Fish Sci (2016) 82:1–15
DOI 10.1007/s12562-015-0938-8

ORIGINAL ARTICLE

Fisheries

Spatio-temporal distribution and abundance patterns of red crab *Pleuroncodes planipes* related to ocean temperature from the Pacific coast of the Baja California Peninsula

Juan Antonio De Anda-Montañez[1] · **Susana Martínez-Aguilar**[2] · **Eduardo F. Balart**[1] · **Tania Zenteno-Savín**[1] · **Lía Méndez-Rodríguez**[1] · **Edgar Amador-Silva**[1] · **Manuel Figueroa-Rodríguez**[3]

Received: 8 October 2014 / Accepted: 20 September 2015 / Published online: 26 October 2015

Abstract Latitudinal and bathymetric patterns in the distribution and abundance of the deep sea red crab *Pleuroncodes planipes* along the Pacific coast of the southern part of the Baja California Peninsula were analyzed. Six research cruises were conducted between autumn (October–November 2004) and spring (March 2007). During this time, El Niño events occurred, allowing for exploration of the effect of this phenomenon on the dynamics of red crab distribution and abundance. The highest estimated biomass was 436,804 metric tons with a yield of 2014 kg h^{-1} of trawling. Red crab specimens were widely distributed in the study area with varying abundance, notably around Bahía Magdalena. Results from this study suggest that environmental changes have had a significant effect on the distribution and abundance of red crabs. El Niño events of 2004 and 2006 changed red crab behavior and affected the resource's availability. Data were also analyzed with a general linear modeling (GLM) framework to assess the variability in presence/absence data and catch rates (dependent variables) across the simultaneous effects of the season, latitude and depth gradients and bottom temperature (independent variables). The best binomial model selected on the basis of Akaike´s information criterion suggests that the variable season significantly contributed to the presence/absence of red crab. The best gamma conditional model for positive occurrences suggests that the explanatory variables of season, depth stratum and bottom temperature significantly contribute to explain the catch rate.

Keywords Abundance · Catch rates · Distribution · El Niño · Generalized linear modeling · Red crab

Introduction

Most stock assessment methods calculate absolute values or relative abundance from a fishery; however, for species that do not have an established fishery, the challenge is to cover extra research costs. This is the case of the red crab *Pleuroncodes planipes*, a small decapod crustacean belonging to the family Munididae [1] and distributed from San Francisco, California to Central America [2]. This species has attracted the attention of biologists for more than 50 years because of its massive occurrence along the west coast of the Baja California Peninsula [3]. Its life cycle in this area is closely linked to oceanographic conditions [4], such that the seasonal intensity of the California Current, local upwellings and offshore surface transports, as well as the magnitude of water productivity, are key factors.

A relevant feature of the red crab's life cycle is its massive presence in the epipelagic zone during the first larval stages to young adult stage, then alternating between pelagic and benthic life at carapace lengths between 12 and 31 mm, and finally it becomes strictly benthic on the outer continental shelf and slope at least to 500 m deep [5]. This characteristic behavior contributes to explaining why the

✉ Juan Antonio De Anda-Montañez
jdeanda@cibnor.mx

Susana Martínez-Aguilar
susykey5@yahoo.com.mx

Manuel Figueroa-Rodríguez
figuer@cicese.mx

[1] Centro de Investigaciones Biológicas del Noroeste, S.C. (CIBNOR), Instituto Politécnico Nacional 195. Colonia Playa Palo de Santa Rita Sur., La Paz B.C.S. 23096, Mexico

[2] La Paz, Baja California Sur, Mexico

[3] Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Carr. Ensenada-Tijuana 3918, Zona Playitas, Ensenada B.C. 22860, Mexico

red crab is an important component of the trophic web of the upwelling ecosystem of the Baja California Peninsula, connecting the pelagic and benthic web through its life cycle; it shifts from a primary consumer during its pelagic phase, grazing heavily on phytoplankton, to being mostly a secondary consumer in its benthic phase [6]. It is also a common prey of many marine predators, reducing the food chain as do anchovy and sardine [7, 8]. The differential bathymetric distribution also suggests different degrees of vulnerability to environmental changes along its life cycle, affecting its distribution and abundance. Thus, contrasting estimates of the red crab biomass are found in the same area (Bahía Magdalena, Gulf of Ulloa, Bahía Sebastián Vizcaíno), but in different years, e.g., 84,300 and 460,217 metric tons [9, 10].

Due to its abundance and distribution in dense aggregations, the red crab has been identified as a species with potential for exploitation in Mexico [11, 12]. However, environmental effects on marine resources are a continuous process; highly variable environmental conditions can cause wide fluctuations in abundance with no stable patterns or periodicity. For these reasons, the abundance of red crab and the dynamics of its distribution over a range of latitudes and bathymetric gradients were assessed. Analyses were performed on the catch of six research cruises conducted from October 2004 to March 2007, in the course of which El Niño and La Niña events occurred. This allowed for exploring the effects of such environmental conditions on red crab dynamics in the study area. Also, the generalized linear modeling (GLM) approach was used in order to assess the variability in catch rates across the simultaneous effects of temperature, season, latitude and depth. We expected to find a significant relationship between the catch rate of red crab specimens and the variables hypothesized to affect the south portion of the west coast of the Baja California Peninsula, Mexico.

Materials and methods

Study area

The study area is located on the continental shelf and slope of the west coast of the Baja California Peninsula and corresponds to a system of bays. To the north stands Bahía Sebastián Vizcaíno, in the middle of which the submarine canyon "El Puma" accentuates its slope starting from 90 m deep towards the northwest. The distribution of sediments ranges from sand to sandy clay, with a gradual shift to fine-textured sediment with increasing depth. To the south, the Gulf of Ulloa has higher amplitude without interrupting the topographic relief of the continental shelf. The maximum length of the platform is found in the central part with a gentle slope, which is accentuated to the north and south, where the shelf is reduced. Predominantly silty sand covers almost the entire shelf area, with isolated patches of very fine sand and sandy silt towards the outer shelf. Bahía Sebastián Vizcaíno and the Gulf of Ulloa are separated by a block of ophiolithic rocks, which are manifested at depth. This block of rocks corresponds to the area of Punta Eugenia [13] (Fig. 1).

Oceanographic dynamics of the region are extremely complex and are mainly dominated by the California Current. The California Current moves south along the west coast of North America, ending near the southern end of the peninsula, and brings cool water with low salinity southward. The California Subcurrent is a subsurface current to more than 200 m deep that flows poleward and has a core of high salinity and low dissolved oxygen, in contrast to the California Current and the California Countercurrent [14]. The latter develops close to the coast and is intermittent. South of the peninsula, between 16°N and 20°N, the North Equatorial Current, which marks the northern boundary of the equatorial current system surface, is a superficial current that is influenced by the trade winds; this current occasionally extends into the study area, where the dominant water system is the subtropical surface water system, bringing with it tropical surface water [14, 15]. The effects of strong winds are particularly important in coastal zones, creating cold upwelling. The upwelling water brings nutrients to the surface, leading to abundant plankton and animal life, including species that constitute important fisheries [16]. A review of hydrographic features can be found in Fiedler and Talley [17].

Field surveys

For the present investigation, we used a ship (BIP XII of the Northwest Biological Research Center) with a steel helmet, total length of 21.25 m, main engine of 520 HP, autonomy of 15 days, a refrigeration system in the cellar, an oceanographic winch, and equipped with echo sounders, global positioning system, radar, VHF/VH radios. There were six research cruises distributed between October 2004 and March 2007. The dates of the six cruises were as follows: first cruise 21 October to 10 November 2004, second cruise 15–29 March 2005, third cruise 19–25 November 2005, fourth cruise 16–24 March 2006, fifth cruise 21 November to 4 December 2006 and the sixth research cruise 7–18 March 2007. The first cruise, in autumn 2004, followed a plan of stations from offshore Todos Santos to Bahía Sebastián Vizcaíno (Fig. 2a), and the following five cruises used a modified plan with stations from 23°36′N near Todos Santos to 28°51′N in Bahía Sebastián Vizcaíno (Fig. 2b–f).

A stratified random sampling design was used, with stations along perpendicular lines to the coast (transects),

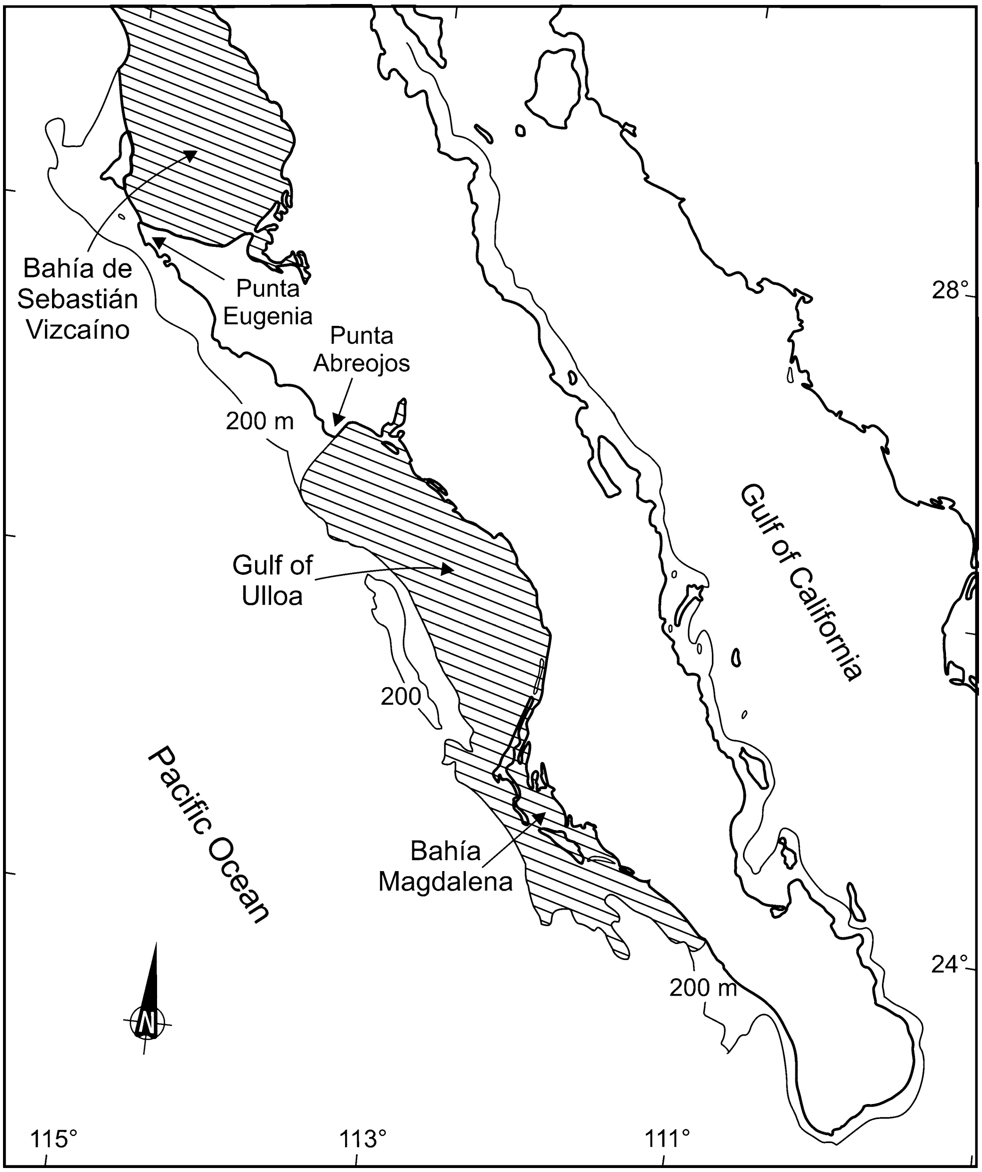
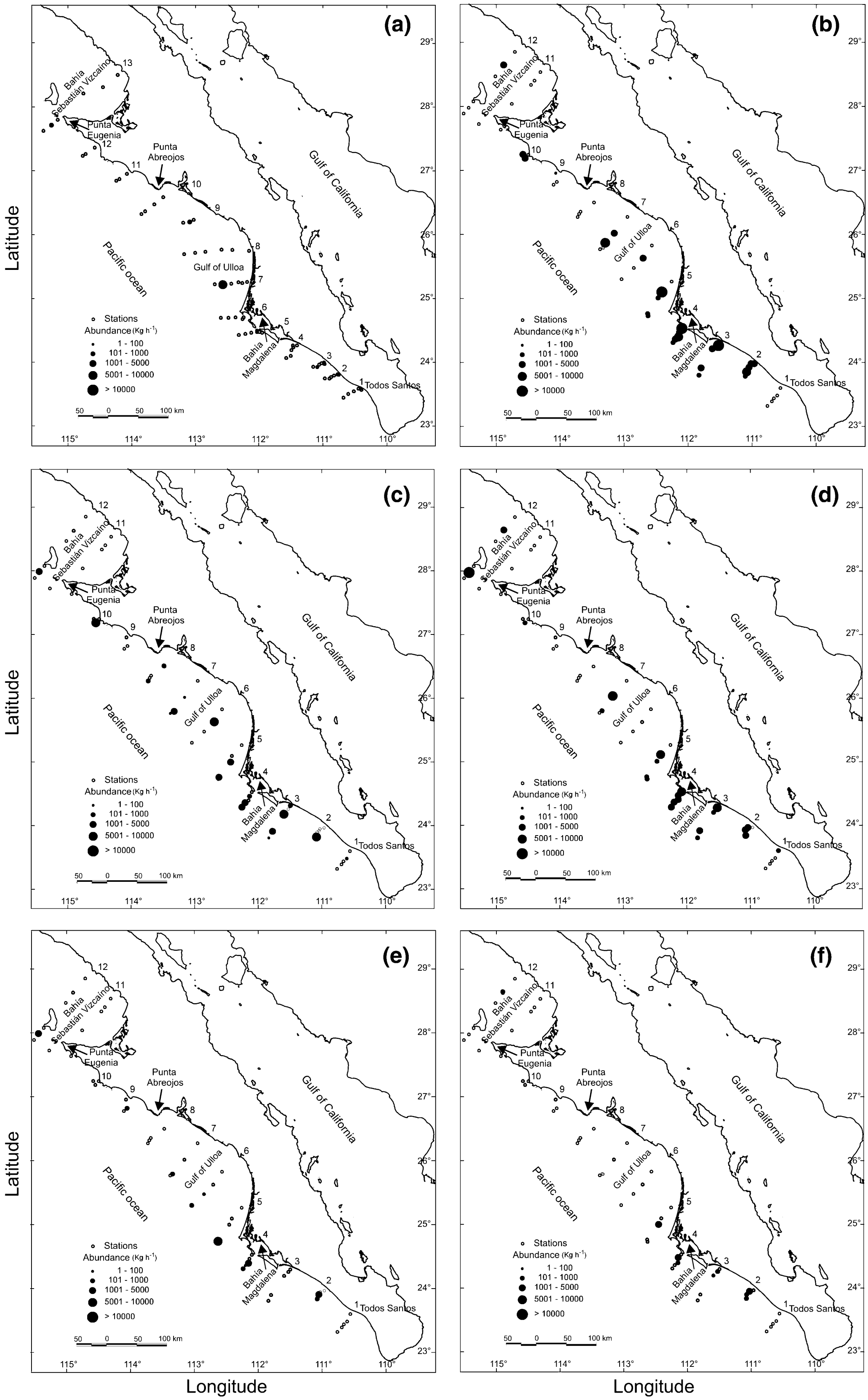


Fig. 1 Study area showing the sediment distribution and the isobath at 200 m (modified from Chávez-López [13])

equally spaced and varying in length according to the topography and bathymetry. At each station, a hybrid conical net, 34 m of upper head-rope, with stretched mesh size tapering from 140 mm in the wings to 45 mm in the codend for fish and crustaceans, was cast and trawled at six depth strata (ranges); (1) 0–50 m, (2) 51–100 m, (3) 101–200 m, (4) 201–300 m, (5) 301–400 m, and (6) 401–500 m, with most trawls concentrated in the 51–100 m range, and with only two trawls in the 401–500 m range. The number of stations per transect and depth strata depended on the topography and bathymetry in each zone; sampling stations, transects and depth strata were maintained during all cruises, except first cruise.

The drags for the first survey were between 20 and 311 m, and the area covered was roughly 27,314 km^2. For subsequent surveys, depth varied from 38 to 401 m and the area covered was roughly 34,233 km^2. These areas and the areas for each station per transect were calculated with the Software ArcGIS version 10.0 (Table 1). The trawl hauls were made at an average speed of 2.5 kn during the day and night with an effective trawl between 5 and 21 min (mean 15 min). The effective haul period started when the winch stopped (the two steel otter boards touched the bottom) and lasted until the otter boards were lifted from the bottom. The total weight of red crab specimens per haul was recorded. It was assumed that trawl efficiency with real times ranging from 5 to 21 min was not affected. It did affect the cath. Therefore, it was reported as catch rates in kg h^{-1} of trawl to be comparable. Studies of trawl efficiency are outside the scope of this study.


(a)
(b)
(c)
(d)
(e)
(f)
Bahía Sebastián Vizcaíno
Punta Eugenia
Punta Abreojos
Gulf of Ulloa
Bahía Magdalena
Todos Santos
Gulf of California
Pacific ocean
1
2
3
4
5
6
7
8
9
10
11
12
13
Stations
Abundance (Kg h^{-1})
1 - 100
101 - 1000
1001 - 5000
5001 - 10000
> 10000
50 0 50 100 km
115°
114°
113°
112°
111°
110°
29°
28°
27°
26°
25°
24°
23°
Latitude
Longitude

◀**Fig. 2** Geo-referenced sampling stations and distribution and abundance of red crab *Pleuroncodes planipes* in the south portion of the Pacific coast of the Baja California Peninsula, Mexico, during the six cruises, **a** October–November 2004 (cruise 1), **b** March 2005 (cruise 2), **c** November 2005 (cruise 3), **d** March 2006 (cruise 4), **e** November 2006 (cruise 5), and **f** March 2007 (cruise 6). The *numbers* over the peninsula indicate the transect number

Population dynamics

The abundance and estimated biomass were determined using the swept area method [18], which assumes that the mean catch per unit of effort or per unit of swept area is an index of stock abundance. The swept area in each haul (a_i) was calculated from:

$$a_i = D_i \mathrm{rs} X_2, \qquad D_i = V_i t_i,$$

where V_i is the velocity of the trawl over the ground (2.5 kn), rs is the length of the head-rope (34 m), t_i is the time spent trawling (5–21 min), X_2 is the fraction of the head-rope which is equal to the width of the path swept by the trawl expressed as a fraction of rs, the "wing spread", rs $\times X_2$. Pauly [19] suggests $X_2 = 0.5$. Effective head-rope width is generally accepted as being approximately 50 % of nominal head-rope width; for the sweep, which is shorter, this value drops to between 40 and 45 % [20]. Because this parameter (wing spread) was unknown in this study, it was defined by a set of possible values (0.5, 0.6, 0.7), selected based on reference values available in the literature [19–22].

The catch in weight per unit of swept area (CPUA expressed in kg km^{-2}) was obtained from:

$$\mathrm{CPUA}_i = \frac{C_i}{a_i},$$

where C_i is the catch in weight of a haul i. Expanding this CPUE$_i$ to the area under investigation per sampling station (A_i; Table 1), an estimate of the biomass (B_i) was obtained:

$$B_i = \frac{\mathrm{CPUE}_i}{X_1} A_i$$

Let X_1 be the fraction of the biomass in the effective path swept that is actually caught ($X1 = 1.0$) [23]. The total biomass (B_T) corresponds to the sum of the estimated biomasses in all the sampling stations (B_i):

$$B_T = \sum_{1}^{e} B_i$$

The coefficient of variation (CV, standard deviation/mean × 100) is shown in the data of estimated biomass.

Table 1 Areas used for each station per transect (A_i) from the west coast of the Baja California Peninsula, Mexico, as calculated with the Software ArcGIS version 10.0

Transect	Cruise 1 area (km^2)	Cruise 2–6 area (km^2)
1	181.53	372.41
2	87.91	276.82
3	92.76	551.50
4	168.92	312.86
5	178.23	648.36
6	308.23	1344.62
7	424.95	795.85
8	667.17	750.60
9	984.50	381.92
10	695.43	223.57
11	478.68	785.35
12	383.37	755.74
13	1158.49	–
Total	27,314	34,233

Environmental variability

In each of the sampling stations, an autonomous CTD, which provides temperature data of the water column, was cast. The superficial and bottom average temperature per season (CTD data) and the catch rates per season of red crab are related. Subsequently, the bottom temperature of each station was used in the generalized linear models (GLM). Distribution maps were drawn from infrared satellite images of the sea surface temperature. Description of the sensors can be found in Baith et al. [24]. Sea surface temperature images were downloaded (http://oceancolor.gsfc.nasa.gov/) on the dates of the surveys. According to NOAA (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml), Pacific warm and cold episodes are based on a threshold of ±0.5 °C for the Oceanic Niño Index (ONI).

Data analysis

Catch rates of red crab specimens were determined for trawl data by dividing the catch by the number of hours trawled (kg h^{-1}). The data set comprised a large proportion of no red crabs caught (zeroes). The generalized linear modeling (GLM) approach [25, 26] was used in order to assess the variability in presence/absence data and catch rates (dependent variables) across the simultaneous effects of the season, latitude and depth gradients and bottom temperature (independent variables), except for cruise 6 (Spring 2007) due to the loss of CTD data. Analyses were performed with Statistica

Software version 8.0 for Windows. Six models were adjusted to the data. In models 1–3, the probability of a non-zero catch was modeled assuming a binomial error distribution (presence = 1; absence = 0). The purpose of using these three models was to determine the factors that predict the binary dependent (response) variable (presence or absence of red crab). With models 4–6, only the positive catch was modeled, assuming a Gamma error distribution. The Gamma distribution was selected because it was not significantly different from the Chi square test ($p > 0.05$), while the log-normal, Poisson, negative-binomial, normal error distribution did show significant differences with the Chi square test ($p < 0.05$). The catch rate was selected as the continuous dependent (response) variable, while season, latitude and depth were included as the categorical explanatory variables, and bottom temperature was considered as a continuous explanatory variable (Table 2).

In model 1, the depth was not included; in model 2, the latitude was not included; and in model 3, the season was not included because very large values were detected for some parameters and the diagonal elements of the parameters variance/covariance matrix; the Hessian matrix may be singular, and the parameter estimates may give inconsistent results. In model 4, all the variables were included; in model 5, the latitude was not included; and in model 6, the season and latitude were not included (Table 3). For the binomial models (1–3), a logit was used as the link function to relate the presence/absence to the categorical and continuous variables. For the Gamma models (4–6), a log was used as the link function to relate the catch rate to the categorical and continuous variables. The three binomial models were validated by visual analysis of the lift chart and residuals, and the three Gamma models were validated by visual analysis of the deviance residual and predicted and observed values [26], and selected on the basis of Akaike´s information criterion (AIC) [27–29].

Table 2 Factors hypothesized to affect catch rates of red crab *Pleuroncodes planipes* caught in bottom-trawl conducted along the southern portion of the west coast of the Baja California Peninsula, Mexico

Variable	Type	Description
Season	Categorical	Autumn 2004 = October–November
		Spring 2005 = March
		Autumn 2005 = November
		Spring 2006 = March
		Autumn 2006 = November
Latitude	Categorical	North: transects 9, 10, 11, and 12
		Center: transects 5, 6, 7, and 8
		South; transects 1, 2, 3 and 4
Depth	Categorical	Depth stratum in which gear operated
		1. 0–50 m
		2. 51–100 m
		3. 101–200 m
		4. 201–300 m
		5. 301–400 m
		6. 401–500 m
Bottom temperature	Continuous	Bottom temperature in which gear operated

Table 3 Factors used in the final generalized linear models (GLM) of catch rates of red crab *Pleuroncodes planipes* conducted along the southern portion of the west coast of the Baja California Peninsula, Mexico

Model	Error	Link	Factors
Trawl catch rate (1)	Binomial	Logit	Season + latitude + temperature
Trawl catch rate (2)	Binomial	Logit	Season + depth + temperature
Trawl catch rate (3)	Binomial	Logit	Latitude + depth + temperature
Trawl catch rate (4)	Gamma	Log	Season + latitude + depth + temperature
Trawl catch rate (5)	Gamma	Log	Season + depth + temperature
Trawl catch rate (6)	Gamma	Log	Depth + temperature

Data models used for catch rates comprised three models of proportion of sets with a non-zero red crab (*binomial error distribution* models 1–3), and three models of positive sets only (*gamma error distribution* models 4–6)

Results

Catch rates

The distribution of red crab specimens per station shows a clear and consistent pattern of heterogeneous distribution. The average catch rates of red crab organisms of the cruises conducted in the spring 2005, autumn 2005 and spring 2006 showed better catch rates (Table 4). Table 4 also shows the average catch rates by day and night for the six cruises; the best catch rate was obtained during the day for spring 2005, autumn 2005 and spring 2006. This pattern is reversed during the autumns of 2004 and 2005, when the best catch rates were overnight.

The catch rate in autumn of 2004 was lower than in the other five cruises, registering a maximum of 1924 kg h^{-1} of trawl in transect 7, in a station away from the coast and at a depth of approximately 200 m located in the Gulf of Ulloa (Fig. 2a). The distribution in spring of 2005 was wider, practically throughout the study area, and the abundance was as high as in the other five cruises, registering a maximum of 5317 and 4424 kg h^{-1} of trawl in transects 3 and 4, respectively, in the depth strata of 51–100 m, 101–200 m and 201–300 m in an area located close to Bahía Magdalena (Fig. 2b; [30]). Red crab distribution and abundance

Table 4 Numbers of trawls and catch rates of red crab *Pleuroncodes planipes* for each season (cruise) conducted along the southern portion of the west coast of the Baja California Peninsula, Mexico, October 2004–March 2007 (for details see text)

Cruise	Season	Trawls (*n*)	Catch rate (kg h^{-1})	Catch rate per day (kg h^{-1})	Catch rate per night (kg h^{-1})
1	Autumn 2004	39	207	2.6	911
2	Spring 2005	43	2014[a]	2298	1581
3	Autumn 2005	44	1087	1278	880
4	Spring 2006	42	1485	1953	793
5	Autumn 2006	41	512	190	1031
6	Spring 2007	45	251	464	24

[a] The results of the second cruise are shown in De Anda-Montañez et al. [30]

Table 5 Catch rate of red crab *Pleuroncodes planipes* by depth strata for each research cruise conducted along the southern portion of the west coast of the Baja California Peninsula, Mexico, October 2004–March 2007 (for details see text)

Depth (m)	Season					
	Autumn 2004	Spring 2005[a]	Autumn 2005	Spring 2006	Autumn 2006	Spring 2007
	Catch rate (kg h^{-1})					
1 (0–50)	0 (11)	0 (0)	0 (0)	0 (0)	0 (2)	0 (2)
2 (51–100)	10 (20)	2297 (21)	194 (22)	1393 (21)	141 (14)	26 (21)
3 (101–200)	1310 (6)	1600 (12)	785 (11)	1742 (12)	481 (14)	839 (11)
4 (201–300)	0 (1)	3223 (5)	4370 (7)	1950 (4)	39 (5)	159 (5)
5 (301–400)	0 (1)	343 (5)	968 (4)	574 (5)	468 (4)	0 (6)
6 (401–500)	–	–	–	–	9474 (2)	–

The numbers in parentheses represent the number of hauls made at each depth

[a] The results of this season are shown per De Anda-Montañez et al. [30]

Table 6 Values assumed for the parameter wing spread and observed trawl velocity for estimating the biomass and the coefficient of variation (CV) by depth strata of red crab *Pleuroncodes planipes* for each season conducted along the southern portion of the west coast of the Baja California Peninsula, Mexico, October 2004–March 2007 (for details see text)

Season	Wing spread	Trawl velocity (kn)	Biomass (metric tons)	CV (%)
Autumn 2004	0.5	2.8	50,442	148
	0.6	2.8	42,018	148
	0.7	2.8	36,015	148
Spring 2005	0.5	2.4	611,525[a]	90
	0.6	2.4	509,604	90
	0.7	2.4	436,804	90
Autumn 2005	0.5	2.6	378,183	79
	0.6	2.6	315,152	79
	0.7	2.6	270,131	79
Spring 2006	0.5	2.6	445,008	93
	0.6	2.6	370,840	93
	0.7	2.6	317,863	93
Autumn 2006	0.5	2.5	151,328	111
	0.6	2.5	126,107	111
	0.7	2.5	108,092	111
Spring 2007	0.5	2.5	57,390	144
	0.6	2.5	47,825	144
	0.7	2.5	40,993	144

[a] Value shown in De Anda-Montañez et al. [30]

were also wider and higher in the autumn of 2005 for transects 2 and 3 with 1579 and 1847 kg h^{-1} of trawling, respectively, in the depth stratum of 201–300 m, located to south of Bahía Magdalena (Fig. 2c).

In the spring of 2006, high abundances with values above 1600 kg h^{-1} of trawling were recorded in stations with depth strata (51–300 m), as in the cruise conducted in spring of 2005, close to Bahía Magdalena, Gulf of Ulloa and Bahía Sebastián Vizcaíno (Fig. 2d). For the autumn of 2006, red crab distribution was registered in stations far from the coast, with the highest abundance recorded in transect 5 (2054 kg h^{-1} of trawling) in the depth stratum of 401–500 m, close to Bahía Magdalena (Fig. 2e). In the spring of 2007, red crab distribution was recorded toward the south of the peninsula with relatively low abundance, transects 2 and 5 being located to the south and north of Bahía Magdalena, respectively, and in the depth stratum of 101–200 m, which showed the highest abundance at 600 kg h^{-1} of trawling (Fig. 2f). Table 5 shows, in general, the average catch rates of red crab by depth strata for each season.

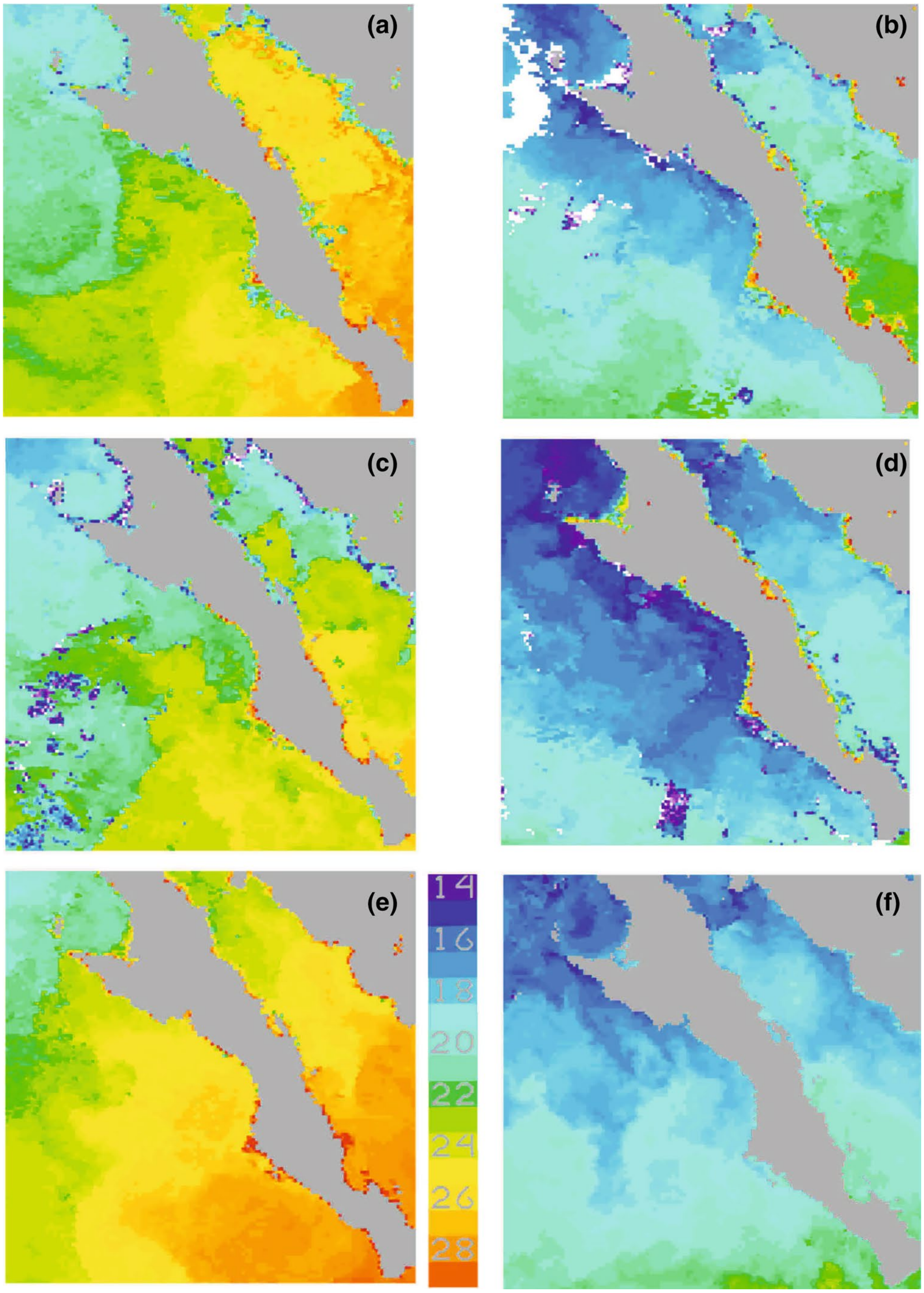


Fig. 3 Sea surface temperatures from infrared satellite images during the six cruises, **a** October–November 2004 (cruise 1), **b** March 2005 (cruise 2), **c** November 2005 (cruise 3), **d** March 2006 (cruise 4), **e** November 2006 (cruise 5), and **f** March 2007 (cruise 6) (NOAA data)

Estimated biomass

Estimated biomass of red crab using three assumed wing spread values and observed trawl velocity for each of the six seasons is shown in Table 6. Although it is difficult to identify which parameter value potentially estimates biomass correctly, the wing spread value of 0.7 produced more conservative estimates. Therefore, this value was adopted as the most plausible for the use of the swept area method for assessing the red crab biomass. These values ranged from 36,015 metric tons calculated for autumn 2004 to 436,804 metric tons estimated for spring 2005. All biomass estimates had high CV ranging from 79 to 148 % (Table 6). These high values of CV show a large variability in the red crab catch data, and therefore, in estimates of biomass.

The distribution pattern of this biomass showed that the best fishing ground was restricted to Bahía Magdalena and the surrounding areas. The next more abundant area was located in the Gulf of Ulloa with a vast continental shelf area, and the less abundant area was around Punta Eugenia. Among the six depth strata where trawls were conducted, the highest biomass was found at depths of 201–300 m and 401–500 m.

Environmental variability

During autumn sampling periods off the southern part of the peninsula, warm waters dominated the coast with the intrusion of subequatorial water masses (Fig. 3a, c y e; NOAA data). Under El Niño environmental conditions (positive anomalies of up to 0.9 and 1.1 °C in 2004 and 2006, respectively; NOAA data), red crab distribution and abundance were poor and restricted to deeper stations, and with the best catch rates obtained overnight (Table 4). The biomass estimates in these two seasons were the lowest of the study period. However, during the third cruise, conducted in autumn 2005, temperatures colder than in the cruises that had taken place in the same season in 2004 and 2006 were registered, and therefore, a La Niña event was catalogued (November 2005 to March 2006) with maximum anomalies of −0.9 °C (NOAA data). Under these environmental conditions, red crab specimens were more abundant and showed a wider distribution, practically throughout the study area (Fig. 2c).

During spring sampling periods, when cold-water masses penetrated the region, the temperature gradient decreased, and the 2005 sea surface temperature anomaly of +0.3 °C was the warmest (Fig. 3b; NOAA data), and the 2006 anomaly of −0.4 °C was the coldest (Fig. 3d; NOAA data). The latter was caused by upwelling along the coast with no input of warm water from the tropics, and for this reason, the waters off the coast of the peninsula were cooler than the offshore ocean waters. Under these environmental conditions, the red crab showed a wide distribution and a high abundance, with the best catch rates obtained during the day (Table 4), which was reflected in the highest biomass estimate (Table 6). During the spring of 2007, with intermediate temperatures (+0.1 °C anomaly; Fig. 3f; NOAA data) between the spring of 2005 and the spring of 2006, respectively, there was a radical change in the catch rate and biomass of the red crab, it being as low as that estimated in the autumn of 2004, but with its distribution near Bahía Magdalena and Bahía Sebastián Vizcaíno, and with the best catch rates also obtained during the day (Table 4).

These changes of catch rate with temperature, the extremes of which are associated with El Niño and La Niña events, can be summarized as follows. The superficial and bottom average temperatures of all sampling stations per season (CTD data) show a lineal and significant relationship with red crab catch rates; the higher the surface temperature or bottom temperature, the lower the red crab catch rates (Fig. 4).

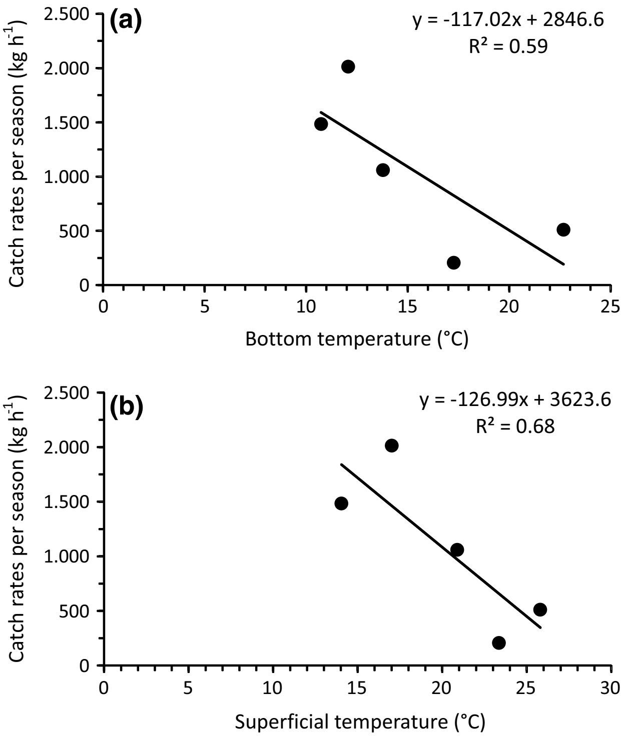


Fig. 4 Relationship between the superficial and bottom average temperature per season (CTD data) and the average catch rates per season of red crab *Pleuroncodes planipes* for each research cruise conducted in the southern portion of the west coast of the Baja California Peninsula, Mexico

Trawl catch rate model

The three binomial models for presence/absence fit the data reasonably well, and there is no evidence of overdispersion, since the ratios of the statistics of goodness of fit (Deviance and Pearson Chi square) over the degree of freedom are close to 1.0 (Table 7). Furthermore, the lift chart summarizes the gain that can be expected by using the respective predictive model compared to using baseline information only, and the residuals of the three models showed a homogeneous variance and a normal distribution as expected for a fitted model (Fig. 5). Also, the Hosmer–Lemeshow test applied to the observed and predicted data by the three models showed no significant difference ($p = 0.25$, $p = 0.58$, $p = 0.22$, respectively) (Table 7). The best model selected on the basis of Akaike´s information

Table 7 Statistics of goodness of fit, parameter estimates and standard error (s. e.) in the different generalized linear models that describe presence/absence of red crab *Pleuroncodes planipes*

Models						
Statistics	(1)		(2)		(3)	
Error	Binomial		Binomial		Binomial	
Link	Logit		Logit		Logit	
n	203		203		203	
Deviance	192		173		177	
Pearson Chi^2	183		172		212	
Loglikelihood	−95		−86		−89	
Df	187		184		184	
Deviance/*Df*	1.02		0.94		0.96	
Pearson Chi square/*Df*	0.98		0.93		1.15	
Level of effect	Estimate	s. e.	Estimate	s. e.	Estimate	s. e.
Intercept	−6.96**	1.69	−6.78	2049	−8.46	2465
Temperature	0.50**	0.11	−0.19	0.12	0.15**	0.05
Autumn 2004	1.28	0.51	1.85	3483	–	–
Spring 2005	0.50	0.44	−9.48**	0.69	–	–
Autumn 2005	0.45	0.40	5.73**	0.59	–	–
Spring 2006	1.04*	0.49	−9.84**	0.68	–	–
Autumn 2006	0.0	0.0	0.0	0.0	–	–
North	0.0	0.0	–	–	0.0	0.0
Center	−0.64*	0.27	–	–	5.47**	0.46
South	−0.74**	0.28	–	–	12.06	3020
1) 0–50 m	–	–	24.89	5524	25.73	4720
2) 51–100 m	–	–	11.43	2049	7.56	2465
3) 101–200 m	–	–	9.30	2049	6.14	2465
4) 201–300 m	–	–	0.06	719	−1.42	2403
5) 301–400 m	–	–	1.14	2049	−1.55	2465
6) 401–500 m	–	–	0.0	0.0	0.0	0.0
Season*Depth (7[a])	–	–	7.99**	0.78	–	–
Season*Depth (12[a])	–	–	5.96**	0.79	–	–
Season*Depth (17[a])	–	–	8.66**	0.78	–	–
Latitude*Depth (7[a])	–	–	–	–	−5.36**	0.63
Hosmer–Lemeshow test	10.16; $p = 0.25$		6.58; $p = 0.58$		10.65; $p = 0.22$	
AIC[b]	224		207		209	
Rank[c]	3rd		1st		2nd	

Values marked with * and ** were significantly different ($p = 0.05$ and $p = 0.01$, respectively) from the intercept

[a] Level of effect

[b] Akaike information criterion

[c] The models were ranked from best to worst according to their AIC values

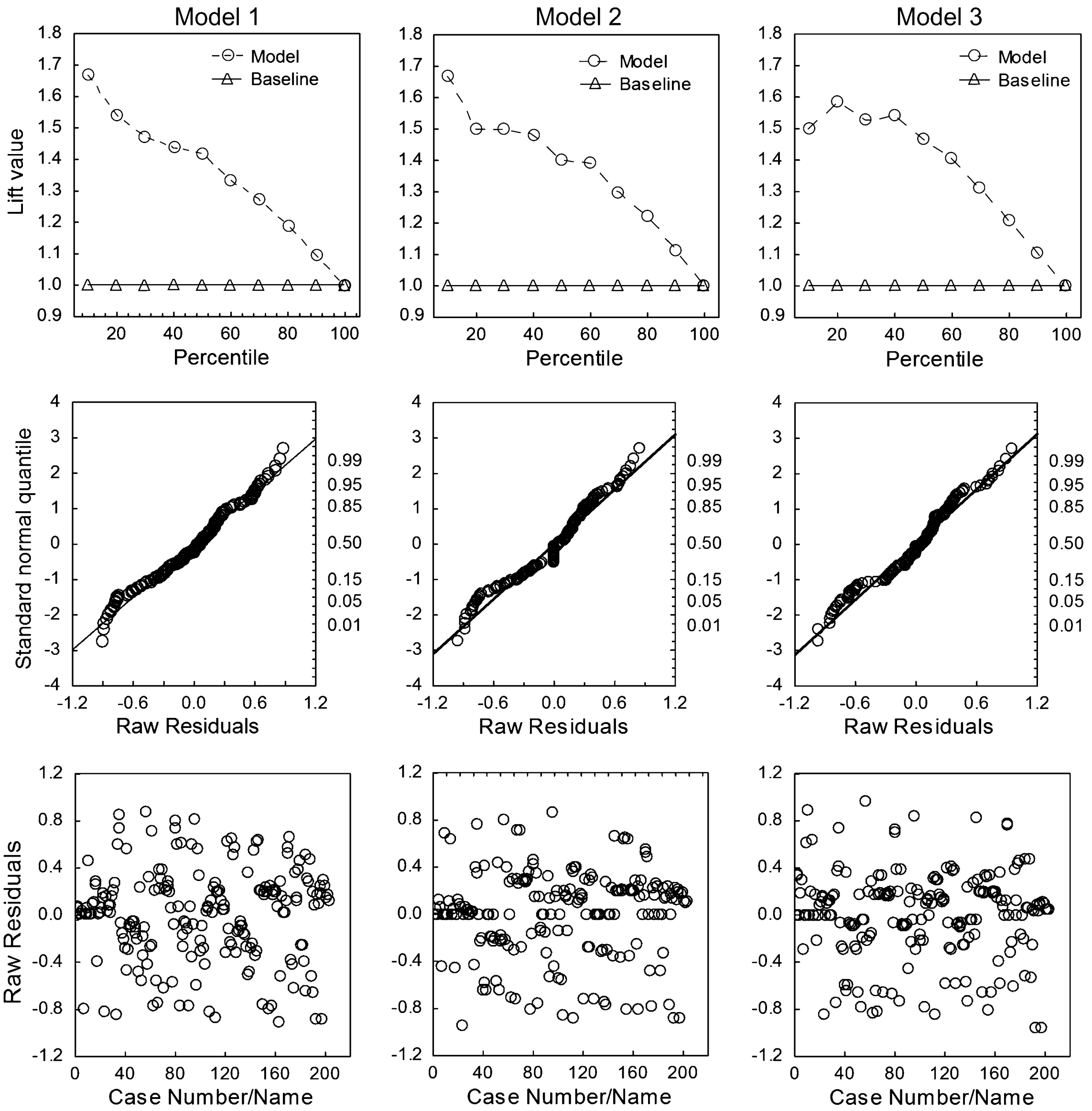


Fig. 5 The lift chart and residuals plots for all three predictive binomial models of red crab from the Pacific coast of the Baja California Peninsula, Mexico

criterion is model number 2. This model started with 12 parameters ($k = 12$), but only six of these ($k = 6$), intercept, presence/absence of the red crab, season (spring 2005, autumn 2005 and autumn 2006) and the interactions, season × depth (7^a), season × depth (12^a), season × depth (17^a) ($\beta = -6.78$, std error 2049, $p > 0.05$, deviance 173, AIC 207), were significant.

The results of the gamma conditional models (model 4–6) for positive occurrences fit the data reasonably well, and there is no evidence of overdispersion, because the ratios of the deviance and Pearson Chi square over the degree of freedom are close to 1.0. The diagnostic of the deviance residual and predicted values, deviance residual and observed values, apparently show that the variance of the residuals is homogeneous over the explanatory variables in the model; it confirms the adequacy of the fitted models. Furthermore, a linear relationship between fitted values and the catch rate (observed values) can be seen, and this shows that the model fits the data (Fig. 6; Table 8). The best model selected on the basis of Akaike´s information criterion is model number 4. This model started with 15 parameters ($k = 15$), but only ten of these ($k = 10$), intercept, catch rate, bottom temperature, season (spring 2005, autumn 2005 and spring 2006), *depth* (201–300 m, 301–400 m) and the interactions season × latitude (2^a), season × latitude (4^a), season × depth (6^a), season × depth (9^a) ($\beta = 5.28$, std error 1.96, $p < 0.01$, deviance 24, AIC 1235), significantly contribute to explain the catch rate.

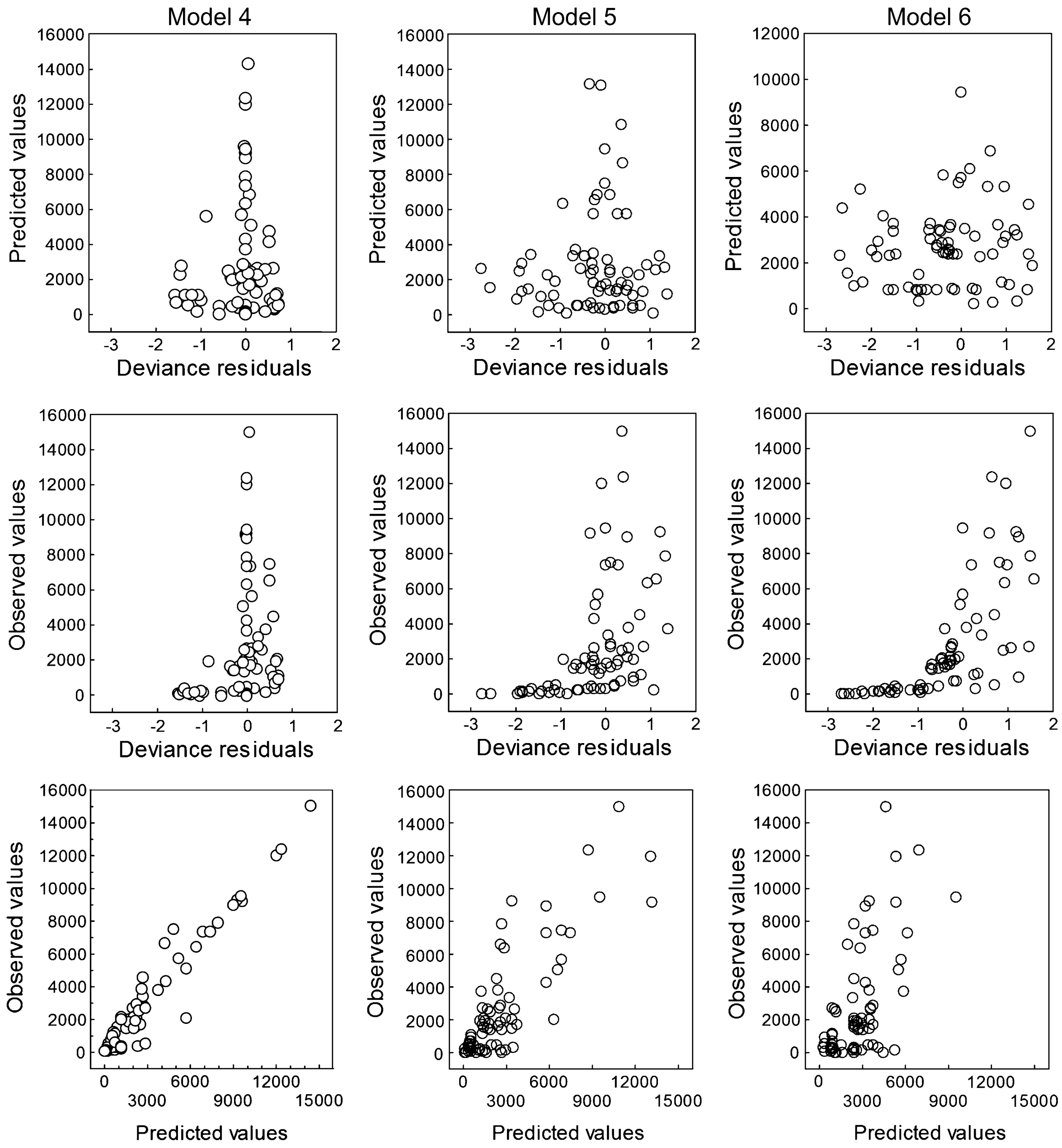


Fig. 6 Residuals plots for all three predictive Gamma models of red crab from the Pacific coast of the Baja California Peninsula, Mexico

Discussion

Two aspects of the results from the surveys of benthic red crab along the soft bottoms of the west coast of the peninsula of Baja California warrant attention. First, the wide and heterogeneous variation in the spatial distribution of catch rates within and between seasons, and second, the huge differences in the estimated biomass in the surveys of the red crab (i.e., 36,015 vs. 436,804 metric tons). Previous red crab assessments, like those of Ehrhardt [9] or Aurioles-Gamboa [5, 10], noted similar results on the continental shelf and suggested an seasonal abundance pattern and a seasonal offshore-inshore migration, at least between 24° and 26°N. Similarly, Gómez-Gutiérrez and Sánchez-Ortiz [31] proposed a model of the life cycle based mainly on the analysis of the pelagic phase of red crab, which also includes a seasonal inshore-offshore migration. The heterogeneous distribution of the adult red crab at a scale of 5° of latitude is addressed for the first time, taking advantage of the GLM models. These models show that benthic red crab distribution (presence/absence) can be explained by the interaction of covariates such as season, depth and bottom temperature, while the density (i.e., catch rate) can be explained by a model that

Table 8 Statistics of goodness of fit, parameter estimates and standard error (s. e.) in the different generalized linear models that describe catch rates of red crab *Pleuroncodes planipes*

Models						
Statistics	(4)		(5)		(6)	
Error	Gamma		Gamma		Gamma	
Link	Log		Log		Log	
n	74		74		74	
Deviance	24		64		96	
Pearson Chi Square	15		39		63	
Log likelihood	−576		−614		−631	
Df	32		53		67	
Deviance/*Df*	0.74		1.20		1.44	
Pearson Chi Square/*Df*	0.47		0.74		0.94	
Level of effect	Estimate	s. e.	Estimate	s. e.	Estimate	s. e.
Intercept	5.28**	1.96	11.20**	1.50	9.32**	0.52
Temperature	0.23*	0.10	−0.11	0.10	−0.09**	0.03
Autumn 2004	−5.26	3.52	0.94	1.99	–	–
Spring 2005	4.69**	1.62	0.22	0.74	–	–
Autumn 2005	3.28*	1.36	0.84	0.72	–	–
Spring 2006	2.46**	0.48	−0.15	0.45	–	–
Autumn 2006	0.0	0.0	0.0	0.0	–	–
North	0.0	0.0	–	–	–	–
Center	0.59	0.86	–	–	–	–
South	0.61	1.33	–	–	–	–
1. 0–50 m	0.0	0.0	0.0	0.0	0.0	0.0
2. 51–100 m	−1.61	1.27	−1.75*	0.85	0.52	0.32
3. 101–200 m	−2.51	1.36	−1.87*	0.75	−0.36	0.29
4. 201–300 m	−2.61**	0.86	−2.02**	0.50	−0.15	0.31
5. 301–400 m	−4.57**	1.35	−3.65**	0.76	−1.67**	0.32
6. 401–500 m	0.0	0.0	0.0	0.0	0.0	0.0
Season × Latitude (2[a])	2.28**	0.45	–	–	–	–
Season × Latitude (4[a])	−1.44**	0.38	–	–	–	–
Season × Depth (6[a])	−2.88*	1.40	–	–	–	–
Season × Depth (9[a])	−4.10**	1.25	–	–	–	–
Season × Depth (9[a])	–	–	−1.73*	0.81	–	–
AIC[b]	1235		1271		1278	
Rank[c]	1st		2nd		3rd	

Values marked with * and ** were significantly different ($p = 0.05$ and $p = 0.01$, respectively) from the intercept

[a] Level of effect

[b] Akaike information criterion

[c] The models were ranked from best to worst according to their AIC values

includes season, latitude, depth, and bottom temperature. This means that if the distribution and biomass are associated with the basic seasonal oceanographic pattern of the area, local variations associated with coastal upwelling, water quality and origin according to depth, interannual anomalies, and large-scale climatic events (i.e., El Niño–Southern Oscillation (ENSO) and La Niña) should also be considered.

Events like ENSO are relevant in a temperate–tropical transition zone such as the southern California Current system, and can particularly affect species with a larval and juvenile pelagic phase and benthopelagic adults with limited locomotive power [31, 32]. Thus, the catch rates per season of the red crab along the Pacific coast of the Baja California Peninsula decrease linearly with an increase in superficial and bottom temperature. This was true bathymetrically, since the highest catches during El Niño, like in autumn 2006, were mostly restricted to deeper stations, and the opposite occurred during La Niña events, such as November 2005 and March 2006, when red crabs were distributed widely and with higher catch rates.

Insights into the potential effects of oceanographic conditions, like active upwelling sites, on the distribution of the red crab enhancing clorophphyll-a production have been shown by Gómez-Gutiérrez et al. [4] and Robinson et al. [8]. Thus, dense swarms of red crab may remain in areas close to the shore regardless of the season.

Robinson and Gómez [33] mentioned that sudden vertical migrations can occur at some locations, contrary to the pattern proposed by Aurioles-Gamboa [6, 10], who found poor evidence for such migrations. Although we did not perform studies of circadian cycles of the spatial distribution of the aggregations of the red crab, we did find differences and consistent patterns in the catch rate by day and night between sampling seasons.

Methodologically, a point deserving comment is the potential effect of the effective headrope width. The biomass estimates by Aurioles-Gamboa [10] and De Anda-Montanez et al. [30] were obtained assuming a wing spread of 50 % (0.5), as it was generally accepted [20]. Today, it is known that using a wing spread value of 0.5 may overestimate the biomass. Results from measurements of trawl geometry reported by GodØ and Engås [21] showed that there was a considerable depth dependence, and suggested that differences in bottom condition from one area to another may add variability to wing spread measurements.

The results of the analysis of the distribution and abundance (spatial, temporal, by transect, by depth, by day–night) and the results of the GLM analysis suggest that red crab is sensitive to environmental conditions along the west coast of the Baja California Peninsula. This sensitivity has implications for fishing efforts, particularly due to the restricted accessibility to the resource. Many species exhibit behavioral changes related to environmental conditions, including depth and climatic changes due to latitude. The results from this study suggest that adult red crabs move to deeper layers with extreme warming of the upper water layers, and that their distribution changes latitudinally, as occurs with larval and juvenile stages [34]. An adequate understanding of this behavior in response to the different environmental conditions according to developmental stage and size can play an important role in the exploitation and management of red crab in this region, as proposed by some authors [11, 12, 30].

Acknowledgments We appreciate the help of the crew and captain, Gabriel Rivera Velázquez, of the research vessel BIP XII (of the Northwest Biological Research Center) during the cruises. Isela Vázquez, Arturo Tecuapleta, Marisol Pérez, Alejandro Ramos, Ismael Mascareñas, Manuel Calderón and Alfredo Zayas provided invaluable assistance in the sampling work on-board. The authors thank Miguel Cordoba for help with an early draft of the paper and Gerardo Hernández García for graphic art. Ira Fogel of Centro de Investigaciones Biológicas del Noroeste, S.C. (CIBNOR) provided extensive editorial services. Funding was provided by Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA) and Consejo Nacional de Ciencia y Tecnología (CONACYT) (grant 2003-002-019) to JADM. Comments and suggestions by the anonymous reviewers and the editor helped to improve the manuscript.

References

1. Ahyong ST, Baba K, Macpherson E, Poore GCB (2010) A new classification of the Galatheoidea (Crustacea: Decapoda: Anomura). Zootaxa 2676:57–68
2. Hendrickx ME, Harvey AW (1999) Checklist of anomuran crabs (Crustacea: Decapoda) from the Eastern Tropical Pacific. Belgian J Zool 129:363–389
3. Aurioles-Gamboa D, Balart EF (1995) The red crab: biology, ecology and exploitation. Northwest Biological Research Center, La Paz, pp 221–233 (in Spanish)
4. Gómez-Gutiérrez J, Domínguez-Hernández E, Robinson CJ, Arenas V (2000) Hydroacoustical evidence of autumn inshore residence of the pelagic red crab *Pleuroncodes planipes* at Punta Eugenia, Baja California, Mexico. Mar Ecol Prog Ser 208:283–291
5. Aurioles-Gamboa D (1995) Bathymetric migration of the benthic red crab in the continental shelf of the Pacific of Baja California Sur. In: Aurioles-Gamboa D, Balart EF (eds) The red crab: biology, ecology and exploitation. Northwest Biological Research Center, La Paz, pp 79–92 **(in Spanish)**
6. Aurioles-Gamboa D, Pérez-Flores R (1997) Seasonal and bathymetric changes in feeding habits of the benthic red crab *Pleuroncodes planipes* (Decapoda, Anomura, Galatheidae) off the Pacific Coast of Baja California Sur, Mexico. Crustaceana 70:272–287
7. Cabrera-Chávez-Costa AA, Galván-Magaña F, Escobar-Sánchez O (2010) Food habits of the silky shark *Carcharhinus falciformis* (Müller and Henle, 1839) off the western coast of Baja California Sur, Mexico. J Appl Ichtyol 26:499–503
8. Robinson CJ, Anislado V, Lopez A (2004) The pelagic red crab *Pleuroncodes planipes* related to active upwelling sites in the California Current off the west coast of Baja California. Deep-Sea Res II 51:753–766
9. Ehrhardt NM, Ramírez E, Aguilera P, Jacquemin P, Lozano M, Romo I (1982) Evaluation of demersal resources accessible to bottom trawl nets in the continental shelf of the west coast of the Baja California Peninsula, Mexico, during 1979 and 1980. Natl Fish Inst Sci Ser 23:10–46 **(in Spanish)**
10. Aurioles-Gamboa D (1995) Distribution and abundance of benthic red crab *Pleuroncodes planipes* in the continental shelf of the west coast of the Baja California Peninsula. In: Aurioles-Gamboa D, Balart EF (eds) The red crab: biology, ecology and exploitation. Northwest Biological Research Center, La Paz, pp 59–78 **(in Spanish)**
11. Aurioles-Gamboa D, Balart EF, Castro-Aguirre JL (1995) Recommendations for the exploitation and use of the red crab. In: Aurioles-Gamboa D, Balart EF (eds) The red crab: biology, ecology and exploitation. Northwest Biological Research Center, La Paz, pp 221–233 **(in Spanish)**
12. Hernández-Llamas A, Balart EF, Ponce-Díaz G, Civera-Cerecedo R (2006) Feasibility of a new fishery based on the red crab *Pleuroncodes planipes* (Stimpson) in Baja California, Mexico: preliminary economic evaluation and risk assessment. Aquat Living Resour 19:173–179

13. Chávez-López S (1995) Sediments and geomorphology of the continental shelf west of Baja California between the parallels 24 & #xB0; and 29 & #xB0; LN. In: Aurioles-Gamboa D, Balart EF (eds) The red crab: biology, ecology and exploitation. Northwest Biological Research Center, La Paz, pp 11–34 **(in Spanish)**
14. Wyrtki K (1967) Circulation and water masses in the eastern equatorial Pacific Ocan. Int J Oceanol Limnol 1:117–147
15. Trasviña A, Lluch-Cota D, Filonov AE, Gallegos A (1999) Oceanography and El Niño. In: Magaña VO (ed) The impacts of El Niño in Mexico, pp 69–101 (in Spanish)
16. Bakun A (1996) Patterns in the ocean: Ocean processes and marine population dynamics. California Sea Gran/Northwest Biological Research Center, La Paz
17. Fiedler PC, Talley LD (2006) Hydrography of the eastern tropical Pacific: a review. Prog Oceanogr 69:143–180
18. Sparre P, Ursin E, Venema SC (1989) Introduction to tropical fish stock assessment. FAO, Rome
19. Pauly D (1980) A selection of simple methods for the assessment of tropical fish stocks. FAO Fish Circ 729:54
20. NEFMC (2011) Essential fish habitat (EFH) omnibus amendment, "The swept area seabed impact (SASI) model: A tool for analyzing the effects of fishing on essential fish habitat". Newburyport, Massachusetts
21. GodØ OR, Engås A (1989) Swept area variation with depth and its influence on abundance indices of groundfish from trawl surveys. J Northw Atl Fish Sci 9:133–139
22. Pezzuto PR, Alvarez-Perez JA, Wahrlich R (2008) The use of the swept area method for assessing the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) biomass and removal rates based on artisanal fishery-derived data in southern Brazil: using depletion models to reduce uncertainty. Lat Am J Aquat Res 36(2):245–257
23. Dickson W (1974) A review of the efficiency of bottom trawls. Institute of Fisheries Technology and Research, Bergen
24. Baith K, Lindsay R, Fu G, McClain CR (2001) SeaDAS, a data analysis system for ocean-color satellite sensors. EOS Trans AGU 82:202
25. Maunder MN, Punt AE (2004) Standardizing catch and effort data: a review of recent approaches. Fish Res 70:141–159. doi:10.1016/J.FISHRES.2004.08.002
26. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York
27. Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108
28. Hobbs NT, Hilborn R (2006) Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. Ecol Appl 16:5–19
29. Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag, New York
30. De Anda-Montañez JA, Perez-Enriquez R, Martínez-Aguilar S, Hernández-Martínez F, García-Rodríguez FJ, Amador-Buenrostro A (2013) Abundance and genetic diversity of the red crab *Pleuroncodes planipes* along the western coast of the Baja California Peninsula, Mexico. Fish Sci 79:21–32. doi:10.1007/s12562-012-0574-5
31. Gómez-Gutiérrez J, Sánchez-Ortíz OC (1997) Larval drift and population structure of *Pleuroncodes planipes* (Simpson) (Crustacea: Galatheidae) off the southwest coast off Baja California, México. Bull Mar Sci 61:305–326
32. Boyd CM (1967) Benthic and pelagic habitats of the red crabs Pleuroncodes planipes. Pacif Sci 21:394–403
33. Robinson CJ, Gómez GJ (1998) The red-crab bloom off the west coast of Baja California, México. J Plankton Res 20:2009–2016
34. Smith PE (1985) A case history of an anti-El Niño to El Niño transition on plankton and nekton distribution and abundances. In: Wooster WS, Fluharty DL (eds) El Niño north: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant, Seattle, pp 121–142