

An update on the biological parameters of the Norway lobster (*Nephrops norvegicus***) in the northwestern Mediterranean Sea**

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Abstract

The Norway lobster, Nephrops norvegicus, is one of the most valuable fishery resources in many coastal countries of the Mediterranean Sea and the northeastern Atlantic Ocean. In the Mediterranean Sea, several stocks are being overexploited, with ecological, economic, and social consequences. To perform an adequate stock assessment and provide guidance on maximum sustainable yield, reliable biological parameters of the species are required. Considering that biological parameters may change over time in overexploited populations, in the present study, we updated key biological parameters for the N. norvegicus stock of the northwestern Mediterranean Sea: size at which 50% (L50) of females were in reproductive condition, length–weight relationship, and individual size structure. Moreover, daily landings were combined with the spatial position of the vessels tracked by their Vessel Monitoring System (VMS), to obtain information on the geographical distribution and time series of Landings Per Unit Effort (LPUE), as well as total landings from 2008 to 2021. Our results suggest overexploitation of the resource, revealing a severe reduction in size at 50% maturity, an earlier spawning and brooding period, and a clear decrease of LPUE over time.

Keywords: fishing resources; landings; N. norvegicus; revisiting biological parameters; size at onset of maturity

Introducton

The future of fishing as a viable economic, social, and cultural activity is uncertain (Pauly et al. [2003\)](#page-12-0). It is estimated that between 40 and 50% of tropical and temperate ecosystems exceed the threshold for the sustainability of fisheries and, therefore, are considered overexploited (Link and Watson [2019\)](#page-11-0). Despite a decrease in fishing pressure over the past decade, leading to the recovery of some fish stocks (Cardinale et al. [2013,](#page-10-0) Fernandes and Cook [2013\)](#page-11-1), there is still a long way to go towards achieving a global recovery of overexploited populations (Froese and Proelß [2010,](#page-11-2) Cardinale et al. [2013\)](#page-10-0). For example, in the Mediterranean and Black Seas, a recent study of 54 commercial fish and invertebrate species revealed that 85% of their stocks were overexploited (Demirel et al. [2020\)](#page-10-1). A key to achieving best management practices is to implement science-based management (Pikitch et al. [2004\)](#page-12-1). To attain this goal, it is imperative to obtain biological parameters of the target species, in order to comprehend the temporal changes in their abundance, distribution, and biology, which may be subject to different alterations, depending on the degree of exploitation (Ligas et al. [2011,](#page-11-3) Galimany et al. [2015\)](#page-11-4).

The Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758), is a benthic crustacean inhabiting muddy bottoms at depths from 10 to 800 m, distributed in northeastern Atlantic and Mediterranean waters (Bell et al. [2013,](#page-10-2) Johnson et al. [2013\)](#page-11-5). Atlantic populations are mainly found on the continental shelf (Eiríksson [2014\)](#page-11-6), whereas in the Mediterranean Sea, the greatest abundance is present on the upper and lower reaches of the continental slope, between depths of 300–600 m (Maynou and Sardà [1997,](#page-11-7) Abelló et al. [2002\)](#page-10-3). It is one of the most valuable European fishing resources with great commercial importance across its entire distribution (Sardà [1998a,](#page-12-2) Bell et al. [2013,](#page-10-2) Ungfors et al. [2013\)](#page-12-3). Its global capture production in European waters has reached ∼60 000 tons per year for the last 30 years (Chapman [1980,](#page-10-4) Bianchini et al. [1998,](#page-10-5) Ungfors et al. [2013,](#page-12-3) FAO [2022\)](#page-11-8). In the Mediterranean Sea, *N. norvegicus* is captured by bottom trawlers, in which other demersal commercial species are also fished, such as European hake (*Merluccius merluccius*), anglerfish (*Lophius budegassa* and *L. piscatorius*), horned octopus (*Eledone cirrhosa*), and blue whiting (*Micromesistius poutassou*) (Sardà [1998a\)](#page-12-2).

Fishery management in Mediterranean European waters relies on biological scientific guidance, involving effort limitation and gear regulation (Sardà [1998a,](#page-12-2) Sánchez Lizaso et al. [2020\)](#page-12-4). Although many European Atlantic fisheries incorporate output limits through total allowable catches, these measures encounter difficulties in their implementation and demonstrate no efficiency when applied to diverse and mixed fisheries, as shown for the Mediterranean (Bellido et al. [2015,](#page-10-6)

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Sánchez Lizaso et al. [2020\)](#page-12-4). The prevailing management approach for *N. norvegicus* involves regulation through the establishment of a minimum conservation reference size (MCRS), set at 20 mm Cephalothorax Length (CL) in the Mediterranean Sea (Regulation (EU) 1380/2013, 11/12/2013 and Regulation (EU) 2019/1241, 20/06/2019; Regulation (EU) [2013,](#page-12-5) Regulation (EU) [2019\)](#page-12-6).

In the Mediterranean Sea, stock assessments are conducted annually by the General Fisheries Commission for the Mediterranean (GFCM) (Cardinale et al. [2021,](#page-10-7) GFCM [2022\)](#page-11-9) and the Scientific, Technical, and Economic Committee for Fisheries (STECF [2023\)](#page-11-10), which meet once a year to present final reports for each stock and help to define new policy decisions for the fishery stocks of the Mediterranean Sea by the European Commission. The evaluation of the *N. norvegicus* stock is mainly based on stock assessment models that require biological reference points essential for proper model validation. However, most of these evaluations that rely on assessment models (e.g. to estimate fishing mortality for which average yield is equal to Maximum Sustainable Yield, MSY) feature biological parameters that need updating, which is important as many resources are overexploited or showing signs of decline may have modified these parameters (Cardinale et al. [2017,](#page-10-8) Rindorf et al. [2017\)](#page-10-8). In the case of *N. norvegicus*, this crustacean has striking differences in the level of exploitation and biological characteristics (such as growth rate, density, or size structure of the population) depending on the geographical variations of the habitat, exploitation patterns, population density, and substrate characteristics (Maynou [1998,](#page-11-11) Sardà et al. [1998,](#page-12-7) Aguzzi et al. [2003,](#page-10-9) Aguzzi and Sardà [2008\)](#page-10-10). For example, in the northwestern Mediterranean Sea (FAO Geographical Sub Area 6–GSA06), where *N. norvegicus* is one of the most valuable stocks for bottom trawl fisheries, earlier studies on its biology suggested a size reduction in individuals caused by fishing pressure (Sardà [1998b,](#page-12-8) Rotllant et al. [2005\)](#page-12-9). Notably, the estimated size at 50% maturity in Catalan waters was already ∼30 mm CL in 1998, as documented by Orsi Relini et al. [\(1998\).](#page-12-10) Consequently, obtaining updated biological information on *N. norvegicus* in this specific area is especially crucial considering that the most recent available biological data for this region were assessed over two decades ago and there are signs of overexploitation following the most recent stock assessments in GSA06 (GFCM [2022,](#page-11-9) STECF [2023\)](#page-11-10).

Therefore, in the present study, we aim to revisit the main biological parameters of *N. norvegicus* in the Catalan Sea to provide relevant data for a revised assessment of this stock, acknowledging its status in terms of exploitation. In particular, we estimated its length distribution, length–weight relationship, demographic structure, and reproduction, evaluated trends in landings and income over the past two decades, and compared our results with those of previous studies in the area.

Materials and methods

Study area

This study was conducted in the northwestern Mediterranean Sea along the Catalan coast [\(Fig.](#page-2-0) [1\)](#page-2-0), where *N. norvegicus* inhabits muddy substrates at depths of 80–550 m on the lower shelf and upper-middle slope of the continental margin (Abelló et al. [2002\)](#page-10-3). Within this region, the bottom trawl fleet is composed of 221 vessels, which operate five days a week for

a maximum of 12 h during daylight hours, commercializing landings daily upon the arrival of trawlers at their respective base port (BOE 502/2022; BOE [2022\)](#page-10-11).

To reexamine the main biological parameters of *N. norvegicus* alongside landings data, we used three distinct types of datasets: (i) a dataset comprising landing records, income information, and fishing effort data sourced from the public repositories of the Department of Fisheries of the *Generalitat de Catalunya* (the Autonomous Government of Catalonia, northeast Spain); (ii) VMS data, which monitor and track the daily and spatial activity of fishing vessels, obtained from the fishery regulatory organization of the *Secretaría General de Pesca* of the Spanish Government; and (iii) a dataset collected directly on-board commercial bottom trawlers as part of the monitoring program of the Catalan Institute of Research for the Governance of the Sea (ICATMAR; https:// [icatmar.cat/en/\),](https://icatmar.cat/en/) a collaborative organization overseeing both recreational and commercial fishing activities along the Catalan coast (ICATMAR [2023\)](#page-11-12).

Temporal landings dataset

Daily landings data on *N. norvegicus* (kg), fishing effort (total number of days of the entire fleet), and fisheries revenue (income in ϵ) from 2000 to 2021 were obtained from the Department of Fisheries of the Autonomous Government of Catalonia, and then summarized by month and year. We also obtained annual and monthly landing data from previous studies (Sardà [1998b,](#page-12-8) Aguzzi et al. [2007\)](#page-10-12) for Barcelona harbor from 1979 to 1994. We compared the temporal evolution of Barcelona Harbor's landings during that period with landings from the same port from 2000 to 2021. In order to examine temporal changes in monthly landings, we conducted a comparative analysis of three distinct time series. These include the period from 1979 to 1994, exclusively focusing on Barcelona harbor landings; a selected timeframe spanning 2005–2010, including landings data from the Autonomous Government of Catalonia; and a time series of catches gathered monthly from commercial bottom trawlers during the years 2019 to 2021 (further details below).

Spatial and temporal variability of LPUE

To estimate the spatial overlap between years of *N. norvegicus* presence from 2008 to 2021, we combined daily landings data on *N. norvegicus*, sourced from the Autonomous Government of Catalonia, with information on spatial fishing effort using VMS data for daily vessel positioning following the methodology described in Sala-Coromina et al. [\(2021\).](#page-12-11) Data regarding fishing spatial effort before 2008 was not available because the use of VMS was not mandatory before 2005, and the first 2–3 years of VMS implementation data is not 100% reliable. Landings were standardized based on fishing effort (duration of fishing activity in hours) and referred to as Landing Per Unit Effort (LPUE). It is important to note that when estimating spatial overlap, fishing effort (measured as the duration of recorded fishing activity in hours) differs from the fishing effort (measured as vessels or landings per day) obtained previously to compare the temporal evolution of landings. The measurement in hours for fishing effort enhances the spatial localization of fishing activities. We represented the spatial distribution of yearly LPUE with a heatmap to observe the bathymetric range (every 25 m, from 50 to 800 m deep) from 2008 to 2021, comparing the LPUE data based on

Figure 1. Spatial distribution of the annual averaged LPUE (Landings Per Unit Effort) of N. norvegicus in the Catalan Sea (northwestern Mediterranean) from 2019 to 2021, obtained by combining Vessel Monitoring System (VMS) information and official daily landings data (European Commission [2022\)](#page-11-13). Trawl surveys conducted from 2019 to 2021 in the study area are represented in the map. Note: For comparative purposes, FAO subgeographical areas (GSA) with available data of N. norvegicus stocks are highlighted on the map of the Mediterranean Sea. The study area along the Catalan coast is located in the northern part of GSA06. Norway lobster illustration by Joan Mir-Arguimbau.

Cohen's Kappa coefficient. This pairwise statistic (McHugh [2012\)](#page-11-14) indicates how much the same spatial units (sites defined by a grid within the study area) overlap in terms of presence of *N. norvegicus* between years. Cohen's Kappa values range from -1 to $+1$, although they usually fall between 0 and 1, where 0 indicates random agreement, and $+1$ indicates complete agreement (in contrast to −1, indicating complete disagreement) (Landis and Koch [1977\)](#page-11-15). To calculate the spatial similarity between the different yearly LPUE distributions, we used the *irr* package (Gamer et al. [2019\)](#page-11-16). We evaluated the overlap of LPUE between years in the bathymetry range (i.e. every 25 m; see above) using Spearman's correlation through the *stats* package (R Core Team [2021\)](#page-12-12). The values of this correlation coefficient range from -1 to 1, indicating the direction and strength of the relationship between two variables, being stronger the closer to -1 or 1, with independent variables closer to 0.

Biological data

Biological sampling of *N. norvegicus* individuals was conducted from January 2019 to December 2021 on board commercial bottom trawlers, harbored in nine of the most important ports of the study area [\(Fig.](#page-2-0) [1\)](#page-2-0). All sampled individuals were obtained from a total of 157 hauls, 54 carried out in 2019, 51 in 2020, and 52 in 2021. The biological samplings were conducted at a frequency of ∼3 to 4 times per month, covering all the Catalan coast throughout the entire year. Trawling vessels were equipped with a commercial fishing net with a 40–50 mm square mesh codend, according to regulation EC No. 1967/2006 (EC [2006\)](#page-10-13). All biological parameters were measured on board, and, whenever available, 90 individuals covering all commercial categories (30 individuals from each category, i.e. small, medium, and large) were collected and transported to the Institute of Marine Sciences (ICM-CSIC) laboratory for further examination. The measurements taken were cephalothorax length (CL, in mm) and weight (W, in g), and all individuals were sexed. Males and females can be distinguished by the position of the genital apertures and the shape of the first pair of pleopods (Powell and Eriksson [2013\)](#page-12-13). In the case of females, total ovary weight (in g) and maturity stage were also noted.

Population structure

Size-frequency distributions were constructed per 1 mm size class of CL for each sex, using density plots. To test for differences in mean size between males and females, we conducted nonparametric Kruskal–Wallis tests. Kolmogorov–Smirnov two-sample tests were also used to detect differences between

Figure 2. Landings of N. norvegicus from Catalan commercial bottom trawlers over different timescales. (a) LPUE of N. norvegicus, landings corrected per the total number of days of the entire fleet (kg × vessel⁻¹ × day⁻¹), and annual landings in tons (t). (b) Nephrops norvegicus annual landings in Barcelona harbor in tons (t) from 1974–1994 (Sardà [1998a\)](#page-12-4) to 2000–2021. (c) Monthly average landings in tons along the Catalan coast over two time periods, from 2005 to 2010 and from 2019 to 2021. (d) Monthly average landings in tons from Barcelona harbor comparing three temporal datasets, from 1979 to 1994 (Aguzzi et al. [2004\)](#page-10-14), 2005 to 2010, and 2019 to 2021.

sexes in size distributions. We obtained size distribution data from 1974 to 1994 for the same GSA06 (Sardà [1998b\)](#page-12-8) to compare the *N. norvegicus* population over time.

The length–weight relationship was analyzed for the sexes, separately and combined, using the equation (Pauly [1984,](#page-12-14) Ricker [1973\)](#page-12-15):

$$
W = a \times CL^b,
$$

where *W* is the body weight (in g), *CL* is cephalothorax length (in mm), *a* is the intercept of the regression curve, and *b* is the slope of the scaling exponent, indicating the pattern of growth, i.e. negative allometry $(b < 3)$, isometry $(b = 3)$, or positive allometry $(b > 3)$. The relationship between length and weight was estimated with the *FSA* R package (Ogle et al. [2023\)](#page-12-16).

Maturity and reproduction stages

Sex ratio was evaluated seasonally from the commercial bottom trawl samplings performed only on the upper slope (200– 500 m), where *N. norvegicus* is found in higher abundances (Sardà [1998a\)](#page-12-2). G-tests (Sokal and Rohlf [1981\)](#page-12-17) were carried out to test for significant differences in sex ratio. Then, male and female percentages by season were estimated. From the total of sampled females, we estimated the percentage of pleopod egg-bearing (i.e. berried) females per season.

Females were classified into five maturity stages determined by macroscopic examination of the color of the ovaries based on Rotllant et al.'s [\(2005\)](#page-12-9) histological examination: stage I white-immature, slender and thin ovaries; stage II resting (also refers to berried females), cream-yellowish ovaries; stage III beginning of maturation, small and light green ovaries; stage IV big, thick, and light green ovaries; and stage V dark green ovaries, advance maturation in pre-spawning phase. All berried females, which were categorized as in stage II of maturity, were also identified and quantified.

The Gonadosomatic Index (GSI), indicating the maturity status of females, was calculated from the ratio of ovary weight to total body weight (Strange [1996\)](#page-12-18):

$$
GSI = \text{gonad weight/body weight} \times 100.
$$

For the estimation of size at 50% maturity, we considered females sampled during the months in which gonads start developing and become mature (from March to August), defining mature females from Stage II (including berried females) to females at Stage V. To estimate size at 50% maturity, a logistic estimation of gonad maturity was run with the *SizeMat* package in the program R (Torrejon-Magallanes [2020\)](#page-12-19), between CL and sexual maturity level determined for both immature (Stage I) and mature (Stage II–V) females. In these analyses, a logistic curve was fitted to the data so that the CL at which 50% of females were in reproductive condition (L50) could be estimated.

Results

Landing trends

During the period 2000–2021, there was a decreasing trend in both *N. norvegicus* total landings (tons) and LPUE [\(Fig.](#page-3-0) [2a](#page-3-0)). Over the course of 21 years, LPUE decreased by 37.81%,

Table 1. Individuals of N. norvegicus by season from the biological samplings conducted on board commercial bottom trawlers from 2019 to 2021 on the upper slope (200–500 m).

Season	n		M		Bd
Winter	21	1049 ± 741	$651 \pm 487(62.06)$	398 ± 284 (37.94)	$7 \pm 11(1.76)$
Spring	21	1191 ± 711	560 ± 369 (47.02)	631 ± 362 (52.98)	0(0)
Summer	20	1158 ± 598	$599 \pm 306 (51.73)$	559 ± 329 (48.27)	$37 \pm 52 (6.62)$
Autumn	17	819 ± 432	$533 \pm 311(65.08)$	$286 \pm 161 (34.92)$	62 ± 49 (21.86)
Total	79	1053 ± 632	$582 \pm 365 (55.27)$	$471 \pm 320 (44.73)$	$28 \pm 44 (5.94)$

^A *ⁿ* indicates the number of surveys conducted in each season on the upper slope; *^T* is the total number of individuals collected per swept area (No. [×] km−2); *M* is the number of male individuals per swept area (No. × km⁻²) with percentage of males (out of total individuals) in brackets; *F* is the number of female individuals per swept area (No. [×] km−2) with percentage of females (out of total individuals) in brackets; and *Bd* is the number of berried females per swept area with percentage of berried females (out of total individuals) in brackets.

Figure 3. Distribution of LPUE of N. norvegicus along the Catalan coast (GSA06) from 2008 to 2021, obtained by combining VMS information and official daily landings data (European Commission [2022\)](#page-11-13). (a) Spatial distribution of LPUE from 2008 to 2021, and (b) bathymetric range of LPUE of N. norvegicus from 2008 to 2021. Values of LPUE per year and bathymetry are indicated in the color bar.

representing a reduction of 210 647 kg in total landings. Moreover, total income also decreased by 39.67%, amounting to €2 190 372 <21 years prior. These time series reached their lowest values in 2021, considering all Catalan Sea fisheries (Supplementary Table S1). The landing trend observed for Barcelona harbor included a more extensive period, from 1979 to 2021, revealing distinct transitions [\(Fig.](#page-3-0) [2b](#page-3-0)). Notably, the lowest landing was reported in 1992 with only 4.69 tons. Subsequently, there appeared to be an upward trajectory in landings until 2014. Starting in 2015 and coinciding with the decreasing trends in all Catalan fisheries, there was a sudden and significant decline in landings. Regarding only Barcelona harbor, landings showed an approximate decrease of 22.95 tons from 1979 to 2021, accounting for a 64.29% reduction from the catch landed in 1979 [\(Fig.](#page-3-0) [2b](#page-3-0)).

The monthly landing pattern in the period 2005–2010 exhibited a peak in late spring months (April, May, and June) and summer (July, August, and September), mainly in July, with mean values ranging between 33.70 and 41.10 tons for monthly landings from May to August [\(Fig.](#page-3-0) [2c](#page-3-0)). Biological samplings from commercial bottom trawls, conducted in the period 2019–2021, revealed a similar pattern to the period 2005–2010, with spring being the season with the highest catch density (1191 \pm 711 No. × km⁻²), followed by summer (1158 ± 598 No. \times km⁻²) [\(Table](#page-4-0) [1\)](#page-4-0). Upon comparing the three distinct time series data (1979–1994, 2005–2010, and 2019–2021) for Barcelona harbor landings, it becomes evident that the largest monthly landings across all-time series coincide, occurring between May and August [\(Fig.](#page-3-0) [2d](#page-3-0)).

Regarding spatial overlap between years, Cohen's Kappa statistic indicated that the distribution of *N. norvegicus* showed moderate overlap, with values ranging between 0.4 and 0.6, indicating no shifts in distribution from 2008 to 2021 [\(Fig.](#page-4-1) [3a](#page-4-1) and Supplementary Table S2). The bathymetric range of *N. norvegicus* remained similar over the years, with 0.92 being the lowest Spearman correlation value (Supplementary Table S3). In 2008 and 2021, 75% of landings came from depths of 300–625 m and 300–675 m, 50% came from between 350–550 m and 375–550 m, and 25% came from between $400-500$ and $425-500$ m, respectively [\(Fig.](#page-4-1) [3b](#page-4-1)).

Population structure

Of the 157 hauls conducted from 2019 to 2021, a total of 15 665 individuals, including 8490 males and 6819 females, were measured and sexed on board commercial bottom trawlers. From these individuals, 6698 individuals, including 4070 males and 2628 females, were collected to estimate more accurately biological parameters in the laboratory (length– weight relationship, percentage of gonad development stage, and size at 50% maturity). The CL from the collected individuals during the sampling period ranged from 18 to 65.5 mm

Table 2. Length–weight relationship for N. norvegicus obtained in the present study compared with this relationship in the same and other GSAs in the Mediterranean Sea.

Area	Year	Sex	No.	a	b	Studies
GSA06	2019-2021	M	4070	0.0004	3.1766	Present study
		\boldsymbol{F}	2628	0.0004	3.1736	
		C	6698	0.0005	3.1166	
GSA06	1994	M	7887	0.0005	3.0520	Sardà et al. (1998)
		F	7574	0.0008	2.9140	
	1995	M	5806	0.0004	3.1180	
		F	4942	0.0005	3.0750	
GSA17	2012-2014	C	4145	0.0003	3.2470	Angelini et al. (2020)
		$\mathbf M$	1842	0.0003	3.2030	
		F	2299	0.0013	2.7620	
GSA17	2012-2016	C	2798	0.0008	2.9670	
		$\mathbf M$	1466	0.0008	2.9610	
		F	1332	0.0010	2.9010	
GSA22	1993	C	275	0.9229	2.9130	Stergiou and Politou (1995)
	1994	C	221	0.4701	3.0850	
GSA22	2008	C	659	0.4800	3.2100	Aydin and Aydin (2011)
		M	305	0.4600	3.2700	
		F	354	0.5200	3.1200	

Sex: $M =$ males, $F =$ females, and $C =$ combined sexes; No.: total number of specimens weighed; a: intercept; and b: slope.

in males, and 18 to 60.35 mm in females, with mean weights of 40.19 \pm 27.26 and 23.94 \pm 14.21 g for males and females, respectively [\(Table](#page-5-0) [2\)](#page-5-0).

The size frequency distribution, calculated from the 15 665 individuals measured, differed between sexes (Kolmogorov– Smirnov tests also indicated a different size distribution between sexes; $D = 0.21$, $P < 0.01$), with males having a higher mean CL than females (males = 32.16 ± 6.59 ; females = 29.60 \pm 4.50; $\chi^2_{1,6697}$ = 1352, *P* < 0.0001; [Fig.](#page-6-0) [4a](#page-6-0) and b). Regarding temporality, there were significant differences between years ($H = 133.08$, $P < 0.01$) and between sexes (H = 1371.72, $P < 0.01$). Mean CLs (mm) for males were 34.34 ± 32.35 in 1974 and 30.35 ± 29.21 in 1994, whereas CLs (mm) for females were 31.51 ± 28.39 in 1974 and 27.89 ± 26.20 in 1994.

The nonlinear regressions between CL and body weight (W) for females, males, and pooled individuals collected from the biological sampling had a good fit, with high correlation coefficients ($r^2 > 0.90$; [Fig.](#page-6-1) [5\)](#page-6-1). The length–weight relationship for females, males, and pooled individuals was similar in the slope of the regression relationships; the scaling exponents (b) were similar between sexes, indicating a slight positive allometric pattern for growth $(b > 3)$ [\(Fig.](#page-6-1) [5;](#page-6-1) [Table](#page-5-0) [2\)](#page-5-0). The regression equations calculated by sex and pooled individuals were:

LogWfemales ⁼ ⁴ [×] ¹⁰−⁴ [×] *^x*3.1736, LogWmales ⁼ ⁴ [×] ¹⁰−⁴ [×] *^x*3.1766, LogWpooled ⁼ ⁵ [×] ¹⁰−⁴ [×] *^x*3.1116.

Maturity and reproduction stages

Sex ratio differed from the expected equilibrium (0.50) in autumn and winter, exhibiting a lower presence of females in landings from October to March [\(Table](#page-4-0) [1\)](#page-4-0). In spring, females showed a higher presence than males (0.53 and 0.47, respectively). G-tests indicated significant differences between sex ratios among seasons ($G = 90.64$, $P < 0.01$). However, a similar sex ratio was found for autumn and winter $(P = 0.18)$ and spring and summer $(P = 0.05)$. Overall, the percentage of berried females out of the total of all collected females was higher in autumn (21.86%) than in the other seasons. Moreover, G-tests conducted with berried females among seasons showed significant differences among all seasons $(G = 164.17,$ $P < 0.01$).

GSI values of females between 2019 and 2021 were higher in summer, specifically in July and August [\(Fig.](#page-7-0) [6a](#page-7-0)). Afterwards, in late summer and the beginning of autumn, GSI decreased, coinciding with a higher percentage of berried females [\(Table](#page-4-0) [1\)](#page-4-0). Additionally, GSI values are shown by maturity stage (I–V) [\(Fig.](#page-7-0) [6b](#page-7-0)). Between 2002 and 2003, GSI monthly values were highest in July, August, and September [\(Fig.](#page-7-0) [6c](#page-7-0)). The estimated size at 50% maturity for females was 25.3 mm CL, with a confidence interval of 24.8–25.7 mm CL [\(Fig.](#page-7-1) [7\)](#page-7-1), which is a lower value when compared to other *N. norvegicus* stocks evaluated within the Mediterranean Sea [\(Table](#page-8-0) [3\)](#page-8-0).

Discussion

Nephrops norvegicus abruptly decreased in annual landings in the northwestern Mediterranean Sea, with a total biomass loss of 65% in just two decades (i.e. from 2000 to 2021). Moreover, we found clear evidence of a substantial reduction, up to 5 mm, in size at 50% maturity for the *N. norvegicus* population, which shows a considerable decrease in mean size in both females and males compared to 1974. In the Mediterranean Sea, this species is mainly regulated by the MCRS, which is set at 20 mm CL [Regulation (EU) 1380/2013, 11/12/2013, Regulation (EU) 2019/1241, 20/06/2019], well below the size at 50% maturity reported thus far [\(Fig.](#page-7-1) [7](#page-7-1) and references herein). Our results may be an indicator of high fishing pressure on *N. norvegicus*, demonstrating that the management measures currently in place are not sufficient to manage the stock sustainably.

Spawning season and stock spatial distribution

Northwestern Mediterranean *N. norvegicus* fishing grounds are still located at depths between 300 and 675 m (Sardà

Figure 4. Plot showing the size frequency distribution of N. norvegicus sampled from 2019 to 2021 (this study) and from 1994 to 1974 (Sardà [1998a\)](#page-12-4): (a) male size distribution and (b) female size distribution. MCRS indicates the minimum conservation reference size for N. norvegicus [Regulation (EU) 1380/2013, 11/12/2013; Regulation (EU) 2019/1241, 20/06/2019].

Figure 5. Relationship between length (CL, mm) and weight (g) of N. norvegicus sampled in GSA06: (a) females, (b) males, and (c) both sexes pooled. The nonlinear regression of the length–weight relationship obtained in a previous study from the same area is also represented (Sardà [1998b\)](#page-12-21).

[1998a\)](#page-12-2). However, we observed how landings have considerably decreased in total number over the years. It is worth mentioning that, despite the reduction of fishing effort in the last several years (ICATMAR [2022\)](#page-11-17), the LPUE of *N. norvegicus* stocks is still decreasing.

Landings preserve a seasonal component, probably related to the behavior of the species (Aguzzi et al. [2023\)](#page-10-17). *Nephrops norvegicus* builds burrows, offering a natural means of protection from bottom trawling activities (Aguzzi et al. [2004,](#page-10-18) [2023\)](#page-10-17). A seasonal pattern in landings was observed, currently peaking in June, although in previous years the largest landings occurred in July–August. The quantity of individuals caught can be considered proportional to the number of individuals emerging from their burrows, which seems to depend on light intensity (Aguzzi et al. [2003,](#page-10-19) [2021,](#page-12-5) Vigo et al. [2021\)](#page-12-22). Spring and summer are the seasons in which a longer photoperiod elicits longer burrow emergence, with animals wandering and meeting. Additionally, *N. norvegicus* mating takes place outside burrows and occurs in spring–summer (Aguzzi et al. [2004\)](#page-10-14). Later, during the brooding period, berried females hide inside their burrows throughout the autumn until the release of larvae in late winter, showing a highly seasonal reproductive period (Farmer [1974,](#page-11-18) [1975,](#page-11-19) Company et al. [2003,](#page-10-20) Rotllant et al. [2005\)](#page-12-23). Possibly, a combination of all these factors may explain the larger catches during these periods and the lower catches in autumn and winter.

Demographic parameters

The population structure of *N. norvegicus* presents different demographic patterns in the northwestern Mediterranean due to area-dependent fishing pressure in combination with variable environmental factors such as habitat characteristics (Abelló et al. [2002\)](#page-12-24). With respect to landings, the largest individuals were always male.The mean size of individuals did not exhibit a reduction over time when compared to the mean size of individuals in 1974. However, it is important to note that the 1974 study was conducted within a specific delimited area near Barcelona, whereas the recorded sizes spanning 2019– 2021 include the entire Catalan coast. It should also be noted that gear devices used on board commercial bottom trawlers at each sampling period (1974, 1994, and 2019–2021) differed in codend mesh size and global gear shape. In 1974 and 1994, the codend mesh size used was a 40 mm diamond mesh (DM40) at the codend of 5 mm knotted PE-netting, while in the present study, fishing vessels used a 40 mm square mesh (SM40) at the codend of 3 mm knotted PE-netting due to a change in legislation for commercial bottom trawlers in the Mediterranean Sea [Council Regulation (EC) No. 1967/2006, Regulation (EU) No. 2019/1241]. The shape of the mesh can significantly change the size-selectivity of the species caught, as codend SM40 selects smaller individuals with larger discards (Bahamon et al. [2006,](#page-10-21) [2007,](#page-10-22) ICATMAR [2021\)](#page-11-20). This could

Figure 6. Gonadosomatic index (GSI) values obtained for females of N. norvegicus. (a) Boxplots of the average monthly (2019–2021) distribution of GSI values, indicating the dominant maturity stage by month. (b) GSI values as a function of ovary maturity stages (S1–S5). (c) GSI monthly distribution of N. norvegicus sampled between 2002 and 2003, graph adapted from Rotllant et al. [\(2005\)](#page-12-23).

Figure 7. Length at 50% maturity (L₅₀) of N. norvegicus females represented in % mature females and confidence limits. Females collected throughout the year, defining mature females from Stage II to Stage V, were considered. The figure presents the size at 50% maturity in this study (2019–2021), the size at 50% maturity obtained in Orsi Relini et al. [\(1998\)](#page-11-21) in GSA06, and the sizes at 50% maturity evaluated in other GSAs in the Mediterranean Sea (see [Table](#page-8-0) [3\)](#page-8-0).

have resulted in the presence of smaller individuals in the length frequency distribution of 2019–2021 due to the better selection of larger individuals. Despite these differences, only the mean size compared from 1974 to 2019–2021 showed signs of overexploitation. Sex ratio was almost equal in spring and summer, yet in autumn and winter the presence of males was greater than that of females, coinciding with the periods in which there is a high proportion of berried females, which apparently spend more time concealed in tunnels (Farmer [1975,](#page-11-19) Aguzzi et al. [2007\)](#page-10-13).

Nephrops norvegicus is considered a long-lived species (Hillis [1979,](#page-11-22) Sardà [1985,](#page-12-2) Castro [1992\)](#page-10-23), with slow growth rates ranging from 4 to 5 mm per year (Bianchini et al.). Our results showed that the length–weight relationship was positively allometric for both males and females. Thus, volumetric growth (body mass) is faster than length growth (body length), with both sexes growing at the same speed. Length– weight relationship can vary significantly, both temporally and spatially (Robinson et al. [2010\)](#page-12-25). Other studies from GSA06 reported a very similar *a* coefficient (ranging from 0.0004 to 0.0008 in Sardà et al. [1998,](#page-12-8) see [Table](#page-5-0) [2\)](#page-5-0), whereas the growth parameter indicated near isometry as *b* values were close to three, with most of them indicating a positive allometric

Table 3. Comparative table of different studies carried out in different GSAs with size parameters of N. norvegicus in commercial bottom trawl fisheries: No.: total number of female individuals; L50: size at 50% maturity; cephalothorax length with a 50% probability of being retained

Areas	Year	No.	L50	Studies
GSA02	1995		36	Orsi Relini et al. (1998)
GSA04	2011-2012	617	33	Bekrattou et al. (2019)
GSA06	1974, 1977, 1978	3595	$30.0 - 31.0$	Sardà (1991)
GSA06	1995		30	Orsi Relini et al. (1998)
GSA06	2019-2021	2628	25.3	Present study
GSA07	1980		27	Morizur et al. (1981)
GSA09	1995		32	Orsi Relini et al. (1998)
GSA ₁₀	1995		32	Orsi Relini et al. (1998)
GSA ₁₇	2012-2014	2299	21.14	Angelini et al. (2020)
	2012-2016	1332	30.83	
GSA17-18			31.69	Mytilineou and Sardà (1995)
GSA18	1995		30	Orsi Relini et al. (1998)
GSA18	2009-2011	744	25.7	Marković et al. (2016)
GSA ₂₂	1995		33	Orsi Relini et al. (1998)
GSA ₂₂	2007	510	28.1	Mente et al. (2009)
Mediterranean Sea	2003		32	ICES (2006)

pattern in both sexes (Sardà et al. [1998,](#page-12-8) Company and Sardà [2000\)](#page-10-25). Compared to other geographical areas of the Mediterranean, the only negative biometric relationship is found in the females of Pomo Pit, a specific area in GSA17, corresponding to the northern and central Adriatic Sea (Angelini et al. [2020\)](#page-10-15). Even if the difference is not significant, the growth rate of *N. norvegicus* seems to vary according to geographical site. Growth in crustaceans is discontinuous because it depends on the frequency and increment of exoskeleton molting (Green et al. [2014\)](#page-11-26). These two factors respond differently to environmental conditions, such as water temperature, which is a major factor influencing marine species, both in physiological and ecological aspects (Kinne [1970,](#page-11-27) Aiken and Waddy [1986\)](#page-10-26). Other factors may suppress growth, such as a high density of individuals in an area, potentially stemming from high recruitment, which, in turn, may subsequently lead to competitive interactions for resources like food and space (Parslow-Williams et al. [2001,](#page-12-29) Briggs [2002,](#page-10-27) Johnson et al. [2013\)](#page-11-17).

The proportion of berried females peaked from September to December, mostly during the autumn months (October– December). This peak occurred just after the spawning period, when females exhibited the highest GSI values (late summer), corresponding to the lowest catches recorded during the year. The GSI monthly values for females sampled between 2002 and 2003 from Rotllant et al. [\(2005\)](#page-12-23) showed a similar pattern to that of the present study, indicating the highest values of GSI in July and August, while also presenting high values in September. The reproductive cycle of *N. norvegicus* has advanced slightly, with the spawning period now beginning in early August. Variations in environmental factors, such as temperature, could directly modify growth patterns (e.g. molting periods) and reproduction periods (e.g. earlier spawning periods), and even induce migrations in some crustacean species (Company et al. [2008,](#page-10-28) Green et al. [2014,](#page-11-16) Le Bris et al. [2018\)](#page-11-28). Climate change has contributed to the decline of vulnerable lobster stocks, such as the American lobster (*Homarus americanus*), and affects community composition due to changes in sea water temperature and salinity (Henderson et al. [2011,](#page-11-29) Caputi et al. [2013\)](#page-10-29). The lower catches observed in August from the most recent landings data series (2019–2020) could be explained by an earlier spawning followed by the brooding period, in which females hide inside their burrows a month earlier than previously recorded (Rotllant et al. [2005\)](#page-12-23).

The breeding cycle of *N. norvegicus* shifts depending on latitude: in lower latitudes, it is suggested to be annual, while in higher latitudes, such as Iceland, it is biannual (Sardà [1991,](#page-12-26) Powell and Eriksson [2013\)](#page-12-30). Our results highlight the fact that *N. norvegicus* females in the Mediterranean Sea have a single yearly spawning event, with an annual and highly seasonal breeding period, as observed for other species dwelling at similar water depths (Company et al. [2003\)](#page-10-20). Specifically, the observed spawning period occurred in late summer (end of August or early September), while hatching was from December to February, as reported in other studies (Rotllant et al. [2005,](#page-12-23) Powell and Eriksson [2013\)](#page-12-30).

The size at 50% maturity estimated for females in this study is 25.3 mm CL, ∼5 mm less than the maturity size (30 mm CL) proposed by Orsi Relini et al. [\(1998\)](#page-11-21) for the same area. In other regions of the Mediterranean Sea, like GSA18 and GSA22, such a reduction has also occurred, substantially diminishing size at 50% maturity (Orsi Relini et al. [1998,](#page-11-21) Mente et al. [2009,](#page-11-24) Marković et al. [2016\)](#page-11-30). Nonetheless, most of the other regions of the Mediterranean Sea describe the size at 50% maturity of *N. norvegicus* at over 30 mm CL [\(Table](#page-8-0) [3;](#page-8-0) Orsi Relini et al. [1998\)](#page-11-21). Our results, however, are similar to those from Atlantic stocks, as average size at 50% maturity is ∼25.6 mm CL among different Atlantic areas (Orsi Relini et al. [1998,](#page-11-21) McQuaid et al. [2006\)](#page-11-31). The variation in size may be the result of differences in growth rate, which could be conditioned by many factors, including fishing pressure. For ex-ample, Marković et al. [\(2016\)](#page-11-23), suggested that overfishing was the cause of the decreased size at 50% maturity (25.7 mm CL) observed for *N. norvegicus* in the South Adriatic Sea, the same size as that found in this research. Indeed, an abrupt decline in population abundance, which may be due to overfishing, is often followed by a shift in size and age at first maturity (Galimany et al. [2015,](#page-11-1) Di Salvatore et al. [2019,](#page-11-32) Molinet et al. [2020\)](#page-12-31).

Previous assessment studies indicate that the *N. norvegicus* stock is being overexploited, recommending a reduction in fishing mortality in GSA06 as well as in other geographical subareas such as GSA09 (GFCM [2022,](#page-11-4) STECF [2023\)](#page-12-18). We therefore hypothesize that fishing pressure is depleting the

biomass stock of *N. norvegicus* in northern GSA06, with small individuals representing the main portion of the population. The biology and behavior of *N. norvegicus* may offer some resilience, but it is a species sensitive to trawl disturbance, which has resulted in a decrease in size at 50% maturity. Apparently, juveniles and berried females spend most time in their burrows, which confers a natural source of protection from bottom trawlers, thereby presenting lower mortality values (Abelló et al. [2002,](#page-12-24) Pauly [2013\)](#page-12-16). However, we suggest that the removal of large males can also affect and reduce size at 50% maturity as previously indicated for Mediterranean stocks (Orsi Relini et al. [1998,](#page-11-21) Abelló et al. [2002,](#page-12-24) Rotllant et al. [2005\)](#page-12-23).It is known that larger males are subject to great fishing pressure because they spend more time outside their burrows, which is the reason males often dominate *N. norvegicus* catches (Briggs [1995\)](#page-10-30). However, fisheries in the Catalan area are also targeting female individuals that are close to the size at 50% maturity, as well as small individuals (juveniles) that will be part of the mature stock. All this information is useful for developing new management approaches to better preserve this fishing resource.

The need for new management approaches

New management measures should be applied to minimize the impact of fishing on the *N. norvegicus* stock (Ridgway et al. [2006,](#page-12-32) Lolas and Vafidis [2021\)](#page-11-33). Here, we observed how fishing pressure may cause a reduction in the size at 50% maturity of *N. norvegicus*, while fisheries have been targeting individuals with lower sizes than the MCRS established for this resource, which is currently 20 mm CL in the Mediterranean Sea. Reducing effort in terms of decreasing the number of fishing vessels, a management strategy applied up to now, does not seem to be enough to sustainably manage the fishery. Thus, we suggest an increase in MCRS and, importantly, an improvement in trawl selectivity, which would help reduce fishing pressure (Bahamon et al. [2007,](#page-10-17) Bahamon et al. [2006\)](#page-10-31), as this may avoid fishing the immature part of the stock, leaving larger individuals to perpetuate the fishery. For example, the addition of escape rings is helping recover the exploited stocks of southern king crab *Lithodes santolla* and *L. confundens* in the southern Atlantic Ocean with an increase in the number of male individuals (no extraction of males, thus no limitation of sperm) and ovigerous females (Varisco et al. [2019,](#page-12-33) Di Salvatore et al. [2021\)](#page-11-34). In fact, the size at first sexual maturity of crustaceans should determine the MCRS (Jewett et al. [1985\)](#page-11-35), which may be reached through different approaches, e.g. establishing improved selectivity measures by increasing the currently utilized commercial 40 mm square mesh codends to reach the average retention rates of the MCRS (ICATMAR [2022\)](#page-11-17). Developing sustainable harvesting guidelines requires the precise quantification of *N. norvegicus* populations across extensive geographic regions. We suggest that this could be achieved through stock assessment methods that rely on animal sampling via fishery-dependent trawls or underwater video cameras (ICES [2016\)](#page-11-36). However, it is important to note that capture rates can be significantly influenced by burrowing behavior (Aguzzi et al. [2021\)](#page-12-5). The integration of novel tools, including ecological monitoring technologies, has the potential to enhance existing stock assessment methodologies (Aguzzi et al. [2022\)](#page-12-6). Other effective measures may include the establishment of no-take reserves, a promising useful management tool to achieve sustainable fisheries management (Sala and

Giakoumi [2018,](#page-12-34) Melaku Canu et al. [2020,](#page-11-7) Vigo et al. [2023a,](#page-13-0) [2023b\)](#page-13-1).

Acknowledgments

We greatly appreciate the assistance of the crew of the fishing vessels that participated during the samplings, along with technical staff of ICATMAR. We acknowledge the Department of Fisheries of the *Generalitat de Catalunya* for access to the Catalan fishing statistics and daily landings of each harbor and the *Secretaría General de Pesca* of the Spanish Government for the access to the VMS data. This work acknowledges the "Severo Ochoa Centre of Excellence" accreditation (CEX2019-000928-S). This work was carried out by members of the Tecnoterra Associated Research Unit of the Scientific Research Council through the Universitat Politècnica de Catalunya (SARTI-UPC) and the Institut de Ciencies del Mar-Marine Science Institute (ICM-SIC). All experimental procedures were conducted in strict accordance with good animal practice as defined by current Spanish, Catalonian, and European legislation.

Supplementary data

[Supplementary](https://academic.oup.com/icesjms/article-lookup/doi/10.1093/icesjms/fsae003#supplementary-data) data is available at *ICES Journal of Marine Science* online.

The following supplementary material is available at ICESJMS online version of the manuscript. Details and information about the current values of total annual landings (in kg), total income (in ϵ), and fishing effort off the coast of Catalonia from 2000 to 2021 are presented in Supplementary Table S1. Cohen's Kappa values of the spatial similarity matrix comparing the presence of *N. norvegicus* from 2008 to 2021 are presented in Supplementary Table S2. The bathymetry range similarity matrix with Spearman's correlation coefficients comparing LPUE from 2008 to 2021 is indicated in Supplementary Table S3.

Funding

This publication was partially funded by the projects RESNEP (CTM2017-82991-C2-1-R) and BITER (PID2020- 114732RB-C31), and the project CGCAT, financed by the Catalan Government through European Maritime and Fisheries Fund (EMFF). M.V. was supported by the FPU program of the Spanish Government (FPU18/01775).

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

Conflict of interest: The authors have no conflicts of interest to declare.

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Handling Editor: Christo Maravelias

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