

journal homepage: www.elsevier.com/locate/ecolmodel

A catch forecast model for the Peruvian scallop (*Argopecten purpuratus*) based on estimators of spawning stock and settlement rate

Matthias Wolff^{a,*}, Marc Taylor^a, Jaime Mendo^b, Carmen Yamashiro^c

^a Centre for Tropical Marine Ecology (ZMT), Fahrenheitstrasse 6, 28359 Bremen, Germany

^b Facultad de Pesquería, Universidad Agraria La Molina, Apto. 456, Lima 100, Peru

^c Instituto del Mar del Peru, Esq. Gamarra y Valle s/n, Apartado 22, Callao, Peru

ARTICLE INFO

Article history:

Received 30 August 2006

Received in revised form

27 June 2007

Accepted 2 July 2007

Published on line 17 August 2007

Keywords:

Peru

El Niño phenomena

Scallop fisheries

Yield prediction

ABSTRACT

The Peruvian Bay scallop (*Argopecten purpuratus*) fishery in Independencia bay (Southern Peru) is being subjected to great inter-annual variability in catch and effort. This is mainly due to the ENSO (El Niño–Southern oscillation)-caused changes in the population dynamics of the stock, which greatly proliferated during the El Niño events 1983 and 1998. As a consequence “gold rush” conditions arose and resource users profited from a multi-million dollar export business. After the El Niño booms, the system normalized and catches dropped to normal levels. This boom and bust situation has made a rational management of the resource difficult, and annual catches are considered unpredictable, just like the stochastic environment. This paper attempts to provide a catch forecast model to enable the scallop fishery to better prepare for and adapt to the ever-changing conditions of the scallop stock. The model proposes that annual catches are mainly the result of the recruitment success of the incoming new cohort, which is a function of adult spawning stock size and the number of settlers to the sea bottom. The latter is considered a function of the larval mortality rate and the temperature-dependent development time to the settlement stage, while the former is proportional to the catches taken over the spawning period (November–April). Using monthly catch and temperature data for the period 1983–2005, we constructed a regression model to predict the catch for the year after the recruitment period (July–June) as a function of (a) the catch during the spawning period (as a proxy for spawning stock biomass) and (b) the settlement factor that was derived from the mean water temperature over the spawning period, an assumed instantaneous larval mortality rate, and the relationship between temperature and larval period to settlement. The resulting multiple regression ($R^2 = 0.930$) proves that both factors can explain a large part of the inherent variability of the data. The model reveals that annual catches greatly depend on the spawning stock size when temperatures are low, while this factor decreases in importance with increasing temperatures, at which the settlement factor is much more influential instead. These findings are relevant for the stock management: at low temperatures, the maintenance of a large enough spawning stock over the spawning period (November–April) is decisive for the yield of the post-recruitment fishing period thereafter, while at increasing spawning temperatures, spawning stock size is of decreasing importance for determining the yield.

© 2007 Elsevier B.V. All rights reserved.

* Corresponding author.

E-mail address: mwolff@zmt-bremen.de (M. Wolff).

0304-3800/\$ – see front matter © 2007 Elsevier B.V. All rights reserved.

doi:10.1016/j.ecolmodel.2007.07.013

1. Introduction

The Peruvian Bay scallop (*Argopecten purpuratus*) is the main target of the multispecies diving fishery of Peru. It is being caught in shallow waters (5–30 m) along the entire coastline, but substantial stocks and fisheries are concentrated around two areas only: Sechura bay in the north and Independencia bay in the south (Fig. 1). In Independencia bay, the largest and most productive natural scallop banks are found.

During the El Niño warming event in 1983–1984 the scallop population of Independencia bay exhibited an unprecedented proliferation, causing annual landings to rise from some hundred tonnes of normal (cold upwelling) years to about 25,000 t during the 3 years following the warming event (Wolff, 1985, 1987; Mendo et al., 1988; Arntz and Fahrback, 1991) (Fig. 1). A scallop export line was established and the scallop fishery became a multimillion dollar business, providing not only work for more than a thousand of divers, but also for a great number of middlemen, factory workers and exporters. This scallop boom thus greatly improved the sustenance basis for thousands of associated families of the nearby town of Pisco.

This “gold rush” period for scallop fishery ended with a normalization of the ecosystem, an almost depletion of the natural scallop stock and the need for scallop divers to shift again to other resources besides the scallops (such as mussels, crabs, clams, octopods among others) and to become

used again to low catches and income levels. Another El Niño event of about the same strength impacted the region again in 1997–1998 and the positive effect on the scallop population of the bay was very similar as during the preceding event 15 years ago. Unfortunately, total scallop harvest was much lower during these years due to a mismanagement (growth over fishing) of the resource (Wolff and Mendo, 2000).

Numerous studies have been conducted on the population dynamics of the scallop during normal years and during the El Niño impact (Wolff and Wolff, 1983; Wolff, 1985; Mendo et al., 1988; Mendo and Jurado, 1993; Wolff and Mendo, 2000) showing that population parameters greatly change over an El Niño-cycle, with recruitment and growth rates increasing with water temperature. These studies revealed that *Argopecten purpuratus* is a relatively short-lived species, whose population sizes greatly depend on the recruitment success of the same year.

Catches are as yet considered unpredictable due to the great environmental stochasticity of the ecosystem and the many abiotic and biotic factors that may affect stock size. As a consequence, the diving fishermen have become used to act like opportunistic predators, searching for and moving towards those areas where scallop abundance happens to be profitable. If this is not the case, other invertebrates are targeted. During the two Niño events mentioned, the diving fleet of Independencia bay increased from less than 100 boats in normal years to over 1000, operating in the zone.

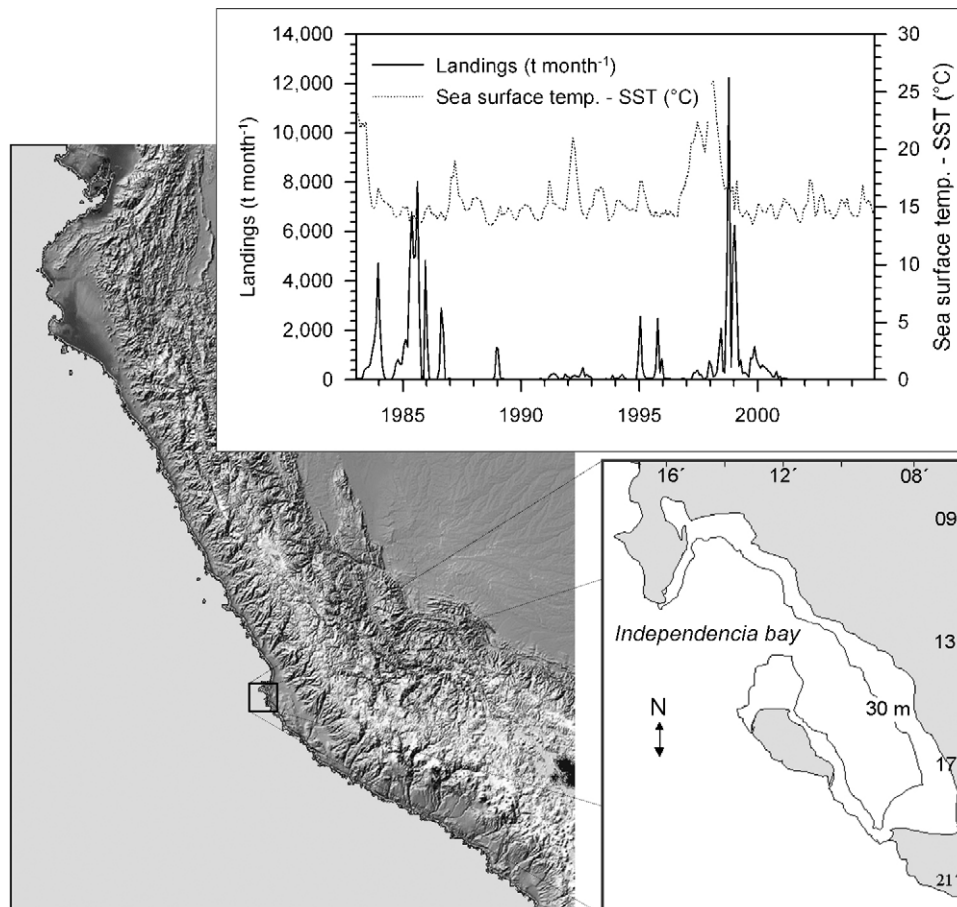


Fig. 1 – Independencia bay (right); scallop landings and SST (°C) (1983–2004) (left).

The ability to predict annual scallop catches would greatly improve the situation of the fishery and the associated export business, since all stakeholders involved would have time to plan and to adjust to the ever-changing conditions.

A first prediction of (at least) the order of magnitude of scallop catches in Independencia bay was attempted by [Mendo and Wolff \(2002b\)](#), who found the mean temperature during the spawning period (November–April) to explain about 77% of the catch variation in the following “biological year” (from July to June).

This first model encouraged us to revisit the available data set of monthly scallop landings and temperatures of the bay from 1983 to 1998, to add more recent data (to 2005) and to try to improve the model.

We started with the above-mentioned simple linear regression, and asked for the possible mechanism behind the observed relationship between the temperature during spawning and the catches in the following year. We reasoned that an increase in the annual recruitment rate of juvenile specimens to the fishery should mainly be the result of the number of spawners (and thus the number of eggs released to the environment) as well as the natural larval mortality during the time period from egg release to settlement to the bottom substrate. While the former is influenced by the fishery, the latter should be greatly dependent on temperature, which accelerates larval development, shortens larval period and thus enhances survival.

Based on this reasoning we constructed a multiple regression model to predict the annual catches after the recruitment period (after July) from proxies for spawning stock biomass and settlement rate. The first was considered proportional to the catches during the spawning period; the latter was derived from a temperature dependent survival rate of the settlers (see below).

2. Materials and methods

2.1. Data used

The data used for the model were monthly scallop catches in Independencia bay and mean monthly water temperatures recorded at the La Vieja Island (see [Fig. 1](#)) by the Instituto del Mar del Peru (IMARPE) in Pisco during the period 1983–2005. Catch and temperature data by IMARPE are taken on a daily basis and are then averaged to monthly values. The first author has surveyed the catches in Independencia bay himself in the early 80s and has compared his own estimates with those of IMARPE finding good agreement ([Wolff and Wolff, 1983](#)). The fourth author of this paper also confirms this. So the landings data are considered reliable.

2.2. Basic assumptions underlying the model

1. Scallop landings reflect the size of the scallop stock in the bay. If the stock increases or decreases, the fishery grows or shrinks accordingly, so that the relative fishing rate remains relatively constant and the catch is proportional to stock size.

2. Scallop landings during the post-recruitment period, which starts in winter (July–August) each year largely depend on the recruits spawned during the preceding summer/autumn period (November–April) ([Wolff, 1988](#); [Wolff and Mendo, 2000](#)), typical for annual “pulse fisheries”.
3. Spawning stock is assumed proportional to scallop landings during spawning (November–April).
4. Larval survival in the natural environment (from egg release to settlement) is significantly lower than the observed 0.1% in the hatchery ([Wolff et al., 1991](#)).
5. Day degrees (dd) for larval development including successful settlement were considered to be approximately 400 for the temperature range relevant for the area (14–25 °C), based on hatchery data by [DiSalvo et al. \(1984\)](#), [Uriarte et al. \(1996\)](#) and [Wolff et al. \(1991\)](#). During typical cold water years (14 °C) larvae would thus need over 28 days to settle, while only about 16 days are needed at the high El Niño temperatures of 25 °C.

2.3. Model construction

The following steps were followed to construct the model:

- (a) An instantaneous daily larval mortality rate was estimated using the negative exponential mortality model below (Eq. (1a)) and a range of assumed survival rates: 0.01, 0.001 and 0.0001%. The period to settlement (24.6 days) was estimated from the mean spawning temperatures of 16.24 °C obtained from our time series ([Table 1](#)) and the 400 dd.

$$M = \left(\frac{\ln(N_t/N_0)}{LP} \right), \quad (1a)$$

where N_t is the number of settlers, N_0 the number of eggs (arbitrary number), M the instantaneous rate of natural mortality per day and LP (t) is larval period (in days).

- (b) Using the values for the larval period (LP) under the different spawning temperatures for the different years ([Table 1](#)), the number of settlers, N_t (“now coined settlement factor, SF”) was calculated rearranging the above Eq. (1a) and replacing LP by the value of 400 for the day degrees (dd) divided by the spawning temperatures (T °C) (Eq. (1b)):

$$SF = N_0 e^{-M \times 400 / T(^{\circ}C)} \quad (1b)$$

We standardized SF as being 1 for the mean spawning temperature (T °C = 16.26) recorded in the study period (1983–2005) and calculated SF at other temperatures accordingly.

A stepwise multiple regression was calculated using the mean monthly catch and the temperature-dependent SF during the spawning period (November–April) as independent variables and the landings from July–June following the annual recruitment as dependent variable. Eq. (1b) was repeatedly calculated with our different range values of M yielding envelop values for SF of different magnitude. These were then iteratively used for the regression analysis and the mortality rate that allowed for the best fit was finally chosen. Following the El Niño outburst 1998, scallop fishermen started to collect small

Table 1 – Model input data

Spawning period (November–April)	Mean T (°C) during spawning	Monthly catches during spawning	Settlement factor (SF) at M=0.558 (day ⁻¹)	Mean catch after recruitment (July–June)
1982–1983	22.5	56.3	45.26	1384.0
1983–1984	15.7	2247.0	0.61	2198.0
1984–1985	14.7	1680.3	0.23	1720.0
1985–1986	14.6	86.0	0.21	408.0
1986–1987	16.9	12.7	1.68	1.0
1987–1988	15.6	0.0	0.56	225.0
1988–1989	15.6	486.8	0.56	7.0
1989–1990	14.8	5.5	0.26	90.0
1990–1991	15.4	74.3	0.46	128.0
1991–1992	18.1	150.8	4.04	115.0
1992–1993	15.7	48.5	0.61	77.0
1993–1994	15.1	124.8	0.35	344.0
1994–1995	16.2	703.3	0.95	355.0
1995–1996	14.4	234.8	0.17	107.0
1996–1997	18.8	65.2	6.40	479.0
1997–1998	24.1	353.8	87.53	2938.0
(1998–1999)*	(14.6)*	(2516.9)*	(0.209)*	(614.0)*
1999–2000	14.5	739.3	0.19	110.9
2000–2001	14.9	65.8	0.29	9.6
2001–2002	15.2	7.8	0.38	6.7
2002–2003	15.3	10.1	0.42	5.2
2003–2004	15.4	5.6	0.46	10.2
2004–2005	15.9	13.7	0.73	12.6

* Data not included.

seed scallop shortly after recruitment (May, June) and transferred this seed to grow out areas in the bay, where scallops were kept until market size (in November, December 1998). For this reason, the bulk of the scallop catch was not taken within the first months of the fishing season (which is usually the case), but later in the spawning season, increasing catches to unprecedented values during these months. The data of this period were therefore not comparable with the rest of the time series data and had to be excluded from the analysis (see Table 1).

3. Results

3.1. Mortality rates, settlement factor (SF), model data input

Out of our seed values for the survival rate, 0.0001% survival to settlement corresponding to a mortality rate of 0.558 day⁻¹ yielded estimates of the settlement factor (SF) that allowed for the best fit of the regression. The improvement of the fit

from the other survival rate values tried (0.01 and 0.001%) was marginal, however (by +0.81 and +0.04%, respectively). When the survival rate was lowered beyond the 0.0001% value, the fit started to decrease. Table 1 contains the input data to the multiple regression model.

3.2. Model output

Fig. 2 show the bivariate scatter plots of relative spawning stock (SS) versus catch (Fig. 2a) and settlement factor (SF) versus catch (Fig. 2b). Evidently, both factors explain a great portion of the variation of the data, and the settlement factor alone is a relatively better predictor for the catch than the spawning stock.

Table 2 gives a summary of the regression statistics of the multiple regression with catch as the dependent (y) and settlement factor (SF) and spawning stock (SS) as the independent variables (x_1, x_2).

Fig. 3 shows the predicted versus the observed monthly catches for the period July–June based on the multiple regression (Fig. 3a), as well as the confidence limits around the

Table 2 – Regression statistics of derived multiple regression

	Beta	Std. Err. B	B	Std. Err. B	t(19)	p-Level
Intercept			-12.195	58.401	-0.209	0.836814
Spawning factor	0.755	0.061	30.095	2.420	12.436	0.000000
Settlement factor	0.638	0.061	0.894	0.085	10.514	0.000000

Regression summary for dependent variable: Catch (July–June) $R=0.96445299$; $R^2=0.93016957$; adjusted $R^2=0.92281900$; $F(2,19)=126.54$; $p<0.000000$; standard error of estimate: 225.71.

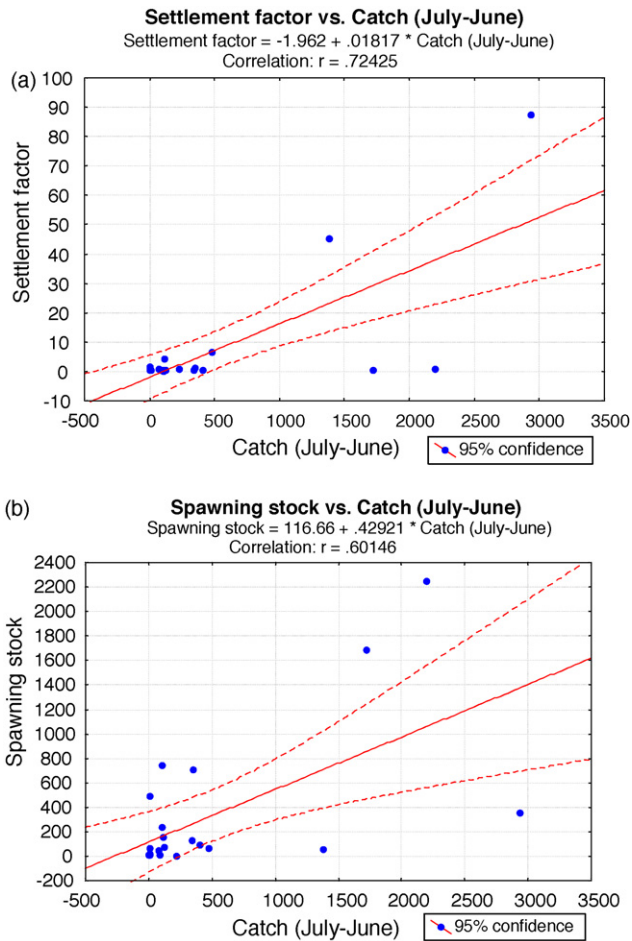


Fig. 2 – (a) Settlement factor (SF) and (b) spawning stock biomass (SS) as related to catches after the annual recruitment period (July–June).

regression line (Fig. 3b). The regression shows that the model is less able to predict low catch levels as many of the observed versus predicted values lie near or outside the 95% confidence limits on the lower end. The following Table 3 summarizes the analysis of the residuals.

Fig. 4 shows the predicted relative catch as a function of temperature and relative spawning stock size (here we used arbitrary values ranging from 10 to 100 t monthly catch during the spawning period). It is evident from predicted catch between low and high temperatures that stock size during spawning (SS) is important at low temperatures (14, 15, and 16 °C), while beyond 20 °C the predicted catch is almost exclusively (>80%) a function of temperature (i.e. settlement factor, SF).

4. Discussion

4.1. Predictive fisheries models and the mechanism proposed for the scallop model

Despite occasional attempts of fisheries scientists to emphasize the importance of environmental variability (EV) for the

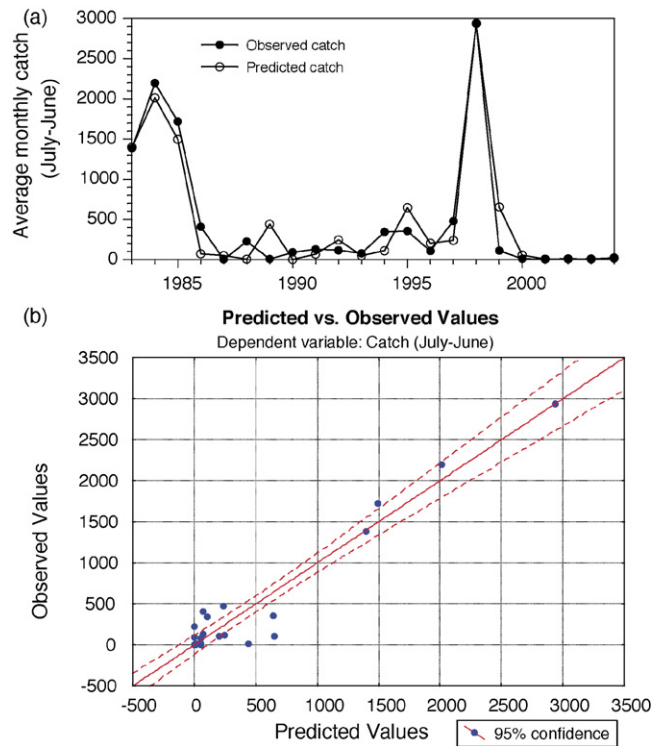


Fig. 3 – Predicted vs. recorded catches for the period 1983–2004 (graph below shows the confidence limits around the regression line).

dynamics of aquatic resources (see early contribution of Ricker (1958), in which he emphasizes the role of the environment in shaping the stock–recruitment relationship in marine fish or the classical book “Climate and Fisheries” of Cushing (1982), a review of models by Wiff and Quiñones (2004) and very recent papers by Chen and Hare (2006) and Nishida et al. (2007), modeling of the influences of environmental variability or environmental change on population dynamics is by many fisheries scientists still considered as not possible or even as not necessary. As Hilborn and Mangel (1997) stated: “Since fishing pressure can be managed but the environment cannot, the default assumption in fisheries models has been to assume that the changes are due to fishing pressure ... thus, we leave the challenge of realistically considering environmental change for the next generation ...”. It has been shown, that most environment–ecosystem interactions are non-linear and that a causal chain is often difficult to detect.

The non-linearity might also explain part of the often observed “breaking relations” described by Myers (1998), who showed that correlations between biological processes and environmental factors may be valid only for a small range of the environmental factor considered.

The model presented here is based on a time series of 22 years of monthly catches and environmental temperatures and a substantial knowledge of the population dynamics and early life history of the species modeled. This allowed us to propose a mechanism—a temperature-mediated change in the larval period, which directly relates to the relative number of survivors to settlement. In addition, we postulate as a sec-

Table 3 – Summary of analysis of residuals

Year	Observed	Predicted	Residual	Standard P.V.	Standard residual	Standard error Pred. value	Mahalanobis distance	Deleted residuals	Cook's distance
1982–1983	1384.0	1400.2	–16.2	1.16	–0.07	106.02	3.68	–20.73	0.001
1983–1984	2198.0	2015.6	182.4	1.95	0.81	170.30	11.00	423.45	0.668
1984–1985	1720.0	1497.4	222.6	1.29	0.99	125.16	5.50	321.38	0.208
1985–1986	408.0	71.0	337.0	–0.53	1.49	55.04	0.29	358.29	0.050
1986–1987	1.0	49.8	–48.8	–0.56	–0.22	56.74	0.37	–52.04	0.001
1987–1988	225.0	4.6	220.4	–0.62	0.98	58.00	0.43	235.97	0.024
1988–1989	7.0	440.0	–433.0	–0.06	–1.92	52.15	0.17	–457.38	0.073
1989–1990	90.0	0.5	89.5	–0.62	0.40	57.98	0.43	95.86	0.004
1990–1991	128.0	68.2	59.8	–0.54	0.27	55.24	0.30	63.58	0.002
1991–1992	115.0	244.4	–129.4	–0.31	–0.57	50.96	0.12	–136.31	0.006
1992–1993	77.0	49.6	27.4	–0.56	0.12	56.05	0.34	29.21	0.000
1993–1994	344.0	109.9	234.1	–0.48	1.04	53.74	0.24	248.18	0.023
1994–1995	355.0	645.3	–290.3	0.20	–1.29	59.24	0.49	–311.83	0.044
1995–1996	107.0	202.9	–95.9	–0.36	–0.43	51.53	0.14	–101.17	0.003
1996–1997	479.0	238.8	240.2	–0.32	1.06	53.03	0.21	254.23	0.023
1997–1998	2938.0	2938.6	–0.6	3.13	0.00	201.05	15.71	–2.86	0.000
1999–2000	110.9	654.6	–543.7	0.21	–2.41	61.33	0.60	–587.08	0.167
2000–2001	9.6	55.2	–45.6	–0.55	–0.20	55.66	0.32	–48.51	0.001
2001–2002	6.7	6.3	0.4	–0.61	0.00	57.80	0.42	0.44	0.000
2002–2003	5.2	9.6	–4.3	–0.61	–0.02	57.67	0.42	–4.65	0.000
2003–2004	10.2	6.7	3.4	–0.61	0.02	57.83	0.42	3.66	0.000
2004–2005	12.6	22.1	–9.5	–0.59	–0.04	57.31	0.40	–10.11	0.000
Minimum	1.0	0.5	–543.7	–0.62	–2.41	50.96	0.12	–587.08	0.000
Maximum	2938.0	2938.6	337.0	3.13	1.49	201.05	15.71	423.45	0.668
Mean	487.8	487.8	0.0	0.00	0.00	73.17	1.91	13.71	0.059
Median	112.9	90.5	–0.1	–0.51	0.00	57.49	0.41	–1.21	0.004

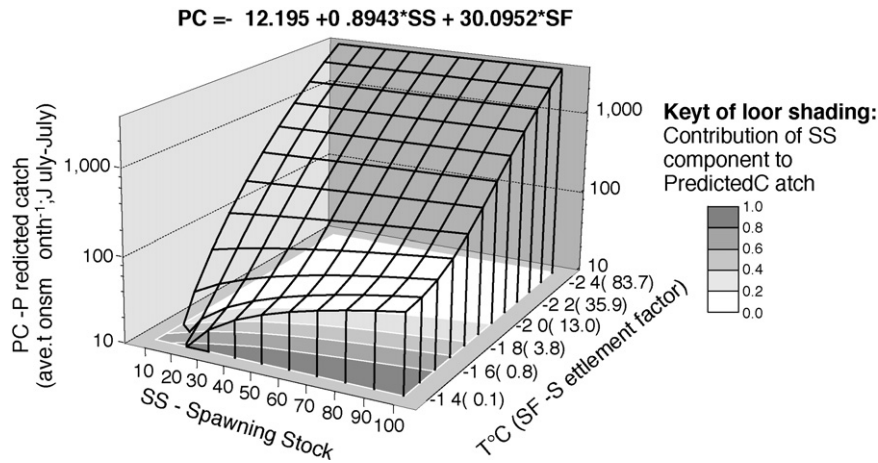


Fig. 4 – Predicted monthly catches, PC (ave. catch in t month⁻¹; July–June), as a function of temperature (settlement factor, SF, in parenthesis) and spawning stock, SS (ave. catch in t month⁻¹ over the previous spawning period, November–April). Floor shading shows the contribution of SS to the value of predicted catch (SS/PC).

ond factor influencing the recruitment success the absolute number of eggs spawned, which is assumed to be proportional to the catches during the spawning period.

We think that the temperature dependence of the larval period used in our model is valid, since it is based on laboratory experiences and since our model data remain within the in situ temperature range (14–25 °C) found for the scallop in Independencia bay. So the problem of “breaking relations” should not occur within this range of the environmental variable used. A key question that arises here is why just this one scallop species responds so favorably to the warming, while most other macro benthic species’ response is rather insignificant or even negative. Shouldn’t the proposed mechanism also hold for other species? Wolff (1987) based on a study on the population dynamics of this species during the El Niño period 1983–1984 and on fossil studies by Waller (1969) offers an explanation by suggesting that *Argopecten purpuratus* is a relict of a tropical/subtropical fauna that once dominated the Peruvian shores during the Miocene. El Niño events may have occurred frequently enough, subsequent to the general cooling of the waters in the late Miocene to preserve the warm water characteristics of this species. Most recent macro benthic species of the bay are more typical upwelling – adapted, cold – water species, however, and rather stressed during the warm El Niño temperatures.

While the assumption of shortening of the larval period at El Niño temperatures is thus based on solid evidence, our estimate of the mortality rate is not. Larval mortality is known to be much higher in situ than in hatcheries, but accurate estimates are not available, since in situ measurements are very difficult. So we had to use an envelope of values of settler to released eggs ratio to search for the best fit of our regression. Surprisingly, all of our envelope values, when applied to calculate the settlement factor, yielded a high regression coefficient ($R^2 > 0.92$), with the ratio of 1:100,000 providing the best fit (0.930). This suggests that the model results are quite robust over a wide range of M-values, and that the “real” in situ larval mortality rate may be in the order of magnitude estimated. This values, expressed as instant daily mortality

rate (0.56), lies in the range of values (0.0754 for *Polydora ciliata* and 0.8 for the bivalve *Mya arenaria*) given for planktonic larvae of benthic invertebrates by Rumrill et al. (1985).

Possibly, the most crucial assumption of our model is that of a constant and temperature-independent instantaneous daily mortality rate. By assuming this, we propose that larval mortality is mainly due to exposure to predation, considered independent of temperature. It could be argued, however, that predation rate may also increase with temperature (see discussion by Moloney et al., 1994 for the Dungeness crab example). While we cannot exclude this to hold true for some species, most predators of the scallop larvae (such as the mussel *Aulacomya ater*, which represents about half of the invertebrate biomass in normal upwelling years and which is greatly reduced during El Niño) seem to be rather cold water adapted, for which the high El Niño temperature may already represent adverse conditions beyond their physiological optimum (Mendo and Wolff, 2002a). Since the total number of days in the plankton is greatly reduced at higher temperatures, total exposure time to predation and to dispersal by currents, which may remove the larvae from the scallop banks, is also reduced and the number of settlers within the bay should greatly be increased.

By standardizing the settlement factor for the average spawning temperature of 16.26 °C recorded, we assumed that recruitment will be (on average) lower and higher at lower and higher temperatures, respectively.

It may be asked if other factors, besides temperature (or co-varying with temperature), may also be influential for the varying recruitment success of the scallops during the study period. Here, we should mention the increased oxygen saturation levels of bottom water of the bay during El Niño events (Wolff, 1987; Wolff and Mendo, 2000), which have been shown to also correlate with scallop biomass to a certain extent (Wolff, 1988). This factor may help to explain why high scallop biomass levels can be sustained in the bay during El Niño conditions (since – according to the Q₁₀-rule – with temperature respiration rate and oxygen demand shall increase), but hardly explains why just scallops were favored to such an

extent. Changing food conditions could also be influential. It may be that a shift in the plankton composition as related to the warming during El Niño (from larger diatoms to smaller dinoflagellates) may have also positively impacted the scallop larvae and juveniles. One would expect, however, that other bivalves of the system should then have also been favored. The same argument holds for a possible release in predation pressure. If the scallop outburst was due to a release in predation pressure, why were other macro benthic species not favored?

Based on the above reasoning, we believe that the proposed mechanism, by which larval survival and recruitment success is increased with temperature, is valid.

The other main pillar of our model—the assumption that catches during the spawning season are suitable proxies for spawning stock size, which is also decisive for the annual recruitment success, may need some further clarification here. Contrary to many other countries of the region, Peru still allows for an open access fishery, so the diving fishing fleet of Independencia bay flexibly grows and shrinks with the natural scallop population, through migrating fishermen from the south and north of the country (Wolff and Mendo, 2000). This means that fleet size and catches have varied over the years and the year's cycle in proportion to the available scallop harvest potential. Thus, catches during the spawning period should be good proxies for the spawner biomass. While the latter can thus be assured, the number of released eggs/spawner may have also changed with temperature, as it has been shown that gonad recuperation was greatly accelerated during higher temperatures (Wolff, 1988). If so, the number of eggs spawned would not just be a function of spawning stock biomass but also of temperature, an effect not considered in our model. It is also possible that egg quality may have been influenced by the temperature regime and the onset of spawning, a factor shown to be important for fish such as Atlantic cod (Scott et al., 2006).

4.2. The model fit and catch predictability

If we examine the relative importance of our two factors – spawning stock and settlement factor – for predicting annual catches, we find that both factors alone may explain a substantial part of the inherent variability of the data. The contribution of the settlement factor was greater, however (Fig. 2a), yielding a better fit in the bivariate correlation ($r=0.724$ compared to $r=0.601$ for the spawning stock). The overall fit of the multiple regression ($R^2=0.930$) can be considered as remarkably good, also reflected in the narrow confidence belt around the regression line (Fig. 3b) and the generally low residuals given in Table 3. It is interesting to note, however, that the differences between recorded and predicted catches is greatest at the lowest recorded catch levels of 1 and 7 t, respectively (Table 3). It is possible that these very low catch levels do not represent well enough the total catchable stock, since divers tend to target other invertebrates when scallop densities decrease beyond a threshold (ca. 0.1 Ind. m^{-2}) (Wolff, pers. observation). However, Fig. 3 shows that the model does not only predict catches well for the two El Niño warming periods, but also for the last years (2001–2004), when low temperatures caused low spawning and low recruitment. Fig. 4 illustrates that the predicted

annual catch greatly depends on the spawning stock size at low temperatures, while this factor decreases in importance at higher temperatures, at which the settlement factor becomes much more influential. These findings are of great relevance for the management of the stock: at low temperatures, the maintenance of a large enough spawning stock (equivalent to a minimum density of scallops in the environment) over the spawning period (November–April) is decisive for the yield of the post-recruitment fishing period thereafter, while at increasing spawning temperatures, spawning stock size is of little importance for determining the yield. The parent stock–recruitment relationship appears thus strong at low temperatures, and weak at the higher El Niño temperatures.

4.3. Concluding remarks and novelty of approach

Compared to age- or size structured population models and Surplus production models, which in addition to catch data require data on size structure, growth, natural and fishing mortality and of fishing effort respectively, and which may also suffer from incorrect assumptions regarding the constancy of growth and mortality rates over longer time periods, our model can do without these data and assumptions. Instead, it only requires mean monthly temperatures and catches during the spawning period. It yielded a 16% improved fit over our first model on the Peruvian scallop (Mendo and Wolff, 2002b), in which we correlated mean $T^\circ\text{C}$ during the spawning period to catches following the recruitment period. While the postulated mechanism behind the observed temperature catch relationship – a temperature mediated shortage of the larval period concomitant with a significant increase in larval survival and enhanced recruitment – has been put forward for invertebrates with pelagic larvae before (Underwood and Fairweather, 1989, Moloney et al., 1994), a catch prediction model based mainly on this mechanism has – to the knowledge of the authors – as yet not been successfully applied to any fishery. This is remarkable since attempts to empirically relate recruitment strength to environmental factors have been followed before and go back to the early work of Ricker (1958). Recent attempts extend mathematically beyond the traditional Ricker spawner–recruit model by using generalized additive modeling approaches (Daskalov, 1999 for Sprat, Anchovy, Whiting and Horse Mackerel in the Black Sea), applying fuzzy logic (Nishida et al., 2007 for Bigeye Tuna in the Indian Ocean) or using neural network analysis (Chen and Hare, 2006 for Pacific Halibut). While the above and other modernized versions have allowed to incorporate environmental variability and to improve the fit to the data compared to the traditional empirical Ricker model, “breaking relations”, nonlinear interdependencies between environmental, physiological and biotic factors and internal feed back processes have often limited the success of these empirical approaches and the question arises, why the here presented model may be an exception.

Our approach is grounded on a functional mechanism behind the recruitment success and the derivation of a temperature dependent new variable, which we called “settlement factor”. This new variable explains a much larger part of the observed variability in annual catches than the spawning stock size, pointing to the very strong role of the environment

in governing the population dynamics of the Peruvian bay scallop. Since the model is built on two factors only, the confidence belt around the predicted estimates is relatively narrow, giving a (statistical) advantage over models of higher complexity.

The special success of our model may lie in the biological characteristics of the scallop, which, as a relict of a formerly warm water fauna of the Peruvian coast, is greatly favored when tropical El Niño conditions appear in Independencia bay. Thus, during these periods the “environmental window” (Cury and Roy, 1989) opens (e.g. the settlement factor greatly increases) allowing the stock to proliferate, while at the same time it closes for other species, among which are competitors and predators of the scallop.

Since the model explains large part of the variability of the data ($R^2 = 0.930$) it promises successful predictions of the Peruvian scallop catches of Independencia bay. Its applicability requires, however, that the present fishing system (diving fishery, absence of closed seasons, no protected areas, minimum landing size of 65 mm shell height, open access) remains essentially unchanged.

Acknowledgements

This study was financed and conducted in the frame of the EU-project CENSOR (Climate variability and El Niño Southern Oscillation: Impacts for natural resources and management, contract No. 511071) and is CENSOR publication No. 0125.

REFERENCES

- Arntz, W.E., Fahrbach, E., 1991. El Niño-Klimaexperiment der Natur. Birkhaeuser Verlag, Basel (Switzerland), p. 264.
- Chen, D.G., Hare, S.R., 2006. Neural network and fuzzy logic models for pacific halibut recruitment analysis. *Ecol. Model.* 195, 11–19.
- Cury, P., Roy, C., 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquatic Sci. (CAN)* 46, 670–680.
- Cushing, D.H., 1982. *Climate and Fisheries*. Academic Press, London.
- Daskalov, G., 1999. Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalised additive models. *Fish. Res.* 41, 1–23.
- DiSalvo, L.H., Alacron, E., Martinez, G., Uribe, E., 1984. Progress in the mass culture of *Argopecten purpuratus* with notes on its natural history. *Rev. Chilena de Hist. Nat.* 57, 33–45.
- Hilborn, R., Mangel, L.M., 1997. *The Ecological Detective. Confronting Models with Data*. Princeton University Press, Princeton, NJ.
- Mendo, J., Jurado, E., 1993. Length-based growth parameter estimates of the Peruvian scallop (*Argopecten purpuratus*). *Fish. Res.* 15, 357–367.
- Mendo, J., Valdivieso, V., Yamashiro, C., 1988. Cambios en densidad, numero y biomasa de la concha de abanico (*Argopecten purpuratus*) en la Bahía de Independencia (Pisco, Peru) durante 1984–1987. In: Salzwedel, H., Landa, A. (Eds.), *Recursos y Dinámica del Ecosistema de Afloramiento Peruano*. Bol. Inst. Mar. Peru-Callao, Callao, p. 382.
- Mendo, J., Wolff, M. (Eds.), 2002a. *Bases Ecológicas y Socioeconómicas Para el Manejo de Los Recursos Vivos de la Reserva Nacional de Paracas*. Universidad Agraria La Molina, Lima, p. 244.
- Mendo, J., Wolff, M., 2002b. Pesquería y manejo de la concha de abanico (*Argopecten purpuratus*) en la Bahía de Independencia. In: Mendo, J., Wolff, M. (Eds.), *Bases Ecológicas y Socioeconómicas Para el Manejo de los Recursos Vivos de la Reserva Nacional de Paracas*. Universidad Agraria La Molina, Lima, pp. 188–194.
- Moloney, C.L., Botsford, L.W., Largier, J.L., 1994. Development, survival and timing of metamorphosis of planktonic larvae in a variable environment: the Dungeness crab as an example. *Mar. Ecol. Prog. Ser.* 113, 61–79.
- Myers, R.A., 1998. When do environment-recruitment correlations work? *Rev. Fish Biol. Fish.* 8, 285–305.
- Nishida, T., Chen, D.G., Mohri, M., 2007. Fuzzy logic analyses for spawner–recruitment relationship of bigeye tuna (*Thunnus obesus*) in the Indian Ocean incorporating the environmental regime shift. *Ecol. Model.* 203, 132–140.
- Ricker, W.E., 1958. Maximum sustained yields from fluctuating environments and mixed stocks. *J. Fish. Res. Board Can.* 15, 991–1006.
- Rumrill, S.S., Pennington, J.T., Chia, F.S., 1985. Differential susceptibility of marine invertebrate larvae: laboratory predation of sand dollar, *Dendroaster excentricus* (Eschscholtz), embryos and larvae by zoeae of the red crab, *Cancer productus* Randall. *J. Exp. Mar. Biol. Ecol.* 90, 193–208.
- Scott, B.E., Marteinsdottir, G., Begg, G.A., Wright, P.J., Kjesbu, O.S., 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecol. Model.* 191, 383–415.
- Underwood, A.J., Fairweather, P.G., 1989. Supply-side ecology and benthic marine assemblages. *TREE* 4, 16–19.
- Uriarte, I., Farias, A., Munoz, C., 1996. Cultivo en hatchery y preengorde del ostio del norte, *Argopecten purpuratus* (Lamarck, 1819) en el sur de Chile. *Rev. Biol.-Mar. Valparaiso* 31, 81–90.
- Waller, T.R., 1969. The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia), with emphasis on the tertiary and quaternary species of eastern North America. *J. Paleontol.* 43, 125.
- Wiff, R., Quiñones, R.A., 2004. Environmental parameterization in fisheries–biology models. A review. *Gayana* 68, 76–92.
- Wolff, M., 1985. Fischerei, Oekologie und Populationsdynamik de Pilgermuschel *Argopecten purpuratus* (L) im Fischereigebiet von Pisco (Peru) unter dem Einfluss des El Niño 1982/1983. PhD Thesis, Kiel University, Kiel, Germany.
- Wolff, M., 1987. Population dynamics of the Peruvian scallop *Argopecten purpuratus* during the El Niño phenomenon of 1983. *Can. J. Fish. Aquatic Sci.* 44, 1684–1691.
- Wolff, M., 1988. Spawning and recruitment in the Peruvian scallop *Argopecten purpuratus*. *Mar. Ecol. Prog. Ser.* 42, 213–217.
- Wolff, M., Mendo, J., 2000. Management of the Peruvian bay scallop (*Argopecten purpuratus*) metapopulation with regard to environmental change. *Aquat. Conserv.: Mar. Freshwat. Ecosyst.* 10, 117–126.
- Wolff, M., von Brand, E., Jollan, L., 1991. Temperature shock treatment for early larval selection in the Chilean scallop *Argopecten purpuratus* (Lamarck, 1819). In: Shumway, S.E., Sandifer, P.A. (Eds.), *World Aquaculture Workshops, 1. An International Compendium of Scallop Biology and Culture—A Tribute to James Mason. Selected papers from the 7th International Pectinid Workshop*. The World Aquaculture Society, Baton Rouge, p. 357.
- Wolff, M., Wolff, R., 1983. Observations on the utilization and growth of the pectinid *Argopecten purpuratus* (L.) in the fishing area of Pisco, Peru, 197–235.