components of adult growth, survival and reproduction and juvenile growth and survival. Darwinian fitness is a result of both survival and fecundity; we can incorporate inter-annual environmental fluctuations, such as El Niño events, through the inclusion of growth and survival.

Constructing the dynamic programming equation. We assume that natural selection leads to patterns of growth, maturity and reproduction that maximizes the long-term number of descendants (Houston and McNamara, 1999; Clark and Mangel, 2000). As a proxy for long-term number of descendants, we use the estimated number of grand-offspring (also see Mangel and Clark, 1988; Clark and Mangel, 2000). For this reason, the model covers a time span of 58 weeks, ranging from an arbitrary starting point, set to the end of February, and running a complete year, to the time at which the last laid eggs have hatched, given a 5-week incubation time in colder waters (Fields, 1965). By completing a full life cycle for a generation, we determine the survival and fecundity of the adult squid, and the size of the following

generation as a proxy for their reproductive output.

We assume two general environments: a warm, low-food availability environment, with higher growth rates but smaller maximum size, and a cold, high-food environment with a lower growth rate but larger maximum size (see Table 1 for symbols and interpretations) (Beverton, 1992; Jackson and Domeier, 2003). These represent El Niño years and non-El Niño or “normal” years, respectively.

Growth in a seasonally and annually fluctuating environment. Yang et al. (1986) fit growth data at a constant temperature to

$$L(t) = A \exp(Bt) \quad t \leq 56, \quad (2)$$

$$L(t) = at^b \quad t > 56, \quad (3)$$

where $A=2.73$, $B=0.0319$, $a=0.034$, and $b=1.477$. Using Eqs. (2) and (3), we will explicitly relate $L(t)$ to $L(t+1)$ in order to analyze growth in discrete time. For $t \leq 56$ days, from Eq. (2), $L(50) \approx 12$ mm, marking the switch point between the two growth curves. Thus for $L(t) < 12$ mm

$$L(t+1) = L(t)\exp(B). \quad (4)$$

We also want to incorporate different environments on an annual scale in the form of El Niño and non-El Niño years, and on a seasonal scale

reflecting within year changes in sea-surface temperature. Grist and des Clers (1999) noted that, based on empirical data for *L. forbesi*, the relationship between the growth coefficient for juveniles, B , and temperature is linear and given by

$$B(T(t), E) = 0.01\{a_0T(t) - a_1\}, \tag{5}$$

where $T(t)$ is temperature ($^{\circ}\text{C}$), a_0 is a species-independent coefficient, and a_1 is species specific. We assume that growth follows the growth trajectory from Yang et al. (1986), where growth for the first 50 days is exponential and determined exclusively by temperature, assuming unlimited food (Forsythe and van Heukelem, 1987). Thus, we modify Eq. (4) to reflect temperature on both annual and seasonal time scales, giving

$$B(t, E) = 0.01\{0.916T(t) - 10.55\}, \tag{6}$$

where we solved for a_1 using the growth coefficients established by Yang et al. (1986) for squid <50 days old at 15°C . The resulting growth rate, reflective of the seasonal temperature variation, oscillates (Fig. 5).

Past the initial growth phase ($L(t) > 12\text{ mm}$) we solve Eq. (3) and $L(t+1) = a(t+1)^b$ for t , and equate them to one another to obtain

$$L(t+1) = (L(t)^{1/b} + a^{1/b})^b, \tag{7}$$

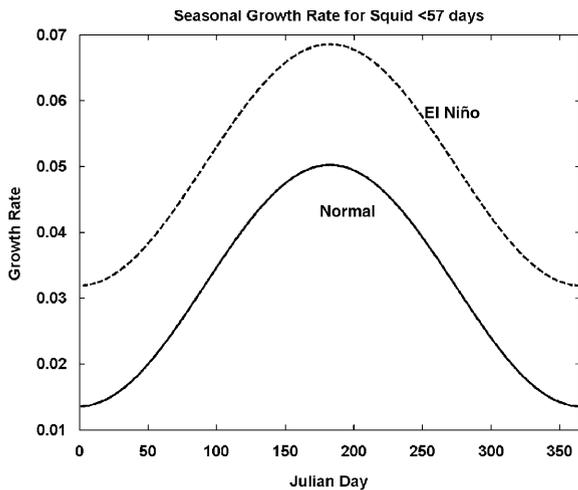


Fig. 5. Squid growth rate used in the life history model in the absence of local variation. The oscillations reflect annual temperature variation; the different curves reflect different environments.

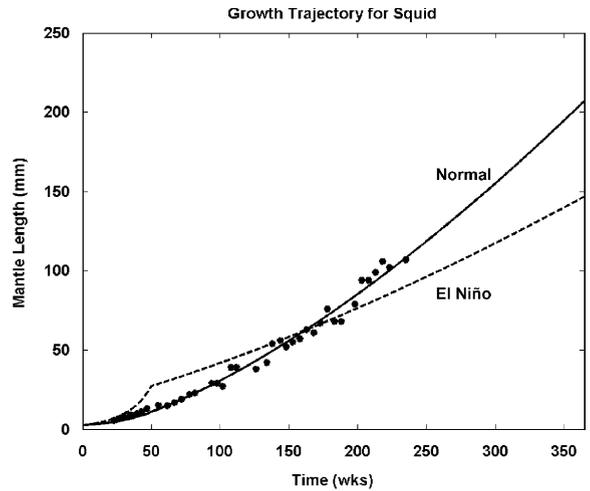


Fig. 6. The length dynamics of squid in the two environments, in absence of local variation. Where the red line shows the growth dynamics in an El Niño environment, the blue line shows dynamics in a normal environment, and * shows data from Yang et al. (1986).

where a is related to food availability, showing additional growth gained in one time step.

To account for annual environmental fluctuations, we assume that B and a are a function of environment where B is determined by temperature and a is reflective of productivity. Thus, B is larger in an El Niño environment and is smaller in a normal environment, while a is bigger in a normal environment and smaller in an El Niño environment. This gives the final model as

$$\begin{aligned} L(t+1) &= L(t)\exp(B(t, E)) & L(t) < 12\text{ mm}, \\ L(t+1) &= (L(t)^{1/b} + a(E)^{1/b})^b & L(t) \geq 12\text{ mm}. \end{aligned} \tag{8}$$

The length dynamics in the two environments are shown in Fig. 6.

3.1. Offspring growth and survival with inter-annual environmental variability

Offspring may experience a different environment than their parents. In the current version of the model, there are four possibilities: (1) normal conditions can remain normal, (2) normal conditions can turn to El Niño conditions, (3) an El Niño year can become normal, or (4) El Niño conditions can persist for 2 years. In each of these environmental regimes, squid have a different

growth pattern due to changes in growth rate, because of the temperatures associated with each environment, and the different levels of food availability. If outcome 1 or 4 occurs, the squid continue to grow on the same trajectory as their parents; however, if outcomes 2 or 3 occur, the offspring squid change their growth pattern at the time that the environment changes, either decreasing the maximum size, thus slowing growth due to decreases in food, in the case of outcome 2, or approaching a larger maximum size, in the case of outcome 3 (Fig. 7).

We allow $L_{bi}(t,E)$ to denote the size of an offspring laid in week t , 6 weeks after the start of the next year’s fishery when the environment this year is E and next year is i . The growth rate and growth trajectory of the juvenile squid are the same as those of the parent squid, including the seasonally varying growth rate, until time at which the environment can change, at which time the juvenile squid growth rate will change according to

the new environment. We assume size-dependent survival for juveniles (Hixon, 1983), so that if $S_b(t)$ denotes the survival of an offspring to week t after birth (suppressing the environment), where i can be environment 1 or 2, we have

$$S_{bi}(t + 1) = S_{bi}(t) \exp\left(-m - \frac{m_b}{L_{bi}(t)}\right), \tag{9}$$

where m_0 is weekly juvenile survival and m_b is size-dependent survival. Although temperature and food availability has been shown to affect larval survival (Vidal et al., 2002), for simplicity we assume that this is included in the length-based survival. Survival is computed from the time the parent goes inshore until the time at which juveniles are recruited to the fishery.

The sooner a parent squid moves inshore, the smaller the spawner, thus the lower the reproductive output, but the larger its offspring are at the beginning of the following year’s fishery, and the

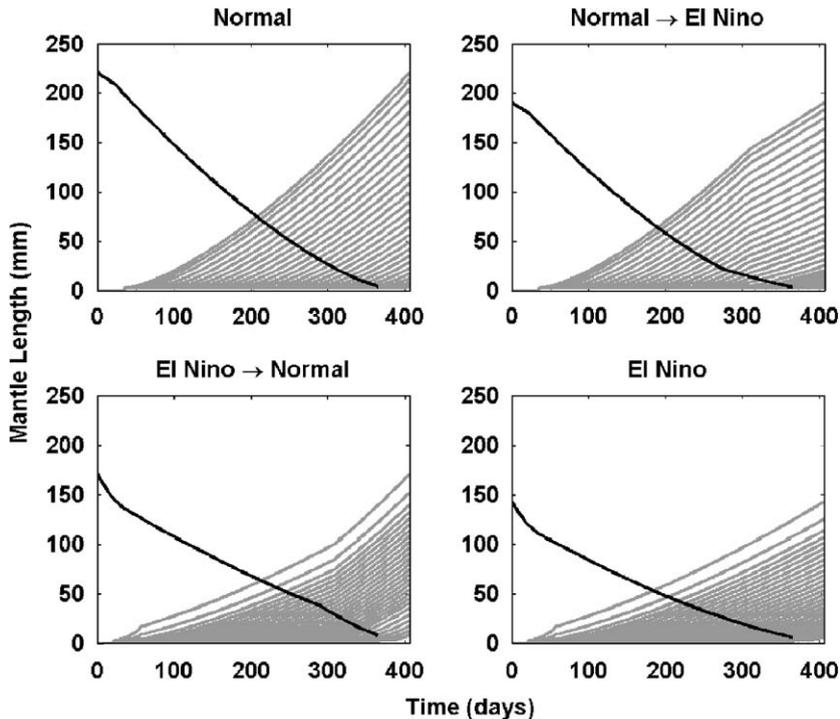


Fig. 7. The resulting growth dynamics of juvenile squid as a function of the date that they are laid and size at the start of the next fishing seasons (curves with negative slope).

greater the risk of juveniles dying. Combining these factors determines adult fitness.

Determining fitness from maturation. Maximum predicted reproductive output (fecundity) must be related to length, given that a female’s gonadal weight is 25–50% of their body weight, and length and body weight are allometrically related. This, however, does not imply that the number of eggs laid is directly related to size (Maxwell and Hanlon, 2000); but for our purposes, we shall assume that each individual achieves its maximum estimated fitness. We let $\Phi(l,t,E)$ denote the fitness from maturation for a squid that moves inshore when the environment is E . If we assume that El Niño events occur about once every 5 years, then when the environment is normal ($E=1$), there is an 80% chance that it remains normal and a 20% chance that there is an El Niño ($E=2$) the next year. Hence

$$\Phi(l,t,1) = \frac{gl^r}{W_0} \{0.8S_{b1}(t)gL_{b1}^r(t) + 0.2S_{b2}(t)gL_{b2}^r(t)\}, \tag{9a}$$

where l , is length at time t , g is gonadal mass, W_0 is egg weight, and r is the allometric measure of fecundity. For modeling purposes, we assume a maximum size of 230 mm ML. If we assume that there is a 5% chance of an extended El Niño event, then the fitness for maturation in an El Niño environment becomes

$$\Phi(l,t,2) = \frac{gl^r}{W_0} \{0.95S_{b1}(t)gL_{b1}^r(t) + 0.05S_{b2}(t)gL_{b2}^r(t)\}. \tag{9b}$$

The first term on the right hand side of these equations denotes the expected number of eggs: it is the gonadal mass (determined allometrically from the length-weight relationship) divided by the mass of a single egg. The term in brackets represents the expected number of offspring (i.e. grandoffspring) produced per juvenile at the time that the juveniles are recruited to the fishery in the next year.

3.2. Backward induction

While a squid is growing offshore, it also faces the risk of mortality before it has a chance to

reproduce. As growth slows, the fecundity gained by increasing length when combined with the risk or mortality has less value than moving inshore to reproduce at a slightly smaller size. We evaluate this tradeoff by stochastic dynamic programming (Mangel and Clark, 1988; Clark and Mangel, 2000). The timeline for our analysis is shown in Fig. 8.

We let $F(l,t,E)$ denote the maximum fitness, measured in terms of expected offspring fecundity (i.e. number of grand offspring), given that $L(t)=l$ and the environment is E . Since squid are an annual species, they have a fixed lifespan, which we set as $t_{\max} + 1$ weeks. Consequently, at week t_{\max} , a squid receives no fitness from remaining offshore and the fitness from going inshore is $F(l,t_{\max},E) = \Phi(l,t_{\max},E)$. For previous weeks, the life history decision is determined as the maximum of moving inshore, and reproducing, or remaining offshore for another week (thus growing and taking the risk of mortality). If $l'(l,t,E)$ denotes

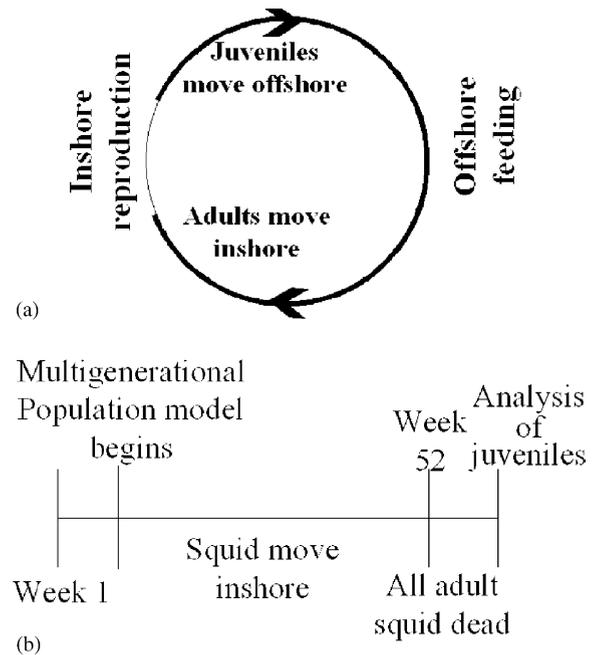


Fig. 8. Timeline of the life history model for calculating adult fitness from juvenile biomass at the time the juveniles are recruited to the fishery from a linear (panel a) or circular (panel b) perspective.

the length in week $t + 1$, given that $L(t) = 1$ and the environment is E we thus have

$$F(l, t, E) = \max\{\Phi(l, t, E); e^{-m}[F(l'(l, t, E), t + 1, E)]\}. \tag{10}$$

go inshore; remain offshore

The solution of Eq. (10) generates a boundary curve (Fig. 9) for the life history decision of remaining offshore and growing or going inshore and reproducing. Thus, individuals at time t , whose sizes are below the boundary curve continue to grow, while individuals with sizes above the boundary curve will move onto the spawning grounds.

Forward iteration of the life history decisions. To follow individual life histories, we simulated a population of squid with initial size normally distributed squid around the mean predicted size at 146 days in both environments and standard deviation of 5 mm, thus establishing a single cohort. We then followed their patterns of growth, maturation and inshore migration. This allowed us

to generate a series of size frequency distributions while squid are offshore. As squid move inshore, they become available to the fishery for harvest. In order to relate the landing volume from the fisheries data to the simulated squid, we computed biomass inshore using an allometric length (cm) to weight (g) relationship for *L. opalescens* (Fields, 1965; allometric exponent = 2.15, coefficient = 0.0013). This allowed us to compute both the weekly values and the cumulative values for biomass inshore. To establish a confidence interval for biomass, we ran the forward simulation 500 times.

The size distribution for the offspring as they enter next year’s fishery is a proxy for the reproductive potential of the next generation, which allows us to consider population dynamics and harvest strategies (to be reported elsewhere).

4. Predictions of the model

4.1. Initial forward simulation

The forward iteration tracks the size distribution of the squid offshore in both environments. The number of squid in the population declines due to mortality offshore and inshore migration; however, for both environments the offshore size distribution remained approximately normal, while biomass inshore was bimodal. In addition, squid moved inshore all year, with peaks in biomass inshore peaks in weeks 13 and 44 in the cold environment and weeks 18 and 38 in the warm environment (Fig. 10).

Biomass inshore each week is predicted to be higher in a normal environment than an El Niño one, with the exception of week 1 (Fig. 10). Cumulative biomass for the forward iteration shows a total biomass inshore to be almost 1.5 times higher in a cold environment than a warm one. The peak in biomass for the warm environment occurs five weeks before the peak in biomass in the cold environment. The mean predicted size for individuals to move to the spawning grounds 104.42 mm ML in the cold environment, and 106.09 mm ML in an El Niño year.

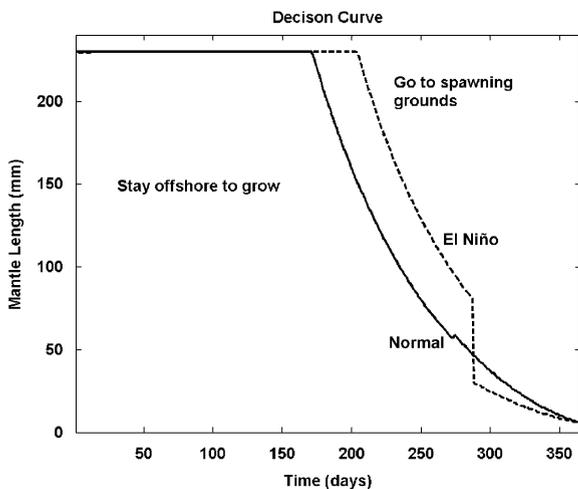


Fig. 9. Boundary curve for the squid life history decision. At any given time, if size is above the value of the threshold curve for a particular environment, the squid is predicted to move inshore. Otherwise, it is predicted to continue growing offshore. When the length at which the optimal size to move inshore is below the boundary curve, there is more value at those times in staying offshore growing than coming inshore to reproduce, and when the length is above the boundary curve a squid gains more from reproducing than growing.

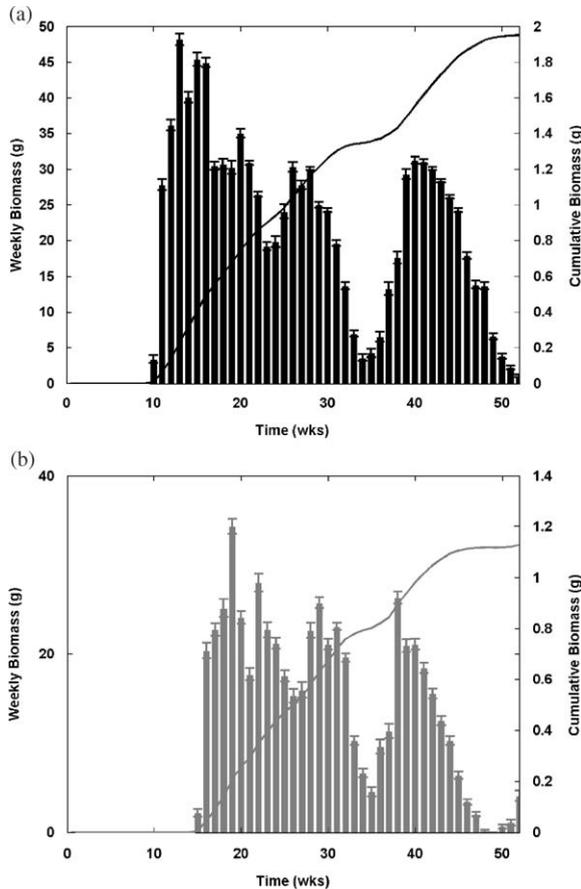


Fig. 10. Biomass distributions inshore for a normal (a) and El Niño (b) environments as predicted by the life history model. We show the weekly biomass inshore (bars) with associated variance and the cumulative biomass inshore (lines)

Sensitivity analysis. Mortality rates affected the boundary curve the most. Increasing adult mortality, which increases the risk of remaining offshore, lowered the size at which squid are predicted to move inshore. Increasing juvenile mortality increased the size at which squid move inshore. To test the importance of fecundity in the boundary curve, we also varied the allometric exponent r . A low value for r causes a sharp decline in the size for the boundary curve. Including the fitness of offspring (rather than just using offspring numbers) in the adult fitness function greatly changed the shape of the boundary curve. When grand-offspring are used as the

measure of fitness, a squid trades both its own mortality with that of its offspring. Early in the season, when the size at which a squid moves inshore is high, it is because most of the fitness a squid would have gained by moving inshore would be lost with high offspring mortality at the beginning of next year's season. As this risk declines, the size of inshore migration declines.

Changing the gonadal to egg weight ratio, W_0 and g , had no effect on the boundary curve in either environment because they appear linearly in the equations. Furthermore, because the value of staying offshore is ultimately related to the value of staying inshore, and these changes affect both values similarly, resulting in no change in the fitness values. The choice of times used throughout the model, whether deciding the starting point for the forward iteration or choosing when to measure the size of the offspring, are arbitrary. Because offspring size affects fitness value, it is important to recognize the effects of, when they are measured on the boundary curve. Changing the setpoints varying the quantitative but not the qualitative predictions of the model.

5. Discussion

Early and late in the season, the values for the size at which a squid moves inshore to breed are near the maximum size and very low, respectively (Fig. 9). This is a manifestation of the timeline assigned to the model. Early in the season, the offspring have a longer time period until recruitment to the fishery. Thus, the benefit of going inshore decreases because of decreased survival. Late in the season, the squid are nearing the end of their lives, and there is less time for the offspring to grow, but the total survival is higher. The maximum fitness is now achieved by an individual sacrificing its own mortality and that of its offspring with reproductive success. Values between these two extremes are a balance of time and length, at the given time, which maximize fitness. Note that the life history decision is size-driven early in the season and time-driven late in the season.

The difference between environments in biomass available in is not as marked as the differences in fishery landings between El Niño and non-El Niño years, but this model does not account for the likely increased mortality during El Niño years, rather it only calculates the differences in food availability and growth rates. The general shape of the distribution in biomass over time remains the same, with fewer squid coming in early and late in the season, reflecting the tails of the size distribution, as well as the mid-sized squid from the initial distribution coming inshore at the midpoint between the other two groups.

Confronting the model with data. The increased biomass inshore in a normal year is due to high food availability in the cold environment, which allows the squid to grow larger. Jackson and Domeier (2003) also attribute the larger size of individuals in La Niña years to increased productivity. This could be one factor explaining why fishery landings decline during El Niño years. Furthermore, because of the effects of environmental state on size, the primary predictions of our model are that squid will come inshore year-round to reproduce and that the timing and size of the inshore migration can be predicted from a combination of life history and environmental information such as temperature and food (krill) availability.

The peak in biomass inshore (Fig. 10) corresponds well to the peaks in harvest for the

Monterey Bay fishery, which occur in late spring and summer (CDFG, 2003) (Fig. 11). The summer spawners are thought to represent those squid born in the previous fall. Since the simulation that generated these figures was based on a normal distribution of sizes with a mean of 50 and 57 mm ML, for normal and El Niño environments, respectively, hatching dates can be back calculated to early September. The spring spawners' offspring could be modeled, and because of increased summer growth rates, one would expect to see their biomass inshore peak in mid- to late-fall.

The modal size for squid collected from the fishery from Marinovic and Gong's data, in 5-mm increments, in Monterey Bay is between 126 and 130 mm ML, and in the Channel Islands is between 146 and 150 mm ML (Fig. 4). In comparison to the model, the mode in both locations is slightly larger than the mean size of squid inshore in an El Niño environment and normal environment, as predicted by the model, which predicts the mean size of squid in a warm environment to be 104.42 mm ML, and in a cold environment to be 106.09 mm ML. The size distributions predicted by the model in the cold environment are just outside the range of sizes found in Monterey Bay and the Channel Islands.

The model is not tuned to either location specifically, thus the difference in the predicted sizes could be due to the extremely high maximum length associated with unlimited food resources that was used in the normal environment of the model. Furthermore, while upwelling indices are similar between Monterey and the Channel Islands (Fig. 12), temperatures, and thus growth rates, are higher in the Channel Islands, resulting in larger individuals. Additionally, the number of squid in the model is much smaller than from the sample data obtained. If the initial size distribution were larger and thus broader, we would likely see a larger spread in the inshore size distribution as the squid reach maturity at different lengths according to the boundary curve.

Implications for fishery management. The model developed here is a theoretical one, rather than an applied calculational tool (Mangel et al., 2001). Indeed, our extremely simple formulation involves only two environmental states ("normal" and

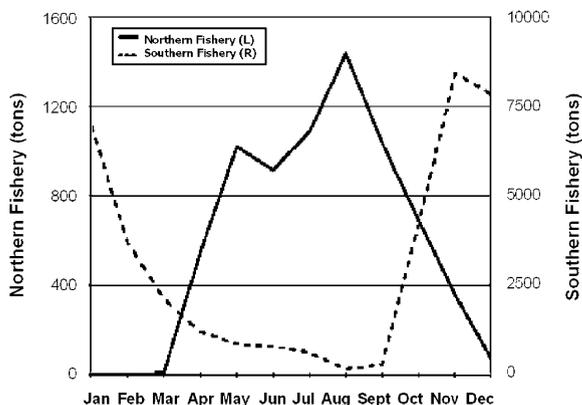


Fig. 11. Average landings for the Northern (solid) and Southern (dashed) squid fisheries (from CDFG, 2003).

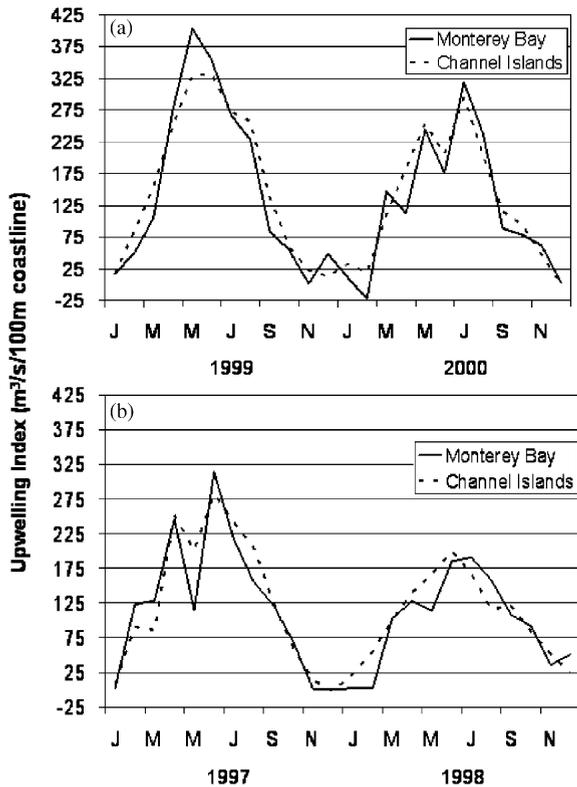


Fig. 12. Upwelling indices for normal (a) and El Niño (b) environments for both the Channel Islands and Monterey Bay. Data from <http://las.pfeg.noaa.gov>.

“El Niño”) in which there is a countervailing effect of temperature and food (low/high and high/low, respectively). One could easily incorporate a broader set of environments, with more complicated correlations, into the model without changing the conceptual flavor.

However, we can draw a number of insights that have implications for fishery management because changes in environment, combined with semelparity and potential harvest before reproduction can cause large inter-annual variations in stock size (Anderson and Rodhouse, 2001). First, understanding how environmental variations affect squid life history is essential to a well-managed fishery (Chavez et al., 2003). The fundamental ecological perspective for doing this will be community, rather than population ecology, because of the need for understanding the linkages in the food webs. For example, feeding rate, which is

the major factor in determining growth rate (Jackson and Domeier, 2003), depends upon krill availability, which depends upon phytoplankton. Thus, factors that affect the distribution and abundance of phytoplankton will affect squid abundance. Second, there is no single stock of squid “sitting” on the fishing ground; rather there is a seasonal influx of individuals to the fishing ground. Thus, within season monitoring and management are crucial, to ensure that a sufficient number of individuals spawn. Third, it will be possible to over-fish the squid fishery even though squid are semelparous. If the fishery intercepts individuals between the offshore feeding grounds and the inshore breeding grounds, before reproduction, then the potential spawn of those individuals is lost to the population.

Assessing the likelihood of this occurrence requires coupling a model for population dynamics in a stochastic environment with the life history model. For example, one may couple the threshold rule that results from the work in this paper with a stock-recruitment curve to establish population dynamics. We could then ask, for example, how selectively of the fishery affects the chance that the stock is put at risk, which could be defined, for example, as the stock size in a particular year falling to less than 20% of its long-term average value. Since the upper limit of the stock recruitment curve will be set by environmental factors such as food and temperature, the interconnection of the environment, the life history, and the fishery is apparent. This is the next step.

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