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Fisheries assessment of *Callinectes arcuatus* (Brachyura, Portunidae) in the Gulf of Nicoya, Costa Rica

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Abstract

The *Callinectes arcuatus* population of the Gulf of Nicoya and its current level of exploitation were investigated based on size frequency analysis of trap and trawl catches. Von Bertalanffy growth parameters ($K = 0.89$; $CW_\infty = 142$ mm for males) are in the range reported for other species of this family and suggest that the male size at first maturity ($CW_{mat} = 94.3$ mm) is reached in about a year. Total and natural mortality ($Z_{yr} = 2.49$; $M_{yr} = 1.32$) were derived from catch curve analysis and age at first maturity, respectively, and indicate that the stock is below full exploitation ($E = 0.47$). A yield per recruit analysis suggests that yield could be maximised, if E was increased to 0.7 under the precondition that recruitment was independent of stock size. Until this has been verified, the use of a precautionary exploitation rate ($E_{0.1}$) of 0.57 is advised allowing for a 20% increase in fishing effort (from 300 traps currently being fished to around 360 traps). A maximum effort of 1600 traps, as recommended by the Instituto Costarricense de Pesca y Acuicultura (INCOPESCA), is unlikely to be sustained by the population, since a decrease in the proportion of large males in the catches has already been observed over the past years under the current fishing regime. This resource is as yet only sold locally, but present catches of around 145 t seem to already cause market saturation. A greatly increased catch (at $E > 0.57$) would thus not only be detrimental to the stock but also to the market price of the resource. Future developments of the fishery should be based on a co-management approach and should involve the exploration of new market opportunities such as the “soft crab market”.

Keywords: *Callinectes acuatus*; Crab fishery; Costa Rica; Population dynamics

1. Introduction

In coastal waters of the Americas, 14 swimming crab species of the genus *Callinectes* are found, of which 11 are restricted to the tropics and subtropics. Although all of these species are suitable for human consumption, fisheries and research has as yet been focused mainly on the Atlantic blue crab *C. sapidus*. In the 1980s, the arched blue crab *Callinectes arcuatus*, which is found in estuaries and coastal lagoons along the Pacific coast off the Americas from Los Angeles, California, south to Peru (Garth and Stephenson, 1966), and which even extends its range to Northern Chile in times of El Niño (Arntz and Fahrbach, 1992), came into focus as a new fisheries resource (Paul, 1982; Castro and De Alteris, 1989). In the Gulf of Nicoya, Costa Rica, a large population of this carnivorous portunid crab (Dittel, 1993) is found (Epifanio and Dittel, 1982; Maurer et al., 1984). Most spawning of *C. arcuatus* occurs in the dry season from December to April (DeVries et al., 1983). At this time most of the ovigerous females migrate from the brackish waters of the upper gulf to high salinity waters in the lower gulf to release their larvae, which unlike the euryhaline adults (1–65‰), require relatively high salinities for their development. These spawning migrations are common in *Callinectes* spp. as also reported for *C. bellicosus* (Arreola-Lizárraga et al., 2003), *C. danae* (Branco and Masunari, 2000) and *C. sapidus* (Tankersley et al., 1998). The crabs re-enter the estuary after about 70 days of larval development and migrate towards the upper gulf as juveniles, where they grow to maturity in seven to nine months (Paul, 1982; Dittel and Epifanio, 1984).

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A small-scale trap-fishery on this species, run by approximately 10 fishermen, has been established in recent years. This fishery is managed by the "Instituto Costaricense de Pesca y Acuicultura" (INCOPESCA) allowing for a maximum fishing effort of 1600 traps, distributed over 40 licences. However, the scientific foundation for this number of traps remains obscure, since the current exploitation level is unknown due to the absence of landing statistics for the crabs and pertinent studies.

The objectives of the present investigation are therefore to study the population dynamics of this species in the upper Gulf of Nicoya, to assess its current state of exploitation and to estimate its potential for a sustainable harvest. Specifically, we determine the growth parameters of the von Bertalanffy growth equation (L_∞, K) using periodic fishery catches for length frequency analysis, and compute total mortality (Z) from the catch curve of samples pooled over the study period (6 months). Our natural mortality estimate (M) was based on the age at first maturity, which was determined by inspecting the maturity stage of crabs sampled over the study period. Own observations and interviews with the fishermen helped to obtain further information about the socioeconomic situation of the fishermen and their personal reflection on the state of the fishery.

2. Materials and methods

2.1. Study area and sampling sites

The Gulf of Nicoya (10°N, 85°W), located at the Pacific coast of Costa Rica, is one of the largest estuaries (1340 km^2) in Central America (Fig. 1) (Voorhis et al., 1983). Due to its shape and bathymetry it can be divided into a shallow northern part, which is no deeper than 20 m and reaches south to San Lucas Island, and a deeper southern part, which opens to the Pacific with depth of up to 200 m (Voorhis et al., 1983). While the upper gulf is fringed by mangroves and tidal flats, beaches and rocky coasts predominate at the lower gulf. The water temperature fluctuates only little over the year (26–30 °C) (Epifanio et al., 1983), average tidal range is 2.3 m (Voorhis et al., 1983). The estuary is strongly influenced by salinity variations, between dry season (typically December–April) and rainy season (typically May–November) (Voorhis et al., 1983). The Gulf of Nicoya is the most important fishing ground of Costa Rica (Vargas, 1995) and accounts for 28% (5070 t) of the countries annual landings. Even though the Gulf fishery is small scale, the high number of fishermen, given as 2300 by INCOPESCA for the year 2000, led to a serious overexploitation of its main fishery resources (Wolff et al., 1998). Most likely, the real number of fishermen is significantly higher than reported and is still increasing, because in Costa Rica, as in many other developing countries, the fisheries-sector serves as an "employer of last resort" (Charles, 2001).

2.2. Sampling

Crab data were obtained from bottom trawl and trap catches. In addition, further information about the fishery was gathered from interviews with crab fishers and through the first author's participation at the fishing operations. Trawling was conducted over muddy to sandy bottoms at 3–5 m water depth at two stations in the upper gulf (Fig. 1). These stations were also sampled during an earlier study of Dittel et al. (1985), allowing for comparison of results. A fibre glass boat with a 65 hp outboard engine was used to tow the semi-balloon shrimp trawl with a head rope of 7.5 m length and 1 cm mesh size. The area swept by the gear was calculated from the distance trawled (as measured with GPS), and an estimated net wingspread of 1/2 the length of the head rope (Sparre and Venema, 1998). Mean crab biomass per area was calculated as the overall biomass caught, divided by the area swept. To consider those individuals not being retained by the gear, a catchability coefficient of 0.5 was used. Trap catches were analyzed monthly from September 2003 to March 2004 at the sites 'Berrugate' and 'Costa Pajaros' onboard of two crab fishermen boats (Fig. 1). At both sites, traps were placed in distances of 40–50 m and set parallel to the edge of a mudflat, where ebb-tide water depth was about half a meter. The traps (60 cm × 60 cm × 20 cm) were baited with 200 g of fresh fish (mostly Clupeidae and Arreidae), which was sliced with a knife to increase its surface and odour. The soak time, or number of hours between two successive hauls, depended on the working habits of the fishermen, tides and weather conditions, but care was taken that each soak included at least one low tide.

Interviews with crab-fishermen were conducted informally during work-time onboard, so some of the answers given could be verified by direct observations in the field. Questions comprised the following topics:

- fishing practice (number of traps fished, number of soaks per day);
- state of the resource (stability of the catches, sex-composition of catches);
- market situation for crabs;
- general problems as perceived by the crab-fishermen.

2.3. Measurements and data analysis

2.3.1. Sex ratio, maturity stage and biometric relationships

C. arcuatus were sexed and females were checked for maturity by the shape of the abdomen (Fig. 2). A sub-sample of males ($n = 1254$) was tested for maturity by trying to move the abdomen with a probe, which is possible in mature males, but leads to the breakage of the abdomen in juveniles as reported by Van Engel (1990) for *C. sapidu*s and by Haefner (1990) for *C. ornatus*. The carapace width (CW) was measured as the distance between the tips of the longest lateral spines and for a sub-sample of crabs, with no

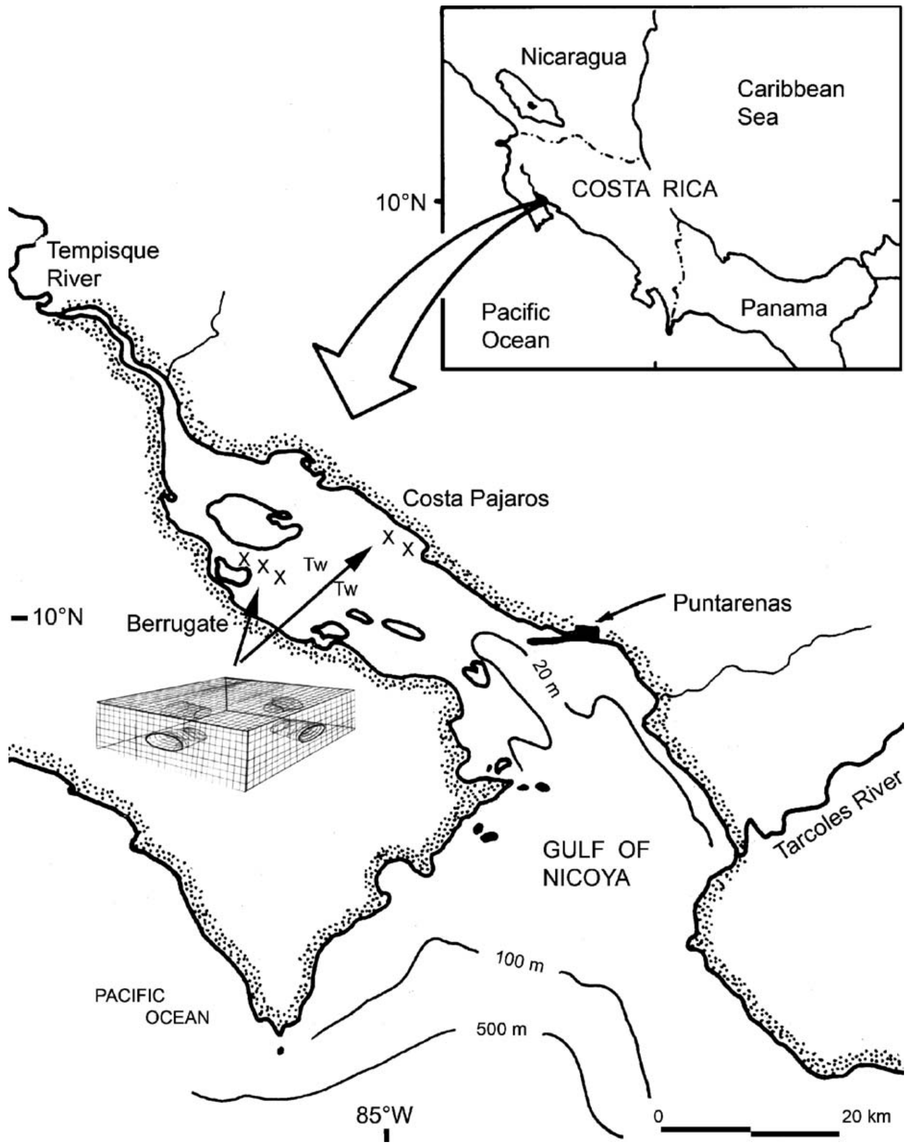

Fig. 1. Sites of trawls (Tw) and traps (*X*) used for captures of *C. arcuatus* in the Gulf of Nicoya at the North Pacific coast of Costa Rica.

pereiopods missing wet mass (*W*) was taken to the nearest *g*. The CW/*W* relationships for both sexes were described by the allometric relationship $Y = aX^b$, which was log-transformed for covariance analysis of the CW/*W* regression lines.

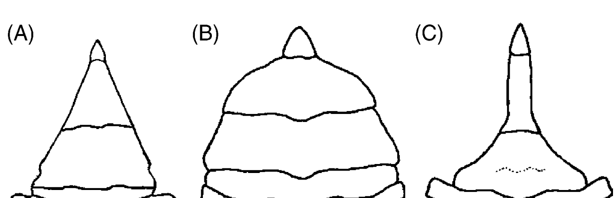

Fig. 2. Assessment of sex and maturity by the stage of the abdomen: (A) immature female; (B) mature female after terminal moult; (C) immature/mature male; males were considered immature when the abdomen was fixed to the carapace and mature when it was moveable with a probe.

2.3.2. Growth rates

The growth and mortality parameters were assessed for male *C. arcuatus* only, as only a very small proportion of females are found in trap-catches, and as growth is limited in females by their terminal moult to maturity, making growth studies based on size frequencies difficult.

The CW-data of the monthly trap catches of male *C. arcuatus* were combined for the two sampling sites and grouped into 5 mm intervals. The Electronic Length–Frequency Analysis ‘ELEFAN I’ routine of the FISAT II program package (Gayanilo et al., 1994) was used to identify the von Bertalanffy growth function (VBGF) that best fits these size-frequencies:

$$\mathrm{CW}_t = \mathrm{CW}_\infty(1 - \exp - K(t - t_0)) \quad (1)$$

where CW_∞ is the asymptotic size, CW_t the size at time *t*, *K* the growth coefficient and t_0 the theoretical age at length

0. A value of $t_0 = -0.18$ year was used, based on results of laboratory studies (Dittel and Epifanio, 1984). As a measure of goodness of fit of the "best" growth curve that is traced through the size frequencies, the programme gives a 'Rn' value (ranging from 0 to 1), by dividing the total number of peaks hit by the curve by the overall number of peaks available. The growth parameters K and CW_∞ were then used to calculate the growth performance index (ϕ') (Pauly and Munro, 1984):

$$\phi' = \log_{10} K - 2 \log_{10} CW_\infty \quad (2)$$

This index was found to be remarkably constant among species of the same genus and thus was employed to compare the results of this study with literature data on other *Callinectes* spp.

2.3.3. Size of first maturity (CW_{mat})

Crabs were grouped into 2 mm intervals, in each sex, and the proportion of mature to immature specimens was recorded for each interval. The Spearman–Karber formula (as cited in Udupa (1986)) allowed for the computation of CW_{mass}:

$$\ln CW_{mass} = X_k + \frac{X}{2} - X \sum P_i \quad (3)$$

where X is the average ln-size increment; X_k the ln-size at which all specimens are mature; P_i the proportion of mature specimens within their size-class. The corresponding 95% confidence limits (CL) were derived from the standard error of the estimated mean ln-size as follows:

$$CL = \text{antilog}\left(\ln CW_{mass} \pm 1.96\sqrt{x^2 \sum P_i \frac{(1 - P_i)}{(N_i - 1)}}\right) \quad (4)$$

where N_i is the total number of specimens within the size-class i and the other parameters as described above. Then the inverted VBGF, with the growth parameters K and CW_∞ derived from ELEFAN, was used to convert CW_{mass} into age of first maturity (t_{mat}) for male *C. arcuatus*:

$$t_{mat} = t_0 - \frac{1}{K} \ln\left(\frac{1 - CW_{mass}}{CW_\infty}\right) \quad (5)$$

2.3.4. Mortality and exploitation rates, yield per recruit estimates

Total mortality (Z) of male crabs was estimated by the 'length-converted catch-curve' method (Pauly, 1983) as contained in the FISAT II program (Sparre and Venema, 1998), separately, for traps and trawl catches. Since the catch curve of the trawl catches showed two discontinuous scatter point groups, which rather conformed to two than only one straight line, the curve was split into two separate catch curves (see Fig. 7). Natural mortality (M) was estimated with the empirical formula of Rikhter and Efanov (1976), which relates M to the age at first maturity (t_{mat}):

$$M = \left(\left(\frac{1.52}{t_{mat}}\right) 0.72\right) - 0.16. \quad (6)$$

Fisheries mortality (F) was calculated two-fold. Firstly, as

$$F = Z - M; \quad (7)$$

and secondly by using the stocks biomass (B), derived from the swept area method, and the annual fisheries yield (Y) as:

$$F = \frac{Y}{B}. \quad (8)$$

The annual fisheries yield (Y) of *C. arcuatus* was assessed as:

$$Y = \overline{T} \times \overline{S} \times \overline{W} \times \overline{CPUE} \times 365 \quad (9)$$

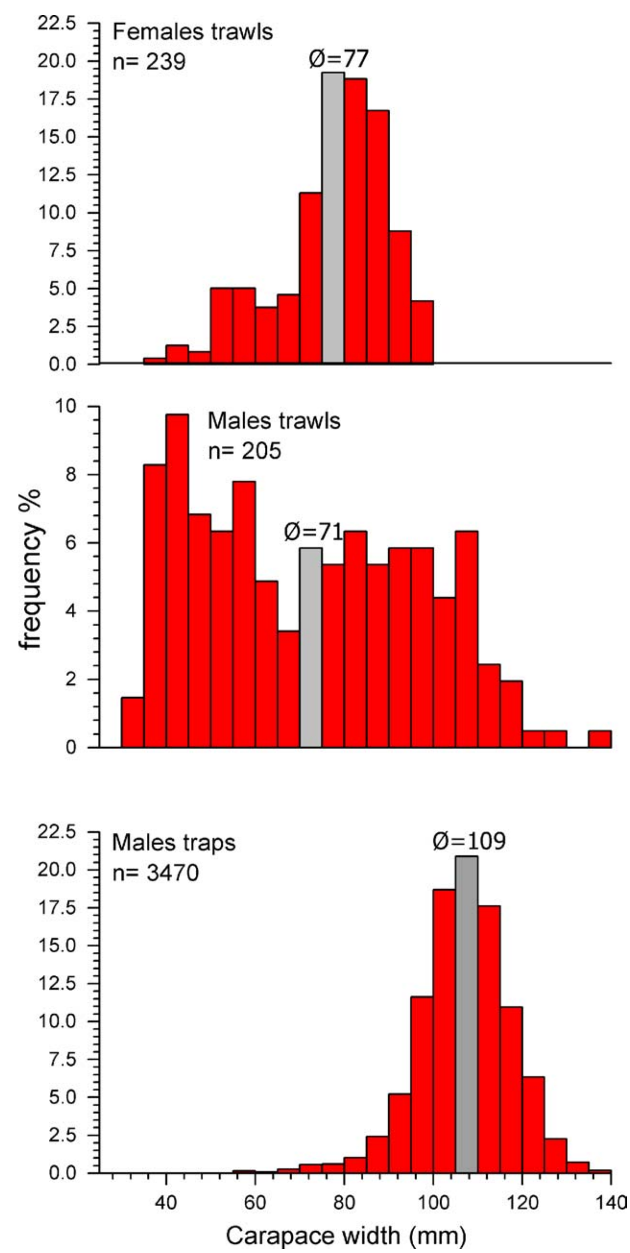

Fig. 3. Pooled size frequencies of male and female *C. arcuatus* caught in trawls and males caught in traps.

with T, being the mean number of traps fished; S, the mean number of soaks per trap/day; CPUE, the mean number of crabs caught per soak; and W, the mean weight of crabs caught in traps.

The exploitation rate (E) was calculated as:

$$E = \frac{F}{Z} \quad (10)$$

The Beverton and Holt (1957) ‘relative yield per recruit model’ (Y'/R), as contained in the FISAT program package, was applied to identify the exploitation rate (E), at which Y'/R is highest. In this model, computation of Y'/R is a function of the growth and mortality parameters of the stock (CW_∞, K, M, F, E) and of the size at which 50% of individuals within that size class are captured (CW_c), which was assessed with the ‘probability of capture’ routine of FISAT.

3. Results

3.1. Catch composition, biometric relationship

Within the trawl catches both sexes were equally distributed (chi^2-test, $p > 0.05$), while trap catches were highly dominated by mature male *C. arcuatus* (Figs. 3 and 4).

The CW–W relationship was significantly different between sexes ($F_{1403} = 10.73$, $p < 0.002$):

$$\text{Males}: \quad W = 0.00008\,\text{CW}^{2.92489}, \quad r^2 = 0.99 \quad (n = 310)$$

$$\text{Females}: \quad W = 0.00003\,\text{CW}^{3.1347}, \quad r^2 = 0.97 \quad (n = 103)$$

Maximum carapace widths (CW_{max}) and the corresponding wet-masses were 150 mm/162 g and 116 mm/79 g for males and females, respectively.

3.2. Growth and maturity

The growth parameters of male *C. arcuatus* were $K = 0.89$ and $CW_\infty = 142$ mm (‘$R_n{}' = 0.477$) yielding a growth performance value of $\phi' = 2.25$ (Fig. 5). Based on these estimates, male *C. arcuatus* reach the size of first maturity ($CW_{mat} = 94.63 \pm 2.06$ mm) in about a year (1.04 ± 0.40) (Table 1). Except for two individuals, all mature males had purple chelae and an olive green carapace, while those males, of which the abdomen was not movable with a probe and that showed uniformly green chelae and carapace, were considered immature. CW_{mass} in females was estimated as 68.72 ± 2.40 mm.

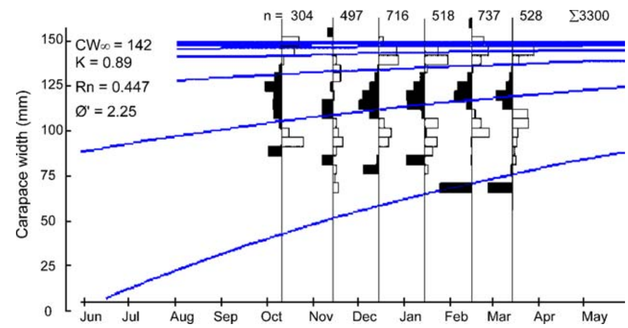

Fig. 5. Growth function of male *C. arcuatus* caught in traps derived with ELEFAN I of FISAT II yielding the growth coefficient K of 0.89 for a CW_∞ of 142 mm.

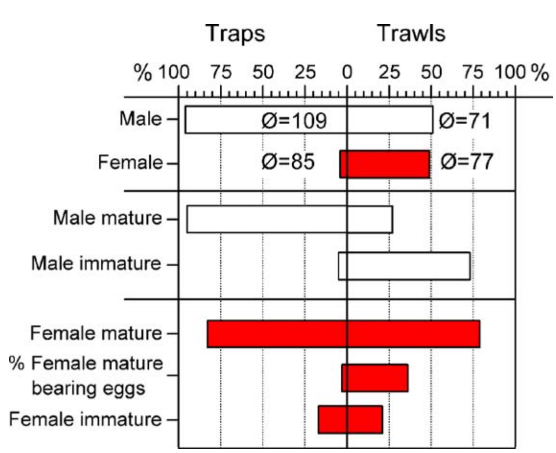

Fig. 4. Catch comparison from traps and trawls for sex and reproductive stage.

3.3. Mortality and exploitation rate

The instantaneous rate of total mortality (Z) estimated from the catch-curve of trap catches of male crabs was 2.49 ± 0.25 (Fig. 6). This catch-curve reveals that male crabs are fully recruited to the trap fishery with an age of approximately 1.4 years at a CW of 108 mm.

For the trawl-catches of male crabs the catch curve was divided into two distinct parts of different slope (Fig. 7). The first corresponds to pre-recruits (<1.4 years age), which are as yet not vulnerable to the traps, and the second to post-recruits (>1.4 years age). The computed Z-values for both

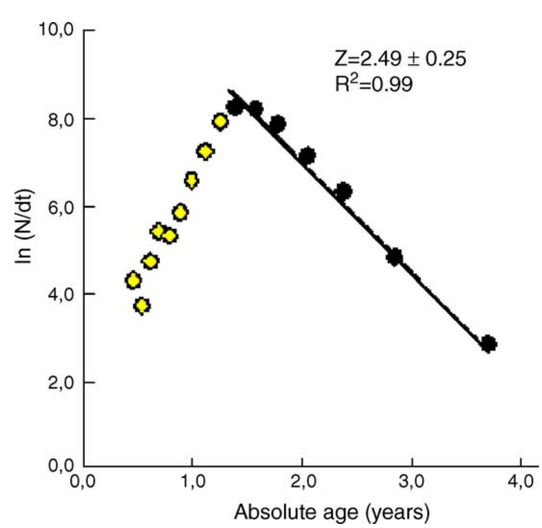

Fig. 6. Total mortality (Z_{yr}) assessed with the length converted catch curve of FISAT II for male crabs caught in traps.

Table 1
Carapace width at first maturity (CW_{mat}) for both sexes and its calculation by the method of (Udupa, 1986)

MI_i	$\ln MI_i$	N_i	M_i	P_i	$\ln MI_{i+1} - \ln M_i$	$1 - P_i$	$P_i\ (1 - P_i/N_i - 1)$
Males							
79	4.3694	7	1	0.13	0.0250	0.87	0.0189
81	4.3944	4	1	0.20	0.0244	0.8	0.0533
83	4.4188	13	5	0.28	0.0238	0.72	0.0168
85	4.4427	7	3	0.30	0.0233	0.7	0.0350
87	4.4659	9	3	0.33	0.0227	0.67	0.0276
89	4.4886	12	5	0.29	0.0222	0.71	0.0187
91	4.5109	8	3	0.38	0.0217	0.62	0.0337
93	4.5326	15	12	0.80	0.0213	0.2	0.0114
95	4.5539	32	8	0.25	0.0208	0.75	0.0060
97	4.5747	27	23	0.85	0.0204	0.15	0.0049
99	4.5951	42	40	0.95	0.0200	0.05	0.0012
101	4.6151	27	27	1.00	0.0196	0	0.0000
103	4.6347	47	46	0.98	0.0192	0.02	0.0004
105	4.6540	69	67	0.97	0.0188	0.03	0.0004
107	4.6728 (X_k)	49	49	1.00		0	0.0000
Sum		368	293	8.71		6.29	0.23
Average ln size increment (X)					0.0217		
Females							
62	4.1271	6	1	0.14	0.0317	0.86	0.0241
64	4.1589	5	1	0.20	0.0308	0.80	0.0400
66	4.1897	2	1	0.50	0.0299	0.50	0.2500
68	4.2195	9	2	0.22	0.0290	0.78	0.0215
70	4.2485	19	11	0.58	0.0282	0.42	0.0135
72	4.2767	11	7	0.64	0.0274	0.36	0.0230
74	4.3041	15	12	0.80	0.0267	0.20	0.0114
76	4.3307	26	22	0.85	0.0260	0.15	0.0051
78	4.3567	26	26	1.00	0.0253	0.00	0.0000
80	4.3820	21	20	0.95	0.0247	0.05	0.0024
82	4.4067 (X_k)	29	29	1.00		0	
Sum		169	132	6.88		4.12	0.3910
Average ln size increment (X)					0.0280		

MI_i = midsize of size-group i; N_i = total number in size group i; M_i number of mature specimen in size-group i; $P_i = M_i/N_i$.
Calculation procedure: $\ln CW_{mat} = X_k + X/2 - \sum P_i$, where X_k = size at which all specimen are mature; X = average ln size increment. 95% confidence intervals $CL = \text{anti log}\left|\ln CW_{mat} \pm 1.96\sqrt{x^2 \sum P_i((1-P)/(N_i-1))}\right|$. Results: CW_{mat} (mm): males = 94.63 (±2.06); females = 68.72 (±2.40).

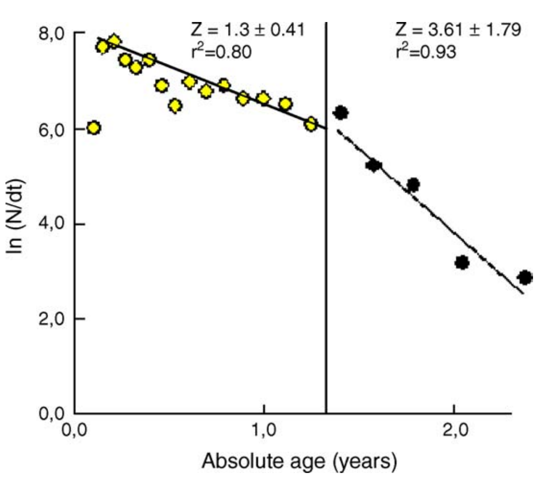

Fig. 7. Total mortality (Z_{yr}) assessed with the length converted catch curve of FISAT II for male crabs caught in trawls (<1.4 years pre-recruits; >1.4 years fully recruited to the fishery).

parts were 1.30 ± 0.41 and 3.61 ± 1.79, respectively. The first value is almost identical to our estimate of natural mortality (M = 1.32 ± 0.04) as derived from t_{mat} (Rikhter and Efanov, 1976). Based on the Z and M-values for male crabs subjected to the trap fishery, fisheries mortality (F) was calculated as 1.17 (±0.22). The second estimate of F from the annual yield (Y) and overall biomass (B) estimates was F = 145/131 = 1.1 (see also next paragraph). The resulting exploitation rate is thus E = 0.47.

3.4. Abundance, biomass and production

The mean crab biomass was estimated as 0.18 g/m^2. Extrapolated to the estimated habitat area of 730 km^2, (630 km^2 Inner Gulf + 100 km^2 eastern shore Outer Gulf) overall *C. arcuatus* biomass in the Gulf of Nicoya can roughly be estimated as 131.4 t. This biomass multiplied with the Z-value of the trap-catch-curve (2.49) thus yields an annual biomass production of 327.2 t.

3.5. State of the fishery: results from questionnaires and observations

The seven active crab fishers identified in the Gulf of Nicoya altogether employ about 300 traps. The number of traps per fishermen varies, however, as traps are frequently stolen, destroyed by other fishing-gear and corrode rapidly in the seawater. As a consequence, they are replaced almost monthly, which generates material costs of $2/trap and 2 h of work for a skilled trap-builder. According to the fishermen (and confirmed by own observations) traps are generally used twice per day, except if the weather is bad or if there is a shortage of bait or some other problem. Based on this information it was assumed that 2 soaks/day are done on 6 days/week, yielding an average daily mean of 1.7 soaks/trap. The overall mean catch was 11.8 crabs/soak, which—at a mean weight of 66 g per crab—amounts to an annual fishery extraction of 145 t. The off board price for *C. arcuatus* ranged between $0.3/kg and $1.0/kg, depending on landing site, season and market situation.

The effect of soak time and fishing site on CPUE was also explored, but results (not included here) did neither show significant differences between sites nor between soak times, suggesting that after about 12 h of soak time traps are generally saturated.

3.6. Relative yield per recruit analysis

Based on the relative yield per recruit analysis, yield would be maximised at an exploitation rate (E_{max}) of 0.7 (Fig. 8), far above the current exploitation rate of 0.47, which is also below the $E_{0.1}$-value of 0.57.

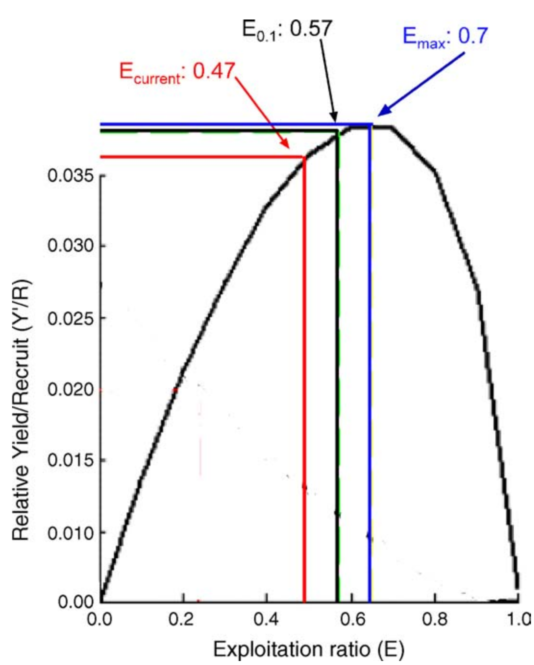

Fig. 8. Relative yield per recruit analysis showing the calculated exploitation ratio ($E_{current}$), $E_{0.1}$ as risk averse target fishing point and the maximum exploitation ratio (E_{max}).

4. Discussion

4.1. Growth, biometry and size at maturity

The difference in maximum weight (W_{max}) and maximum carapace width (CW_{max}) in both sexes is explained by the females' terminal moult to maturity, after which no further growth for females occurs.

The CW_{max} of 150 mm observed for one male *C. arcuatus,* is larger than sizes reported so far. Paul (1982) gives a CW_{max} value of 147.6 mm, Norse and Estevez (1977) mention 55 mm carapace length corresponding to about 138 mm CW, and Arreola-Lizárraga et al. (2003) give a CW_{max} value of 130 mm. As this CW_{max} was thought to be exceptional and not reflecting the growth potential of an average specimen, a smaller CW_{∞} of 142 mm (corresponding to the mean CW_{max} value of the 10 largest individuals) was used for the size frequency analysis. Based on the resulting *K*-value of 0.89, male *C. arcuatus* grow to their size of first maturity (CW_{mat}) in about one year, which is in close agreement with results of laboratory studies (Dittel et al., 1985) and field studies (Paul, 1982) and compares to the growth of *C. sapidus* and *C. rathbunae,* both reaching 110 mm CW in one year (Chazaro-Olvera and Peterson, 2004). The ϕ'-index determined in this study is also within the range of published data for other species within this genus (Table 2), although high individual variability in growth seems to be apparent for *Callinectes* (Ju et al., 2001).

4.2. Total mortality (Z)

Total mortality of male *C. arcuatus*, derived from the catch curve of the trap catches ($Z = 2.49 \pm 0.25$), was lower than the value found with the catch-curve of the trawl catches ($Z = 3.61 \pm 1.79$). This may be due large crabs being more able to avoid trawls through fast swimming reactions. It is thus possible that larger crabs have a reduced catchability in trawls, which would result in reduced relative numbers caught with increasing size, a steeper catch curve and a corresponding higher *Z*-value. Based on this consideration and the fact that the confidence interval was much larger for the *Z*-value derived from the trawl catches, the *Z*-value of the trap fishery ($Z = 2.49 \pm 0.25$) seems to be the more representative for the male crab population of the study area. As total mortality (*Z*) equals production (*P*) per biomass (*B*) ($Z = P/B$) (Allen, 1971), it can be readily seen that *C. arcuatus* has a high turnover rate, which is even comparable to values for penaeid shrimp stocks (Pauly et al., 1984). This is emphasized here, since shrimps used to be very abundant in this area, but are heavily overfished for more than two decades, possibly allowing other species including *C. arcuatus* to enter their food niche (Wolff et al., 1998).

Table 2
Comparison of growth performance index (ϕ') of *Callinectes* spp.

Species	Area	CW_{∞} (mm)	K_{yr}	ϕ'	Reference
C. arcuatus	Gulf of Nicoya/Costa Rica	142	0.89	2.25	Present study
C. bellicosus	Sonara Bay/Mexico	177	0.96	2.48	Montemayer and Cosio (2001)
C. sapidus	Chesapeake Bay/USA	240	1.09 (0.49–1.45)[a]	2.76 (2.45–2.92)[a]	Ju et al. (2001)

[a] Depending on study-site and study-conditions.

4.3. Natural and fisheries mortality, present and potential exploitation rate (M, F, E)

Our estimates for the rates of natural and fisheries mortality seem very reasonable since both were obtained by the use of two independent methods. In the case of M, the catch curve value for the pre-recruits (1.3 ± 0.41), for which the fisheries mortality can be assumed to be zero, is almost identical with the M-value obtained from our estimate based on t_{mat} (1.32). This value is near the $M = 1 -$ value estimated for *C. sapidus* in Delaware Bay (Helser and Khan, 2001).

The two F-estimates obtained in our study (1.17 from $F = Z - M$, 1.1 from $F = Y/B$) also agree quite well and reveal that present exploitation ($E = F/Z = 0.47$) is as yet relatively low.

Our results thus suggest that *C. arcuatus* is as yet underexploited in the Gulf of Nicoya. The relative Y/R analysis indicates that even a maximum exploitation rate (E_{max}) of 0.7 could be sustained by the population (Fig. 8) (if recruitment remains constant). A sensitivity analysis (results not shown here) demonstrated that this E_{max}-value is robust to moderate changes (stepwise up to 30%) in M and K, indicating that our fisheries-strategy seems well justified. An E_{max} of 0.7 is further supported by the fact that *C. sapidus* in Chesapeake Bay withstood such an exploitation rate (0.7 on average) throughout 40 years without evidence of a persistent stock decline (Rugolo et al., 1998). This long-term resistance to extremely high fishing pressure can partly be explained by the fact that cannibalism seems to be a main cause of natural mortality in juvenile *C. sapidus* (Moksnes et al., 1997; Hines, 2003). High juvenile mortality due to adult predation is not uncommon in crustaceans and was also described for the snow crab, *Chionoecetes opilio* (Lovrich and Sainte-Marie, 1997) and for *Cancer polyodon* in Chile, were up to 10% of the stock's production were found to be consumed through cannibalism (Cerda and Wolff, 1993). Thus, high fisheries mortality of adults seems to be somehow compensated by enhanced juvenile survival.

4.4. Population structure, abundance and biomass

The mean abundance found in this study is comparable to other studies of *Callinectes* spp. (Table 3), but somewhat lower than in the study of Dittel et al. (1985) on *C. arcuatus* in the Gulf of Nicoya two decades ago. These comparisons of swept area estimates are difficult, however, due to the uncertainty associated with the determination of a realistic catchability coefficient (q). The value of $q = 0.5$ used in the present study is substantiated by personal observations that only about 50% of the *C. arcuatus* specimens retained in a beam trawl were found in an otter trawl. While the *C. arcuatus* population is thought to be underexploited, effects on the crab stock can already be seen at the given fishing effort. In two studies in the Gulf of Nicoya (Dittel et al., 1985; Dittel, 1990, unpublished), which are thought to represent a virgin state of the population because virtually no fishery existed on *C. arcuatus* at this time, the stock was dominated by large specimens. While this still holds true for the female part of the stock (in 1990 mean CW: 80 mm; present study: 77 mm), the mean size of male crabs has decreased from 97 mm (1990) to 71 mm at present. This decrease might be due to the current trap fishery, whose catches are almost exclusively comprised by mature male crabs. This one-sided exploitation is not uncommon for *Callinectes* fisheries. In Mexico, at least 85% of the *C. bellicosus* specimens caught in traps are males (Montemayer and Cosio, 2001), and in a study in Ecuador on the fisheries potential of *C. arcuatus* (Castro and De Alteris, 1989) mostly mature males (mean CW: 103 mm) were caught. The authors of the latter study concluded that females were not present in the trapping area and are rather to be found in deeper waters. Equal proportions of sexes found in the nearby trawl catches in this study rather suggest the following explanation, how-

Table 3
Comparison of abundances of *Callinectes* spp. (all studies were conducted with otter trawls and a catchability coefficient (q) of 1 if not indicated otherwise)

Species	Area	Mean (N/m^2)	Reference
C. arcuatus	Gulf of Nicoya/Costa Rica	0.0050[a]	Present study
C. arcuatus	Gulf of Nicoya/Costa Rica	0.0044–0.0168	Dittel et al. (1985)
C. arcuatus	Pacific Coast/Mexico	0.0038	Arreola-Lizárraga et al. (2003)
C. bellicosus	Bahia Magdalena/Mexico	0.0024	Chavez et al. (2003)
C. sapidus	Chesapeake Bay/USA	0.006–0.015[b]	Sharov et al. (2003)

[a] $q = 0.5$.
[b] Beam trawl.

ever: large male crabs prevent smaller individuals, such as females and juveniles from entering traps, due to aggressive or even cannibalistic behaviour. The female-spawning stock is thus almost untouched by the trap fishery and recruitment over fishing seems unlikely. However, the one-sided exploitation of males still might have negative effects on the females' reproductive potential as females mate only once in their lifetime during their terminal moult. Thus, the fertilization of all egg-masses produced in a female's life depends on the amount of ejaculate, which is a function of male size and of the male's mating frequency, received at this time (Jivoff, 2003). A reduction in the number of large males increases the opportunity for small males to mate leading to females receiving reduced supply of seminal fluid (Kendall et al., 2001; Hines et al., 2003).

4.5. *Current state of the fishery and the market for C. arcuatus*

The trap fishery on *C. arcuatus* differs from the main types of fisheries in the Gulf of Nicoya such as gill net, long line and trawling in various aspects. If assistants are included, only around 15 persons participate in the crab trap fishery, which is less than 0.5% of the estuary's total number of fishers (Charles, 2001). Nevertheless, they contribute to a disproportional large amount of the Gulf's total catches (145 t) that as yet do not appear in the INCOPESCA fisheries statistics, but would make up around 3% of the Gulf's annual catch. Given the long-term overexploitation of the Gulf's main fishery resources, as described for penaeid shrimps by Tabash and Palacios (1996) and fin fish of the sciaenid family by Araya (1984), it is surprising that so few fishermen target *C. arcuatus*. The explanation seems to be the current market situation for *C. arcuatus* in Costa Rica. The species seems too small for the international markets (Oesterling, 1998) (not explicitly stated for *C. arcuatus*, but for other *Callinectes* spp. being larger). The mean size of 109 mm found in this study is even smaller than the minimum legal harvest size of 123–127 mm (depending on state) for *C. sapidus* in the USA (Guillory and Hein, 1998). However, access to international markets might be possible in the future, as stocks of other portunid crabs further decline and as the demand for marine resources increases worldwide. Local demand is slowly increasing for *C. arcuatus* in Costa Rica as reported by fishermen. Even though crabs are not highly priced (0.3–1.0 $/kg), the crab fishery has advantages to the fishermen over other types of fishery as catches are very stable over time (personal observation). Consequently, crab fishermen harvest every day, while other fishermen work irregularly—'on a satisfying basis'. However, the market price rapidly drops if fishing effort and catches increase, which has been observed when new crab-fishermen enter the market, or if one of the current crab fishers substantially increases the number of traps employed. Another problem is the theft and destruction of traps commonly encountered among crab fishers. This generates high effort and costs for trap replacement for all fishers involved.

4.6. *Recommendations for C. arcuatus fisheries management*

Higher exploitation rates could be sustained by the stock, but the E_{max} value is not recommended as target fishing level, because negative effects on recruitment cannot be excluded. Thus, a lower exploitation rate is advisory, substantiated by the already observed decrease in males' mean size in trawl catches, the risk of sperm depletion, and the uncertainty about the species' importance in the Gulf's trophic structure. Rather, the precautionary $E_{0.1}$-value is recommended as target fishing level. Exploitation should not go beyond this point unless further investigations have shown that recruitment is not negatively affected by a further reduced adult stock. Fishing at $E_{0.1}$ allows for an increase in fishing effort up to a mean annual number of 363 traps fished (assuming a linear relation of effort and catches). Based on our findings, the maximum effort of 1600 traps (40 fishers/40 traps), suggested by INCOPESCA, is very unlikely to be sustained by the stock. The current fishery management and enforcement of regulation measures is clearly ineffective, shown by the fact that only one of the fishermen has a fishing licence, a situation quite typical for the Gulf of Nicoya, where many fishermen have no licence, use illegal gear or catch within closed seasons (personal observation). Since traps are static gears, control and enforcement should be relatively easy. However, instead of a top-down approach, community-based management of the crab fishery seems more advisory, and requires that fishermen and other stakeholder involved in the chain from fishing to selling/exporting agree upon a certain fishing effort and allowable total catch for the gulf, which lies within the biological limits of the stock. Only by co-management, the problems of market over-saturation, and thus decreasing prices and the theft and destruction of traps, could be overcome. In order to enhance the current market situation, a diversification of the 'product' *C. arcuatus* could be attempted. Crab meat could be extracted for local consumers in small-scale processing plants. Additionally, pilot studies could explore the feasibility of *C. arcuatus* for soft crab production, which seems very promising for *C. arcuatus*, because here the overall crab's size is not as important as for meat extraction. In the USA soft crabs are products of a very high price. 'Soft-crabs' would not only be of interest for export, but also for direct sale to tourist resorts and restaurants.

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