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Abstract—This study, which included examination of the distribution and life history and a stock assessment of the flathead lobster (*Thenus orientalis*), is the first of its kind in the waters of Saudi Arabia in the Arabian Gulf, also known as the Persian Gulf. The flathead lobster is widely distributed in this region, although it is more abundant in the central and northern Arabian Gulf. Carapace lengths at 50% and 95% maturity are 59 and 65 mm for females and 58 and 71 mm for males. The fecundity of 4 berried females ranged from 26,000 to 76,000 eggs per spawning, and the fertilization rate exceeded 97%. Length–frequency data were consistent with just 2 cohorts, indicating that this species has a short life span and high growth coefficient (K=0.846 year^{-1}). Large fishing boats (called *dhows*) accounted for more than 98% of the total landings. Estimates of natural mortality rates from use of generalized depletion models have high statistical precision and a magnitude compatible with short life history. In addition, abundance levels estimated with the depletion model are sufficient to support a sustainable small-scale fishery either as bycatch of shrimp trawlers or as a resource targeted with specialized gear. A targeted fishery for flathead lobster could be set during the off months of the shrimp trawl fishery (February–July), reducing interference with the reproduction cycle.

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Ecology, life history, and fisheries potential of the flathead lobster (*Thenus orientalis*) in the Arabian Gulf

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The flathead lobster (*Thenus orientalis*) is a highly valued commercial lobster species, with increasing importance in the world (Spanier and Lavalli, 2006). It has a wide distribution in the Arabian Gulf, also referred to as the Persian Gulf, including in waters of Saudi Arabia in the northwestern part of the gulf, where it has been traditionally captured as bycatch by local, small-scale fishing operations during the season (August–January) of the trawl fishery for the green tiger prawn (*Penaeus semisulcatus*). Landing this lobster species was forbidden by managers because of a lack of scientific knowledge for determination of sustainable catch rates and development of regulations oriented toward sustainability. This measure, implemented in 2008 and still enforced, was taken as a precautionary action pending studies of the life history and biological reference points of and a stock assessment for this species.

The distribution of species of *Thenus* and other slipper lobsters (Scyllaridae) depends on several environmental factors (Spanier and Lavalli, 1998; Wardiatno et al., 2016), as observed in palinurids (Herrnkind et al., 1997; Butler et al., 2006). The nature of sediments and the depth of water are the 2 major factors that influence the abundance of slipper lobsters (Jones, 2007; Lavalli et al., 2019). The flathead lobster prefers soft, sandy sediment areas with medium-to-coarse particle size. Tropical slipper lobsters, including species of *Thenus*, may live at densities of 1–10 individuals/ha in areas that reflect the habitat preferences of the species (Jones, 2007). There is no evidence of aggregation due to reproductive stimuli in species of *Thenus*, but the presence of other species, such as prey, predators, and competitors, may influence the density of these species in a particular habitat (Jones, 2007).

Species of *Thenus* have greater mobility because of the highly developed swimming ability that sets this genus apart from other slipper lobsters. They are capable of moving long distances by swimming, and their life history can be described as nomadic and not directed or migratory. Jones (1988) and Courtney et al. (2001) studied the mobility of species of *Thenus* by using tagging. Data from recovery of tagged individuals indicate that individuals of *Thenus* species can move as far as 24 km in 183 d (Courtney et al., 2001). They are more active during late evening and early morning, the foraging time of the lobster (Jones, 2007).

Most of the species of *Thenus* mature in 1 year (at about 45 mm in carapace length for most species) with a fecundity of up to 67,000 eggs (Jones, 1988; Radhakrishnan et al., 2007). Like other tropical species, *Thenus* species breed almost throughout the year, with at least 2 spawning peaks, the timing of which might vary in different regions (Kagwade and Kabli, 1996; Jones, 2007; Radhakrishnan et al., 2007). Flathead lobsters carry eggs in their pleopods (swimming legs) for about 25 d before releasing phyllosoma larvae that have a larval life of 30–45 d involving 4 stages, the last one of which is the nisto stage in which larvae molt for settlement. Water currents and eddies play a role in the distribution and settlement of *Thenus* larvae because they are mostly retained within the area of release as a result of their shorter life in comparison to that of palinurid larvae, which are carried long distances offshore.

Flathead lobsters have been caught in the Saudi waters of the Arabian Gulf since 1980, yet to date little scientific information is available about the biology and population dynamics of this species and the fishery that targets it. In view of this knowledge gap, this study was carried out with the following aims: 1) to determine the spatial distribution and abundance of flathead lobsters, 2) to examine the life history of this species, and 3) to assess the stock of flathead lobsters in the waters of Saudi Arabia in the Arabian Gulf.

Material and methods

Study area

The Arabian Gulf is a semi-enclosed, shallow sea located between the Arabian Peninsula and Iran. It is bounded on the south by Oman and the United Arab Emirates, on the west by Qatar, Bahrain, and Saudi Arabia, on the north by Kuwait and Iraq, and on the east by Iran (Fig. 1). It is about 990 km long with a width of 200–370 km and an average depth of 36 m. The waters of Saudi Arabia in the Arabian Gulf host a great variety of habitats and a rich biodiversity, including nursery habitats (Rabaoui et al., 2017, 2019; Lin et al., 2021a; Rabaoui et al., 2021a), coral reefs (Lin et al., 2021b, 2021c), spawning habitats (Lin et al., 2021a), and rich pelagic habitats enhanced by manmade structures (Rabaoui et al., 2015a) with abundant mammals (Rabaoui et al., 2021b).

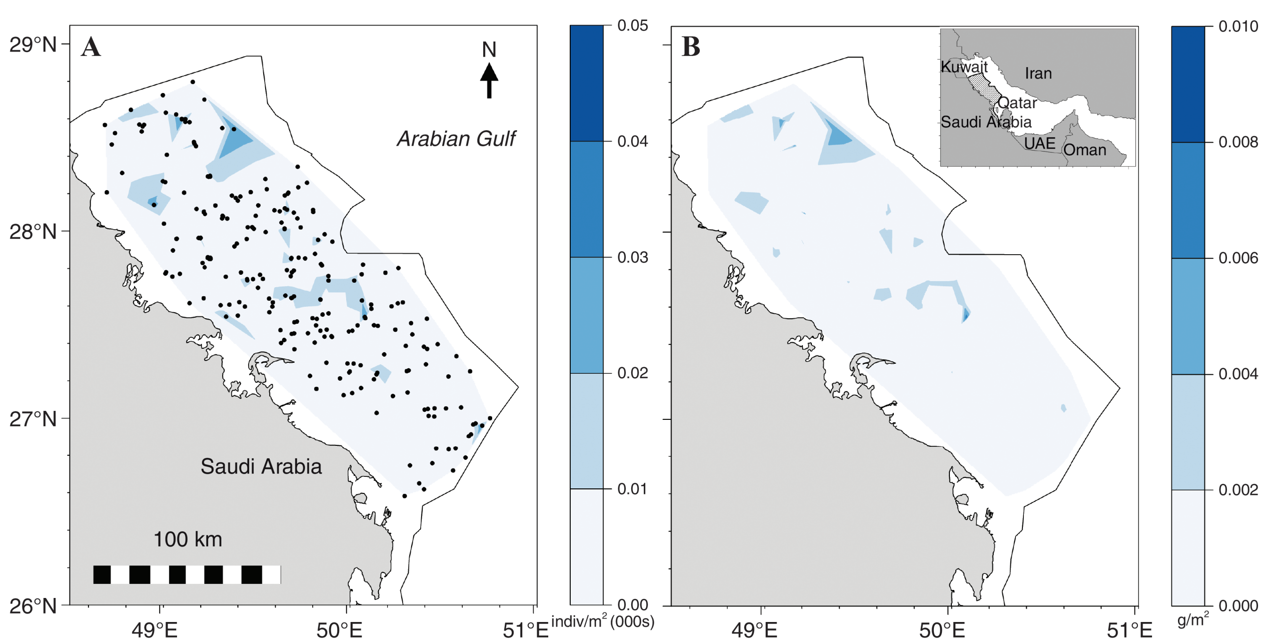

Figure 1

A map showing (**A**) abundance (in thousands of individuals per 100 square meters) and (**B**) biomass (in grams per 100 square meters) of flathead lobsters (*Thenus orientalis*) sampled in the waters of Saudi Arabia in the Arabian Gulf during trawl surveys conducted between 2013 and 2016. Dots indicate stations where surveys were conducted. In the inset, the outlined area in the Arabian Gulf indicates the study area. UAE=United Arab Emirates.

Spatial distribution and abundance

The spatial distribution and abundance of flathead lobsters were determined by using the data collected during 5 trawl surveys conducted in the waters of Saudi Arabia in the Arabian Gulf between 2013 and 2016. Three trawl surveys were conducted on the commercial outrigger *Afrah* (which had a trawl net with a knot-to-knot mesh size of 15 mm) in March and July 2013 and in May–November 2016. Two trawl surveys were completed on the Kuwaiti RV *Bahith II* (which had a trawl net with a knot-to-knot mesh size of 36 mm) in June–July 2014 and in May–June 2015. In total, trawl surveys were conducted at 189 stations (88 stations in 2013, 31 stations in 2014, 40 stations in 2015, and 30 stations in 2016).

A systematic grid design was applied for the trawling surveys. In 2013, equally spaced stations were set along predetermined transects perpendicular to the coast, covering all territorial waters of Saudi Arabia in the Arabian Gulf. In 2014 and 2015, we visited stations set as close as possible to ones we previously surveyed, with a few additions or reductions in station numbers because of constraints, such as poor weather and validity of fishing permits. In 2016, the team surveyed the locations where flathead lobsters occurred often in previous surveys, to increase sample size for biological analysis and habitat characterization. We assumed that there were no differences in size selectivity between the gears used by the 2 vessels employed for the surveys. This assumption is justified because the mesh size of both trawlers is selective for fish under 40 mm in total length, meaning carapace length plus the tail (Lin et al., 2021a), and the smallest total length of all flathead lobsters caught during surveys was 52 mm. Therefore, given this assumption of equal selectivity, we pooled the lobster catch and biological data from the surveys conducted on the 2 vessels to increase the sample size.

Standard operating procedures were applied in all surveys. In other words, the following actions were taken: 1) at each station, we recorded environmental variables, such as temperature, salinity, and depth before trawling; 2) the duration of each trawl was fixed at approximately 30 min; 3) once the catch was on deck, the bottom type (sand, mud, or rock) was determined by examining debris; 4) the entire catch was photographed and weighed; and 5) 5–100% of the catch, including the debris, was randomly sampled for further analysis in the laboratory.

The catch per unit of effort, expressed as kilograms per hour of trawling, was determined for each survey and included only the stations where at least one flathead lobster was encountered. The abundance and biomass of lobsters for the trawled area, expressed as the number of individuals per 100 square meters of trawling and grams per 100 square meters of trawling, were calculated for each survey. The spatial distributions of abundance and biomass of flathead lobsters were plotted for the cruises from 2013 through 2016 by using the packages rworldmap (vers. 1.3-6; South, 2011) and rworldxtra (vers. 1.01; South, 2012) in R, vers. 4.0.2 (R Core Team, 2020). The spatial heatmaps were plotted by using the package akima (vers. 0.6-2.1; Akima and Gebhardt, 2020) in R.

Reproductive biology and growth

A total of 302 flathead lobsters, collected during trawl surveys and from auction centers, were used for detailed morphometric studies. All collected lobsters were transported to the laboratory, where they were measured (for total length) and weighed (for total weight) and their sex was determined. The reproductive biology of the flathead lobster was studied by recording the morphological and morphometric changes that occur at maturity, the gonadosomatic index (GSI), and the maturity stages of gonads. The maturity stages of female gonads were determined following the classification proposed by Kennelly et al. (1997) and Haddy et al. (2005) (see Suppl. Table 1). Similarly, 5 maturity stages of male gonads were determined by dissecting the lobster as well as by using histology. The color and condition of the fresh gonads were noted, and their wet weight was recorded to the nearest 0.001 g after wiping water from the gonads with blotting paper. Fecundity was examined by counting the eggs in the pleopods of berried females. We estimated fecundity by taking the total weight of eggs carried by the female after stripping it, counting the eggs in a minimum of 3 samples weighing from 0.1 g to 1.0 g, and extrapolating the numbers to get the total count in the whole egg mass. The fertilization rate of eggs was estimated by counting the number of unfertilized eggs in the egg mass. Unfertilized eggs are cream or pink in color, and fertilized eggs are dark yellow or orange (Kizhakudan[1]).

The GSI was calculated for each mature female as the percentage of body weight accounted for by ovary weight. The maturity status of the lobster by carapace length was estimated by using a logistic model:

$$S(L) = \frac{1}{1 + e^{g+hL}}, \tag{1}$$

where $S(L)$ = the proportion of mature individuals at carapace length L in millimeters;
g = the intercept parameter; and
h = the slope parameter.

The model was fit to data of counts of immature and mature individuals at length categories with logistic regression. The carapace lengths at which 50% (L_{50}) and 95% (L_{95}) of individuals were mature were calculated by using the following equations (Roa et al., 1999):

$$L_{50} = \frac{-\hat{g}}{\hat{h}} \text{ and} \tag{2}$$

$$L_{95} = \frac{\ln\left(\frac{1}{19}\right) - \hat{g}}{\hat{h}}. \tag{3}$$

[1] Kizhakudan, J. K. 2016. Hatchery technology and seed production of lobsters. *In* Course manual: winter school on technological advances in mariculture for production enhancement and sustainability (I. Joseph and B. Ignatius, eds.), p. 106–113. Cent. Mar. Fish. Res. Inst., Kochi, India. [Available from website.]

The standard errors of L_{50} and L_{95} were calculated with the delta method by using the package msm (vers. 1.6.9; Jackson, 2011) in R, and a Wald-type confidence interval was also calculated. The differences between sexes in the maturity model parameters were examined by applying information theory. The Akaike information criterion (AIC) was calculated to select the best model:

$$AIC = 2p - 2\ln(Lik), \tag{4}$$

where p = the number of parameters; and
Lik = the maximum likelihood of the model.

Candidate models were fitted with data for the sexes pooled or separated, and then the AIC values for the models were compared. The model with the lowest AIC value was selected as the best working model.

Histological techniques were used to record different phases during the development of gonads. The gonads from fresh specimens were removed, weighed, and fixed in Bouin solution for 2 h and preserved thereafter in absolute ethanol. By using an ATP1 automated tissue processor, TBS[2] (VWR International, Radnor, PA), small portions (anterior, posterior, middle, oviduct, and vas deferens) of these gonads were dehydrated through the use of a series of graded ethanol solutions finalized with a clearing step in xylene. The gonad tissues were thereafter embedded in paraffin wax, sectioned at 5–6 µm with an automated TBS SHUR/Cut 4500 microtome (Cole-Parmer Instrument Co., Vernon Hills, IL), and stained with eosin and hematoxylin (Bancroft and Stevens, 1990) with a TBS SHURStain 3030 automated slide stainer (General Data Co. Inc., Cincinnati, OH). The stained sections were examined under a binocular microscope (Olympus BX51, Olympus Corp., Tokyo, Japan). The sections were photographed by using an Olympus DP72 microscope camera (Olympus Corp.). Identification and description of the different maturity stages in the ovary and testis were done on the basis of the works of Haddy et al. (2005) and Kizhakudan (2014).

Because aging data are not directly available for the flathead lobster, statistical techniques were used to determine the number of cohorts sampled over 4 years that underlie the length–frequency data. The method involves 1) a statistical model for estimating the number of cohorts underlying the length–frequency data on the basis of the multinomial distribution, 2) biological criteria to resolve the aging of the cohorts, and 3) a hierarchical statistical model based on the multivariate normal distribution to fit a growth model to the mean length and the assigned age of each cohort. Details of the mathematical and statistical models and the software used to fit the models to data have been described in Roa-Ureta (2010).

Statistical analysis of the age structure was conducted with aggregated data, without distinction by year or sex, owing to the small sample sizes (n) for all years (2013: n=21; 2014: n=15; 2015: n=31; 2016: n=235; total: n=302).

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

In selecting a model for estimation of the number of cohorts underlying the length–frequency data, we tested models that included 2, 3, 4, 5, 6, 7, and 8 cohorts. This wide range of hypotheses for the number of cohorts was tested because nothing was known about the age structure of the stock in waters of Saudi Arabia in the Arabian Gulf. A low number of cohorts would indicate a short-lived stock, and a high number of cohorts would point to a long-lived stock. Among the 7 models fit to the length–frequency data, the best model was selected by using the AIC. Age assignment for the resulting number of cohorts was based on previous biological knowledge about the number of spawning events, the duration of life at the larval stage, and size at settlement.

Once the number of cohorts composing the length–frequency data and associated parameters were estimated and once age assignment was completed, we fitted the following 2-parameter version of the von Bertalanffy growth function to the mean length and age data:

$$L(a) = L_\infty\left(1 - \left(\frac{L_0}{L_\infty}\right)e^{-\mathrm{Ka}}\right), \tag{5}$$

where $L(a)$ = carapace length at age a;
L_∞ = asymptotic carapace length;
L_0 = carapace length at birth; and
K = the growth coefficient.

The model is used to estimate only 2 parameters, L_∞ and K, because L_0 is assumed to be known from previous biological information and is equal to 8 mm. Both the multinomial model for length–frequency data and the multivariate normal model for the growth data were fitted by using in AD Studio, vers. 1.0, the AD Model Builder (vers. 12.0; Fournier et al., 2012) code in the supplementary material accompanying Roa-Ureta (2010).

This method has been used in many previous studies and has been useful for studying the growth of other crustaceans, such as the green tiger prawn (Rabaoui et al., 2017) and a blue swimming crab, *Portunus segnis* (Rabaoui et al., 2015b, 2021b).

Old bycatch fishery and stock assessment

The official Saudi government fisheries statistics for landings and fishing effort (MEWA[3]) that were collected for the 2 fleets of small boats (called *tarad*) and large boats (called *dhow*), in Saudi Arabia from 1995 through 2008, include landings of flathead lobster as valuable bycatch of the trawl fishery for the green tiger prawn, the main Saudi fishery in the Arabian Gulf, both by volume and value. The number of boats operating in this fishery is close to 2000 (Roa-Ureta, 2015). Almost half of them are traditional Arabic dhows with lengths ranging from 15 to 20 m, and the other half are smaller tarad boats with lengths of less

[3] MEWA (Ministry of Environment, Water & Agriculture). 1995–2008. Official fisheries statistics of Saudi Arabia. [Available from Fish. Dep., Minist. Environ. Water Agric., Riyadh 11195, Saudi Arabia.]

than 10 m (Roa-Ureta, 2015). Dhows may remain at sea for nearly a week, and tarads conduct 1-d operations. Both fleets are motorized. The dhow fleet is more important throughout the landings time series. It accounted for an average of 93% of the monthly catch of flathead lobster along the entire time series.

We carried out a stock assessment of the flathead lobster with the method described in Roa-Ureta (2015), developed to assess data-poor fisheries. We fitted 2-fleet multiyear generalized depletion models to 14 years of monthly landings and fishing effort spanning the 168-month period from January 1995 through December 2008. Subsequent landings data were not available because landings of the flathead lobster were banned. The particular version of the model that was used is as follows:

$$C_t = \sum_l C_{t,l} = \sum_l k_l E_{t,l}^{\alpha_l} \left(N_0 e^{-Mt} - e^{\frac{-M}{2}} \left[\sum_{i=1}^{i=t-1} C_{i,l} e^{-M(t-i-1)} \right] + \sum_{j=1}^{j=P} R_{j,l} e^{-M(t-\tau_{j,l})} \right)^{\beta_l} e^{\frac{-M}{2}}, \quad (6)$$

where C_t = the true catch in numbers in month t;
l = a value of 1 or 2, and indexes the fleet;
E = the observed effort in boat-days of fishing;
N_0 = the initial abundance;
M = the natural mortality rate;
k = the scaling;
α = the effort response;
β = the abundance response;
i = the index of the time step (i=1–168);
R_j = the annual recruitment with index j (j=1,...,14 for a total of 14 annual recruitments); and
τ_j = the timing of annual recruitment with index j (in seasonal fisheries, the timing is always the first month of the season).

In these models, parameter k is similar to catchability except that it is not affected by changes because of its relationship with abundance, and the effort response α and abundance response β accommodate nonlinear dynamics, namely the potential of effort to be saturated (α<1), effort synergy (α>1), hyper-stability (β<1), and hyper-depletion (β>1).

We tried model fits with 4 alternative likelihood functions by using the data from each fleet (4 functions for each fleet data set) and 2 numerical methods to minimize the negative log-likelihood, leading to 32 model versions (4×4×2). The likelihood functions were exact normal, exact lognormal, and adjusted profile (i.e., with the dispersion parameter eliminated) approximations of the normal and lognormal. Precise formulas of these likelihoods are detailed in table 2 in Roa-Ureta (2019). Numerical procedures were the spectral projected gradient and the conjugate gradient methods. These numerical techniques have worked well with generalized depletion models because they can handle moderately large optimization problems. With 14 years of data, the 2-fleet multiyear generalized depletion models include 36 (adjusted profile approximations) or 38 (exact likelihoods) free parameters that can be estimated. The models were fit by using the package CatDyn (vers. 1.1-1; Roa-Ureta, 2019) in R.

Results

Spatial distribution of abundance and biomass

The percentage of stations where flathead lobsters were caught varied between 16% and 25% of the total number of stations sampled, during 2013–2015. The frequency of occurrence increased to 60% during the 2016 trawl survey, mainly because of the increase in the fishing effort over the areas where flathead lobsters were caught during the previous surveys. The catch per unit of effort at the stations where flathead lobsters were caught ranged from 0.434 kg/h in 2013 to 0.593 kg/h in 2014. The overall catch per unit of effort of all stations was the lowest (0.067 kg/h) in 2013 and the highest (0.339 kg/h) in 2016 (Table 1).

Results from the trawl surveys conducted from 2013 through 2016 indicate that the flathead lobsters were patchily distributed in the Arabian Gulf, from the northern border between Saudi Arabia and Kuwait to the southern border with Bahrain. The abundance and biomass of the lobsters were both higher in the central and northern parts of the western Arabian Gulf (Fig. 1). The abundance at the stations where flathead lobsters were caught ranged from 0.5×10^{-3} to 4.8×10^{-3} individuals/100 m^2 (Fig. 1A), and the biomass ranged from 0.001 to 0.800 g/100 m^2 (Fig. 1B).

Reproductive biology

The sex ratio of flathead lobsters captured in waters of Saudi Arabia was 1:1, with mature lobsters being dominant in the samples collected during November 2016. Few berried and many spent flathead lobsters were also present in the samples. Few immature flathead lobsters were collected, and most of them were above 40 mm in carapace length and were in the preadult or adult stage. Maturity data support a sex-separate maturity model for the flathead lobster with a high AIC difference of 6.01. Therefore, the maturity curve was fitted to data for females and males separately (Fig. 2). The carapace lengths at 50% and 95% maturity were 59.5 mm (standard error [SE] 0.6) and 64.6 mm (SE 1.5) for females and 57.8 mm (SE 1.1) and 71.0 mm (SE 3.0) for males. Supplementary Figures 1 and 2 show the maturity stages of female flathead lobsters, as well as the variations in their percentages. Four berried flathead lobsters (Suppl. Fig. 3) were collected during the study period, and the eggs they carried were in the advanced developmental stage (Suppl. Fig. 4). The weight of an egg mass varied from 18.74 to 60.62 g, and the weight of a single egg ranged from 796 to 849 mg. The fecundity of the 4 berried lobsters ranged from

Table 1

Catch per unit of effort (CPUE), mean abundance, carapace length, and weight of flathead lobsters (*Thenus orientalis*) collected during trawl surveys conducted between 2013 and 2016 in waters of Saudi Arabia in the Arabian Gulf. A range of carapace lengths is not given for 2015 because only 1 individual was measured. Standard deviations (SDs) are given in parentheses.

Year	2013	2014	2015	2016
Total no. of stations	88	31	40	30
No. of stations with lobsters	14	8	11	18
Mean lobster abundance (individuals/station)	0.278 (0.687)	0.454 (0.904)	0.026 (0.460)	0.590 (0.946)
CPUE (kg/h) of stations with lobsters	0.434	0.593	0.426	0.567
CPUE (kg/h) of all stations	0.067	0.153	0.117	0.339
Mean carapace length (mm)	90 (22)	78 (19)	95	64 (9)
Carapace length (mm) range	27–134	50–107	–	22–86
Mean total weight (g)	149 (78)	105 (74)	206 (33)	101 (180)
Total weight (g) range	3–329	24–250	46–243	97–318

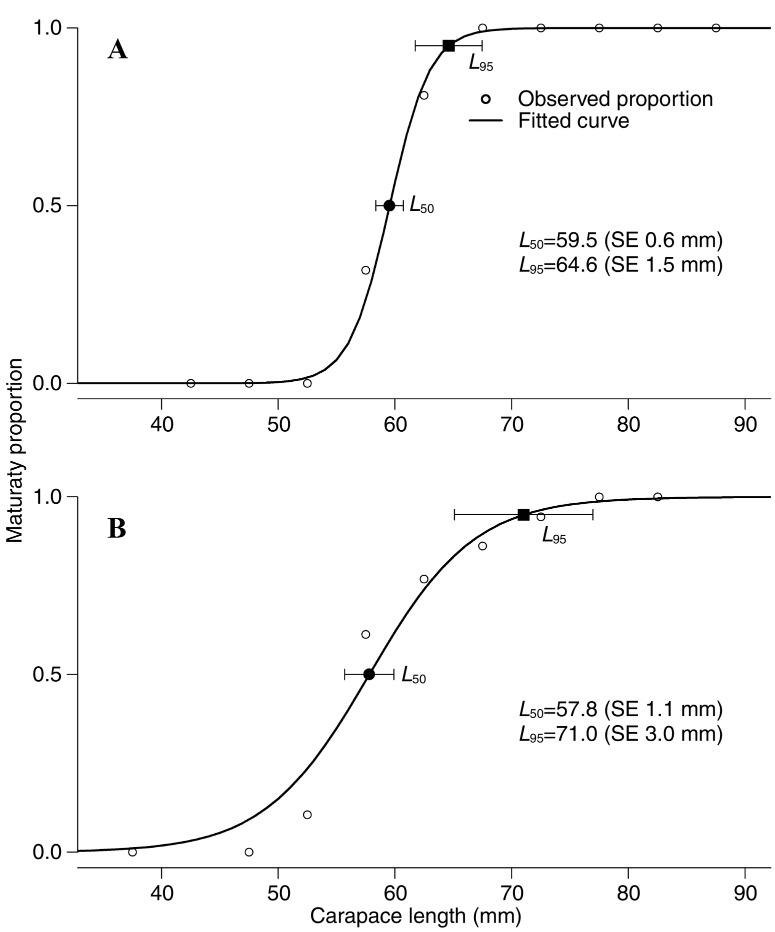

Figure 2

Maturity curves for (**A**) female and (**B**) male flathead lobsters (*Thenus orientalis*) collected between 2013 and 2016 in waters of Saudi Arabia in the Arabian Gulf. Open circles along the fitted curve indicate observed proportions. The black circle and square indicate the carapace lengths at 50% maturity (L_{50}) and 95% maturity (L_{95}), respectively. Error bars indicate the standard errors of these lengths.

26,000 to 76,000 eggs (Suppl. Table 2). The fertilization rate was very high, above 97% in all the lobsters.

Age and growth

Out of the 7 hypotheses tested, only 3 had successful numerical convergence under the multinomial likelihood model for the data. Those models are the ones with 2, 3, and 5 age cohorts. Of these 3 models, the best model is clearly the model with 2 cohorts, according to AIC values: −2182.1 for the 2-cohort model, −2174.4 for the 3-cohort model, and −2157.5 for the 5-cohort model. The model with the best fit to the length–frequency data is shown in Figure 3. The presence of only 2 cohorts indicates that this species has a very short lifespan and rapid growth. Estimated parameters of the best-fit normal mixture distribution model are shown in Supplementary Table 3. As can be seen in Figure 3, very few individuals belonging to the youngest cohort were observed. Nevertheless, all the parameters of the model could be estimated with satisfactory statistical precision, as evident from the low SEs. We were able to use the marginal likelihood model to estimate the parameters of the von Bertalanffy growth function in spite of the low number of cohorts estimated for the model underlying the length–frequency data (Suppl. Table 4). The growth was very rapid (with a high K of 0.846 year^{-1}). Given these results, life history theory predicts that M must be very high (Table 2).

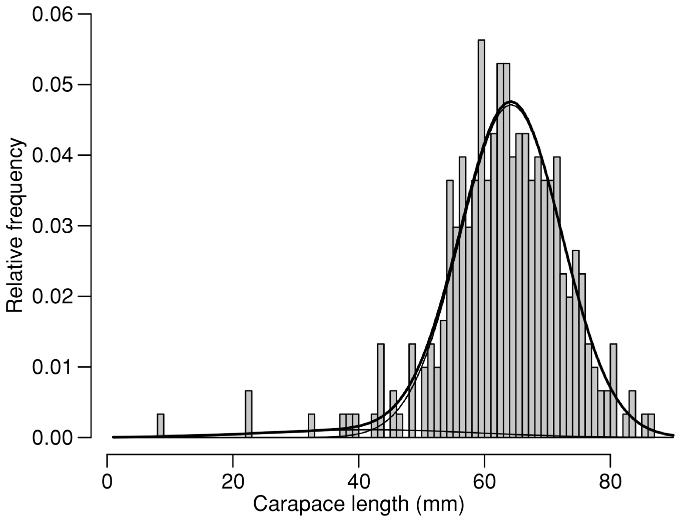

Figure 3

Aggregated length–frequency data (bars) and the fit of the model with 2 age cohorts (lines) for flathead lobsters (*Thenus orientalis*) collected from 2013 through 2016 in the waters of Saudi Arabia in the Arabian Gulf.

Lobster fishery and stock assessment

The landed catch has been increasing substantially since 2000, amounting to 43 metric tons (t) in 2008, the last year before the ban (Fig. 4A). Considering the mean weight of flathead lobsters in our sampling during 2016, that catch translates to over 200,000 individual lobsters. Dhow fleets had a dominant role in contributing to the landings, from 50% in 1995 and >98% in 2008 (Fig. 4A). The rise in landings is totally attributable to the dhow fleet, with approximately 15,000 trips per year (Fig. 4B) or 70,000 days per year (Fig. 4C) after 2003. The catch rate in kilograms per day of fishing was similar in both fleets, 0.436 kg/d for the dhow fleet and 0.300 kg/d for the tarad fleet (Fig. 4D), or around 2 flathead lobsters per day.

The best fit of the generalized depletion model to the data and the predicted biomass per month are shown in Supplementary Figure 5 (also see Supplementary Material). Estimates from the model closely follow the observed catch of both fleets (Figs. 5 and 6), although there are signs of deviation from distributional assumptions in the residual cloud for the dhow fleet, and this deviation tends to widen toward the end of the time series. Predicted biomass on the other hand indicates wide fluctuations driven by recruitment (Fig. 7) and intense M (Table 3), but the prediction is fairly imprecise, with wide statistical margins. Parameter estimates and their precision are presented in Table 3. Natural mortality is very high, at an annualized rate of 1.8 year^{-1}, and abundance inputs (N_0 and recruitment) vary widely from nearly 1 to 100 million individuals. Estimates of M, N_0, and all recruitment pulses higher than 50 million individuals have fairly good precision (coefficient of variation <50%). The operations of the dhow fleet, which accounts for over 97% of the landings in the latest years, are proportional with respect to effort and are hyperstable with respect to abundance.

Discussion

With the results of this study, we have provided for the first time the necessary scientific information for managing a sustainable fishery for flathead lobsters in waters of Saudi Arabia in the Arabian Gulf. We determined the spatial

Table 2

Published estimates of parameters of the von Bertalanffy growth function, growth coefficient (K) and asymptotic length (L_∞), and estimates of natural mortality (M) for species of *Thenus* in different regions around the world. Also provided are mean values from this study for comparison, with standard errors given in parentheses. The estimates for this study in the Arabian Gulf are based on data pooled for both sexes. Values of L_∞ for male and female *T. unimaculatus* are not provided in the consulted reference. CL=carapace length.

		K (year^{-1})		M (d^{-1})		L_∞ (mm CL)		
Species	Country	Males	Females	Males	Females	Males	Females	Source
T. australiensis	Australia	0.511	0.584	0.0022	0.0023	77.45	89.04	Courtney[4]
T. parindicus	Australia	0.949	0.834	0.0035	0.0034	61.23	72.44	Courtney[4]
T. unimaculatus	India	1.387	1.059	0.0017	0.0019	–	–	Radhakrishnan et al. (2013)
T. orientalis	Kuwait	1.789	1.679	0.0068	0.0071	71.6 (max: 74)	81.7 (max: 85)	Hussain (1996)
T. orientalis	Saudi Arabia	0.840 (1.497)		0.0048 (0.0012)		106.52 (11.06)		This study

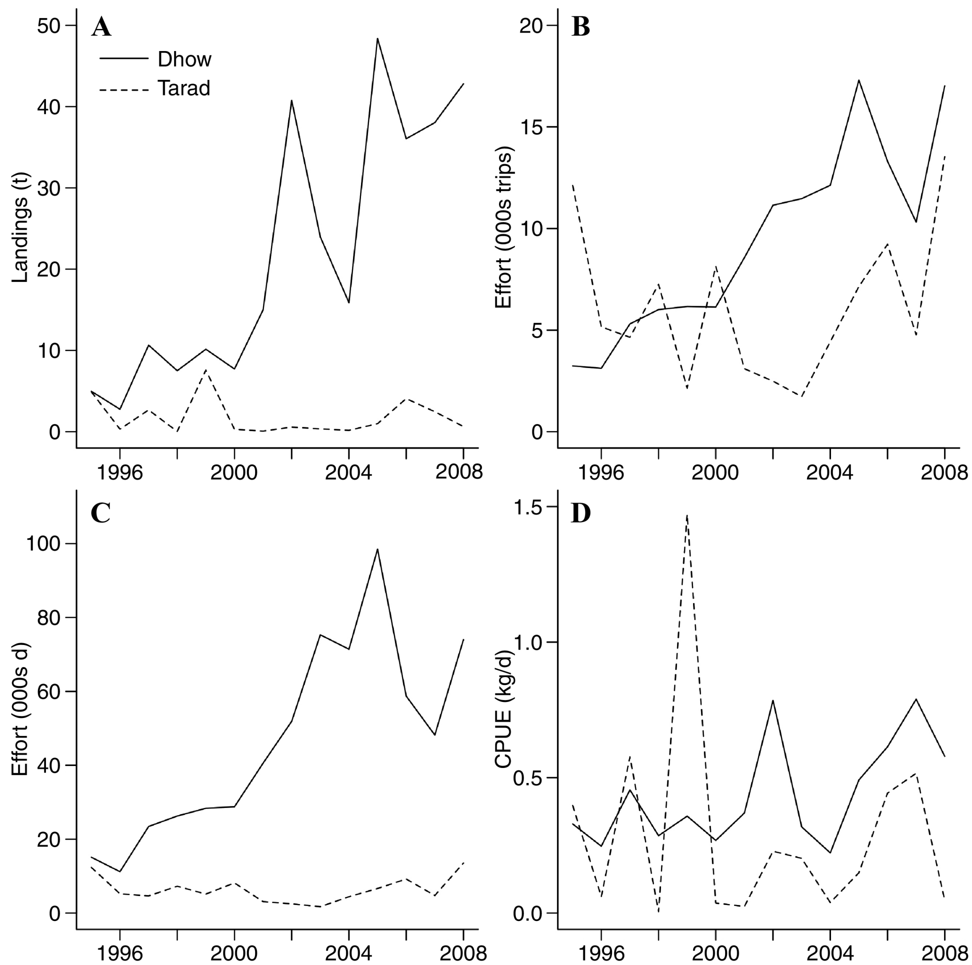

Figure 4

(**A**) Landings in metric tons (t), (**B**) fishing effort measured as the number of trips, (**C**) fishing effort measured as the number of days at sea, and (**D**) catch per unit of effort (CPUE) in kilograms per day from 1995 through 2008 for the fishery that targets flathead lobsters (*Thenus orientalis*) in the waters of Saudi Arabia in the Arabian Gulf. The fishery includes large boats called *dhow* (solid lines) and small boats called *tarad* (dashed lines).

distribution of the stock and the sexual maturity and somatic growth of the samples, and we conducted a stock assessment with a validated method that has been used for other lobster stocks (Meissa et al., 2021). The stock is distributed over the whole region at low densities, on average one order of magnitude less than those observed for *T. parindicus* and *T. australiensis* in Australia (Jones, 1988). Females and males have slightly different maturity schedules, with both sexes of flathead lobster reaching 50% maturity at about 60 mm carapace length. The growth of this species is fast, and its population structure is composed of just 2 cohorts. Recruitment dominates abundance, and the life history of this species is characterized by a short life, rapid maturation and growth, and high M.

Our findings regarding sexual maturity and somatic growth in general are fairly consistent with results from studies of other *Thenus* lobsters in regions of the Indian Ocean. Female flathead lobsters in the Arabian Gulf attain sexual maturity at a slightly higher size than the sizes reported for *T. parindicus* and *T. australiensis* (Jones, 2007). The major pulse of spawning occurred in November–December with a minor peak in May–June. Other *Thenus* species across various regions also have 2 spawning peaks (Jones, 1988; Courtney; Jones, 2007; Radhakrishnan et al., 2013). The maximum fecundity of flathead lobsters in this study (76,144 eggs) was higher than the maximum fecundity that has been reported for *T. parindicus*, *T. australiensis*, and *T. unimaculatus* (Jones, 1988; Radhakrishnan et al., 2013).

The growth rate of flathead lobsters was quite similar to the rates reported for other *Thenus* species from other regions (Table 2). The von Bertalanffy growth coefficient,

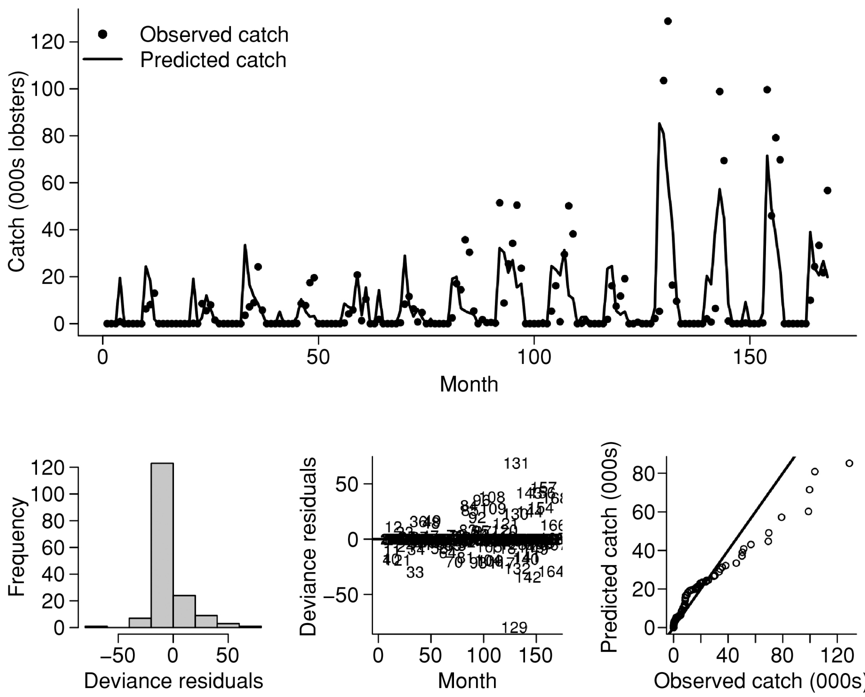

Figure 5

Fit of the stock assessment model to observed data on catch of flathead lobsters (*Thenus orientalis*) by large fishing boats, called *dhow*, from 1995 through 2008 in the waters of Saudi Arabia in the Arabian Gulf (top panel). Diagnostic plots for the model are also provided (bottom panels).

K, and M for *T. parindicus* in Australia (Courtney[4]) are fairly close to those estimated in our study, and L_∞ was lower. The K obtained in this study matches that of *T. unimaculatus* from India (Radhakrishnan et al., 2013), and M reported for the latter was lower than that of this study. On the other hand, Hussain (1996) reported higher K and M but lower L_∞ for flathead lobsters in Kuwait. Growth modeling was based on just 2 observed cohorts, with the juvenile cohort barely represented in the length–frequency data. The hierarchical method of inference accounted for the different contributions of the 2 cohorts; nevertheless, the scant information available for the juvenile cohort resulted in an imprecise estimate of K, with an SE almost double the value of the estimate (see Table 2).

There are striking similarities between the life history of flathead lobsters and that of the green tiger prawn in waters of Saudi Arabia in the Arabian Gulf. The green tiger prawn also is a short-lived, fast-growing crustacean (Rabaoui et al., 2017). One of the reasons for the fast growth of these 2 species could be the effect of temperature. Growth rates generally increase with temperature, but mortality also increases at the highest viable temperatures (Hartnoll, 1982). Located in an arid climatic zone, the western Arabian Gulf has high sea-surface temperatures of 36–40°C during summer months, with an annual sea-surface temperature of 24°C (Sheppard et al., 1992; Al-Abdulkader et al., 2019). There is a southward increase in temperature due to the greater stagnancy toward the south. Preen (2004) observed average monthly sea-surface temperatures <19°C for 4 months in Kuwait Bay, but for only 2 months 300 km farther south in Ras Tanura, Saudi Arabia, and for only 1 month at the southernmost station of Aziziah. This variation in temperature can be linked with the higher occurrence of flathead lobsters in the northern and central parts of the Saudi waters of the Arabian Gulf, indicating avoidance of high temperatures by flathead lobsters. In the Mediterranean Sea, wild slipper lobsters have been reported to migrate offshore to avoid the extreme temperatures found in shallow waters (Spanier et al., 1988; Spanier and Lavalli, 1998).

Although the availability of fisheries data ends in 2008, the fact that there has been no directed fishery for the flathead lobster since the ban supports the view that the results of our analysis presented here are relevant for the current management of flathead lobster. The most remarkable finding pertinent to the potential

[4] Courtney, A. J. 2002. The status of Queensland's Moreton Bay bug (*Thenus* spp.) and Balmain bug (*lbacus* spp.) stocks. Queensland Dep. Prim. Ind., Inf. Ser. QI02100, 18 p. [Available from website.]

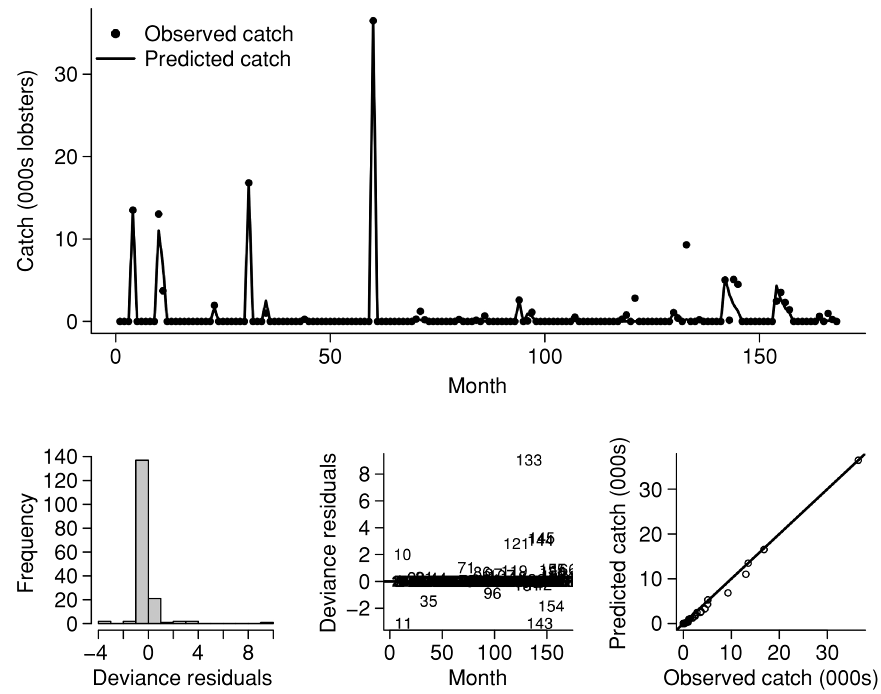

Figure 6

Fit of the stock assessment model to observed data on catch of flathead lobsters (*Thenus orientalis*) by small fishing boats, called *tarad*, from 1995 through 2008 in the waters of Saudi Arabia in the Arabian Gulf (top panel). Diagnostic plots for the model are also provided (bottom panels).

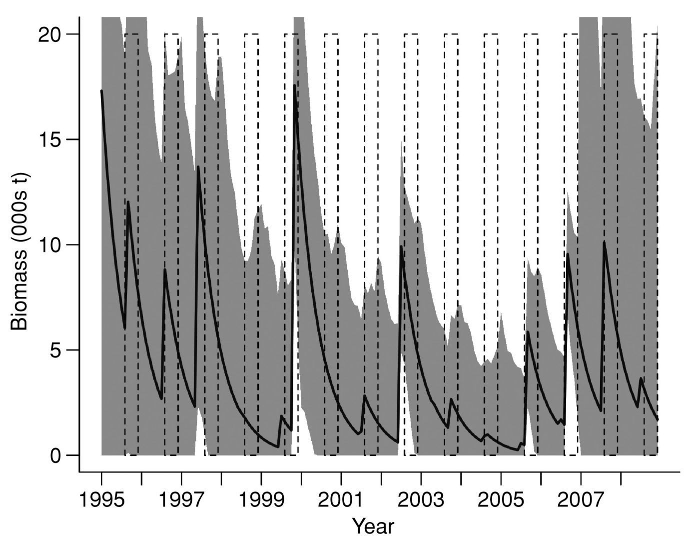

Figure 7

Predicted biomass (solid line) of flathead lobster (*Thenus orientalis*) caught in the waters of Saudi Arabia in the Arabian Gulf during 1995–2008. The gray polygon indicates the 0.5 standard error. The rectangles formed with dashed lines indicate the fishing season for the flathead lobster.

for development of a new fishery is the very wide fluctuations in abundance, driven by fluctuations of 2 orders of magnitude in recruitment and by intense M. In 8 months of the time series, stock biomass was below 500 t or 2.7 million flathead lobsters, and in the months of higher abundance the stock could have over 10,000 t or 55 million flathead lobsters. Because of the wide fluctuations in stock size, it would be necessary to adopt a precautionary stance regarding the potential to resume landings either as allowed bycatch of shrimp trawlers or as a targeted stock in a specialized small-scale fishery. Nevertheless, it should also be noted that the highest landings recorded as bycatch of the shrimp trawlers (~50 t in 2005) amount to just 10% of the minimum monthly biomass. Therefore, it should be safe to resume allowed landings of flathead lobsters as a commercially valuable bycatch of shrimp trawling, but the development of a targeted small-scale fishery would require careful fine-tuning of gear efficiency, magnitude of effort, and seasonal closures, considering that the very low biomass of the stock may drop during natural fluctuations.

Table 3

Parameter estimates from the selected best stock assessment model for flathead lobsters (*Thenus orientalis*) fished as bycatch from the trawl fishery for the green tiger prawn (*Penaeus semisulcatus*) in waters of Saudi Arabia in the Arabian Gulf from 1995 through 2008. The estimated parameters include natural mortality (M), initial abundance (N_0), recruitment for each year (in millions of individuals), scaling (k), effort response (α), abundance response (β), and dispersion. Data are from 2 fleets in the shrimp fishery: small boats (called *tarad*) and large boats (called *dhow*). CV=coefficient of variation.

	Dhow boats			Tarad boats		
Parameter	Timing (month)	Estimate	CV (%)	Timing (month)	Estimate	CV (%)
M (month^{-1})	–	0.1500	25.6	–	0.1500	25.6
N_0 (millions)	–	109.1	14.5	–	109.1	14.5
Recruitment 1995 (millions)	Oct	2.13		Oct	40.86	–
Recruitment 1996 (millions)	Sep	41.08	34.5	Nov	0.55	–
Recruitment 1997 (millions)	Sep	0.09	641.6	Jul	73.72	14.3
Recruitment 1998 (millions)	Sep	0.41	–	Jul	0.38	–
Recruitment 1999 (millions)	Aug	9.60	178.0	Dec	104.23	13.2
Recruitment 2000 (millions)	Sep	0.05	2050.4	Sep	0.05	1986.4
Recruitment 2001 (millions)	Sep	11.69	235.1	Aug	1.60	1810.1
Recruitment 2002 (millions)	Aug	59.10	23.8	Sep	1.12	460.5
Recruitment 2003 (millions)	Jun	0.95	277.6	Oct	9.62	106.6
Recruitment 2004 (millions)	Sep	2.07	137.8	Oct	1.23	164.4
Recruitment 2005 (millions)	Jul	2.24	334.5	Oct	34.30	98.2
Recruitment 2006 (millions)	Jul	2.56	182.0	Oct	52.26	21.6
Recruitment 2007 (millions)	Aug	52.14	–	Oct	1.65	–
Recruitment 2008 (millions)	Jul	8.65	210.6	Jul	1.87	799.7
k (1/number of days)	–	3.3969×10^{-8}	473.9	–	3.3420×10^{-8}	41.6
α	–	1.2433	39.2	–	0.0028	511.6
β	–	0.7138	30.4	–	3.1669	2.3
Dispersion	–	2.1160×10^{-4}	14.1	–	8.6299×10^{-7}	13.7

No targeted fishery for the flathead lobster exists anywhere in the world, and flathead lobsters form only a small percentage of the bycatch in the shrimp trawl fishery in waters of Saudi Arabia in the Arabian Gulf. Fishermen in the area have observed that flathead lobsters can be attracted to bright lights when swimming close to the surface and then caught with scoop nets. This type of fishing is done under bright illumination around oil platforms, or any other structure built in the sea that may act as a fish aggregating device. This method of fishing, which can be highly selective and non-destructive, must be scientifically studied to determine its efficiency and whether it targets a specific fraction of the population, particularly in connection with berried females. The results of our study indicate that a small-scale targeted fishery could complement landings by shrimp trawlers with a production level similar to the bycatch of flathead lobsters in the shrimp trawl fishery. This rate of exploitation would still take only 20% of the minimum biomass observed in some months during the fluctuation cycle observed in our stock assessment modeling. In addition, considering the main spawning period of November–December, a targeted fishery could be set during the off months of the shrimp trawl fishery (February–July), reducing interference with the reproduction cycle.

Conclusions

The results of this study indicate that the flathead lobster caught as bycatch in the shrimp trawl fishery in waters of Saudi Arabia in the Arabian Gulf could be the basis of a sustainable fishery connected to shrimp trawling. The percentage of juveniles in bycatch of trawl surveys was negligible, and a majority of the samples in the catch were above the size at which 50% of females attain sexual maturity. Preventing the catch of berried flathead lobsters, especially during peak spawning in November–December, would further secure sustainability. Furthermore, a targeted small-scale fishery that would operate in the off months of the shrimp trawl fishery could be developed as long as its output is similar to that of the bycatch of shrimp trawling.

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