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Population dynamics of brown shrimps (Crangon crangon) in the Belgian coastal waters*

1. Consumption-production-model

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Abstract.

A quantitative model, describing the most important trophic relationships of the shrimp stock (Crangon crangon) in the Belgian coastal waters is formulated. This model includes estimates of total abundance and biomass of the post-larval shrimp population, consumption of food, production of eggs and larvae, production by growth, mortality during the embryonic stage, predation-mortality due to demersal fishes and fishing mortality.

Résumé.

Un modèle quantitatif, qui décrit les plus importantes relations trophiques de la population crevettière (Crangon crangon) dans les eaux côtières belges, est formulé. Ce modèle comprend des estimations de l'abondance et de la biomasse totales de la population de crevettes post-larvaires, l'ingestion de nourriture, la production d'oeufs et de larves, la production par croissance, la mortalité durant les stades embryonaires, la mortalité due à la prédation par les poissons démersaux et la mortalité due à la pêche.

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1. Introduction.

In order to clarify some problems in the ecology of brown shrimp (Crangon crangon) a quantitative study on its trophic relationships was started in 1973. The most important results are discussed in this contribution. The objectives of this study comprise :

a. a determination of the abundance and biomass of postlarval shrimp in the Belgian coastal waters ;

b. a quantitative analysis on a yearly basis of the consumption and production by this population, including a detailed description of fishing- and predation mortality ;

c. the formulation of a quantitative consumption-production-model which describes the trophic relationships of this population.

2. Qualitative consumption-production-model.

The population of postlarval Crangon crangon in the Belgian coastal waters is considered as a "black box". This implies that the intraspecific relationships between individual organisms belonging to the same "black box" (e.g. cannibalism), are left out of consideration. Only the ecological relationships between the "black box" of brown shrimp and the other compartments of the ecosystem are subject to further investigations.

The Belgian coastal waters comprise an area with a total surface of 1150 km^2, bordered in the SE by the outermost offshore limit of the shrimps' nursery area (i.e. the 4 m isobath), in the SW and NE by respectively the Belgian-French and the Belgian-Dutch border and in the NW by a parallel to the coastline, 10 miles offshore (figure 1).

The ecological relationships of the Crangon population in this area can be summarized as follows (figure 2). Postlarval Crangon extract organic matter and energy from the ecosystem by consumption (C). The main food sources are meiobenthos (C_{me}), macrobenthos (C_{ma}), epi- and hyperbenthos (C_{eh}), hypoplankton (C_{hp}) and detritus (C_{om}) (BLEGVAD, 1915 ; HAVINGA, 1930 ; PLAGMANN, 1939 ; GERLACH, 1969). Part of the ingested matter and energy is recycled into the ecosystem as a consequence of defecation (F), respiration (R) and excretion (U) (HAGERMAN, 1970 ; SUSCHENYA, 1970). The other part is transformed into specific organic substances by metabolic activity, leading to the production (P) by the population.

Part of this production serves for growth and weight-increase of the individuals in the population (P_g) (TIEWS, 1954 ; MEIXNER, 1966, 1969a ; SCHOCKAERT, 1968 ; DECLERCK and REDANT, 1972 and others). During moulting some of the organic production is recycled into the ecosystem as exuvae (P_{ex}) (PASSANO, 1960 ; MEIXNER, 1966, 1969a). A final part of the production is used in ovogenesis (P_e) (JENSEN, 1958 ; TIEWS, 1967 ; SUSCHENYA, 1970 and others). A fraction of the eggs is lost, mainly due to mortality of ovigerous females (P_{em}) (BODDEKE and BECKER, 1976) ; the other eggs develop into planktonic larvae (WILLIAMSON, 1901 ; HAVINGA, 1930 ; PANDIAN, 1967 ; WEAR, 1974 and others).

The biomass increase (P_g) and the losses of eggs (P_{em}) are "consumed" by natural mortality (i.e. non-predatory mortality) (P_{om}) (MEIXNER, 1969a, b ; SCHLOTFELDT, 1972), fishing mortality (P_{fi}) (MISTAKIDIS, 1958 ; BODDEKE, 1970, 1972 ; SCHUMACHER and TIEWS, 1976 and others), predation mortality by Laridae (P_{la}) (KOCK, 1974) and by demersal predators (P_{dp}) (GILIS, 1952 ; TIEWS, 1965, 1975 ; BODDEKE and DAAN, 1971 and others). Finally a part of the production leaves the population by emigration (M_e).

The in- and outputs of matter and energy by immigration (M_i) and emigration (M_e) are greatly independent of the physiological consumption-production-process. Both immigration and emigration proceed in two directions : immigration during autumn from the nurserys and in early spring from the wintering areas further offshore, emigration during winter to the wintering areas and in late spring to the nurserys (HAVINGA, 1930 ; BODDEKE, 1963;

1975, 1976 ; TIEWS, 1969 and others) (a complete list of references can be found in REDANT, 1978).

3. Abundance and biomass.

3.1. Sampling methods.

The estimates of abundance (i.e. population size in number of individuals) and biomass of postlarval Crangon crangon are based on in situ investigations, which lasted from 07.1973 till 06.1976. Monthly samplings were carried out with an ottertrawl (12.2 m)headrope, 18 mm mesh size in the codend) on 10 fixed stations : 5 stations inshore along the Belgian W-coast and 5 stations offshore along the E-coast (figure 1). Additional spring- and autumn surveys on 30 sampling stations, covering the whole of the Belgian coastal waters, were performed with a beamtrawl (6 m beam length, 18 mm mesh size in the codend) (figure 1). Neither otter-, nor beamtrawl were electrified or rigged with tickler chains. Each experimental haul lasted 15 minutes. The area swept by the trawl was calculated from the towing distance and the horizontal opening of the trawl (6 m for the beam trawl, 12.4 m on average for the opening between the doors of the ottertrawl). Sampling always took place between 8 a.m. and 6 p.m.

On each station a random shrimp sample of 1500 cc was collected and preserved in a 20 % formaline solution. The laboratory analyses of the shrimp samples included counting and weighing of the total number of individuals, grading of the shrimps into 5 mm length classes (total length from tip of scaphocerite to tip of uropods), counting of the number of ovigerous females and determination of the stage of development of the abdominal eggs, using Meyer's colour scale (MEYER, 1935).

3.2. Efficiency of the sampling gear.

It is generally admitted that shrimp trawls only "catch" a fraction of the fauna present on the seafloor (REYS and SALVAT, 1971). The efficiency with which a trawl collects burrowing organisms like Crangon, largely depends upon the disturbing effect of the trawl on these organisms. This effect can be intensified by tickler chains or electrical pulses (BOONSTRA and DE GROOT, 1970 ; DE WIT, 1973). Comparative trials on shrimp trawls with 4 tickler chains and without tickler chains however showed no marked difference between the shrimp catches in both nets (DE GROOT, 1973). Similar comparative experiments with an electrified trawl on the other hand clearly demonstrated that such a trawl catches on average 2.00 times more shrimp than a normal trawl. This proportion was the same for all size groups of shrimp (BOONSTRA and DE GROOT, 1970, 1974 ; VAN DEN BROUCKE, 1973). From these data we concluded that the standard shrimp trawl used during our investigations collected maximally 50 % of the shrimps present in or on the seabed.

The efficiency with which a trawl retains the collected shrimps mainly depends upon the mesh size of the gear (i.e. the selectivity of the trawl). The codend as well as the large-meshed anterior part of the net contribute to its selectivity (BOHL and KOURA, 1962 ; BOHL, 1963). Comparative trials with a completely small meshed trawl and a normal shrimp trawl showed that the former one catches 1.27 times more undersized shrimp (smaller than 50 mm) and 1.11 times more commercial shrimp (larger than 50 mm) (BOHL, 1963). These proportions give an idea about the influence of selectivity in the anterior part of the net on the composition of the catches.

In order to evaluate the influence of selectivity in the codend we used a hypothetical selectivity curve (figure 3) with a 100 % retention value for shrimps of 60 mm and over (BOHL and KOURA, 1962). Combination of the correction factors for the selectivity in the large-meshed anterior part of the trawl and the reciprocals of the retention-values for the codend leads to overall correction factors for the influence of selectivity or "retaining efficiency" for each size group of shrimp (table 1). Combination of these values with the overall correction factors for the "collecting efficiency" of the trawl (see first paragraph of this section) results in gross correction factors for the sampling efficiency of the trawl (table 1).

3.3. Estimates of abundance and biomass.

The samplings and analyses of the postlarval shrimp population produced values for its abundance and biomass observed on each sampling station and for each sampling month. Next, these values were corrected for the sampling efficiency of the trawl and for the loss of weight due to formaline preservation, resulting in estimates of the real abundance and biomass of the population on each station and in each month. The yearly average abundance and biomass of shrimp on each station was derived from these data, taking into account the different time-intervals between succesive samplings. From this set of yearly averages per station (10 sampling stations) and per year (3 years of investigations) were calculated the final estimates of average abundance and biomass of postlarval shrimp in the coastal area as a whole.

The average abundance of postlarval Crangon in the Belgian coastal waters was estimated at 7.11 ± 3.78 individuals/m^2. From these 0.20 ± 0.13 were larger than 50 mm total length. The average biomass of the population was 1830 ± 1088 mg wet weight/m^2 or 106 ± 63 mg-C/m^2 (figure 4).

4. Consumption.

4.1. Daily food uptake.

The daily food uptake of the population was computed from

(1) the results of aquarium experiments on the cumulative food uptake and the growth of Crangon (MEIXNER, 1966, 1969a),

(2) the relation between total length and weight of Crangon,

(3) the estimated length distribution of the individuals in the population and

(4) the sex ratio of the various length classes (BODDEKE, 1962 ; TIEWS, 1967).

The total amount of food ingested by male or female shrimp to grow from length L_o (i.e. 10.5 mm) to length L_2, or consumption C_{o-2}, for a number of discrete lengths L_2 (20, 30, 40, 50 and 55 mm), were derived from Meixner's original cumulative food uptake curves, obtained from aquarium experiments (MEIXNER, 1966). The quantities of food ingested to grow from length L_1 to length L_2 or specific consumption C_{1-2} for each growth interval L_{1-2}, were deduced from the C_{o-2} values (table 2). Next, the ages A_1 at length L_1 and A_2 at length L_2 for males and females were derived from Meixner's growth curves of Crangon under similar aquarium conditions (MEIXNER, 1969a).

The difference $dA = A_2 - A_1$ is the number of days male or female shrimp need to grow from L_1 to L_2 (table 2). The quotient C_{1-2}/dA gives the daily food uptake per individual shrimp, $C_{d,I}$, expressed in units weight/day. The average weight $\bar{W}$ of the individuals in each growth interval or size class L_{1-2} was calculated from the biometric relation between length (L) and live weight (W) of Crangon. The regression between these parameters is expressed by

$$W = 3.212 \, . \, 10^{-6} \, L^{3.178}$$

(r = 0.999)

(number of observations n = 1200)

The quotient $C_{d,I}/\bar{W}$ is the daily food uptake of each sex and size class, expressed in units weight/day/unit weight of Crangon, $C_{d,W}$ (table 2). Finally, the average daily food uptake of the population as a whole, $C_{d,P}$, was calculated, taking into account the relative importance of each size class in the population and under different assumptions on the sex ratio of the various length classes, related to the eventual occurrence of a sex change in male *Crangon*. The resulting values of the daily food uptake showed no marked difference, whatever assumption was made on the sex ratio, and amounted 0.032 mg C/day/mg C *Crangon*.

4.2. Estimate of consumption.

The mean yearly consumption (C) by the population, computed as the product of the daily food uptake multiplied by the mean biomass and by 365, is 1238 ± 736 mg C/m^2 (figure 4).

Since no quantitative data on the food composition of *Crangon* were available, any detailed estimate of the fluxes connecting the shrimp black box with the other benthic compartments of the ecosystem was excluded. Live preys seem to be more attractive to *Crangon* than dead organic matter (DAHM, 1975), indicating that detritus is not the major food component for shrimp. From the living food sources macrobenthic, epi- and hyperbenthic and hypoplanktonic organisms are probably the most important. Meiobenthos indeed is considered as a complementary food source for shrimp (GERLACH, 1969).

5. Production.

5.1. Production by growth.

The gross growth-efficiency or Ivlev's K_1 (SUSCHENYA, 1970 ; WINBERG, 1970) was calculated in analogy to the daily food uptake. The average gross growth-efficiency of postlarval *Crangon* is 51.2 %. It is difficult to compare this value with bibliographic data because most of them refer to pelagic organisms (KINNE; 1970 ; SUSCHENYA, 1970). In comparison to the few benthic organisms for which K_1-values are known, the gross growth-efficiency of *Crangon* is fairly high. The reason for this can be found in the kind of food, namely *Artemia*, used during Meixner's aquarium experiments (MEIXNER, 1966, 1969a). Indeed, *Artemia* is very rich in protein and energy (SLOBODKIN and RICHMAN, 1961). As a consequence it is likely that the shrimp's gross growth-efficiency will be lower in vivo than under aquarium conditions and that the in vivo consumption by the population, needed to obtain a same production by growth, will be higher than the one estimated (see previous section).

The production by growth (Pg) was computed from the consumption of the population and the average gross growth-efficiency and was 633 ± 376 mg C/m^2/year. The production of exuvae (P_{ex}) was not estimated because data on the weight or carbon content of the exuvae were not available (figure 4).

The turn-over (production by growth/biomass) of the population of postlarval *Crangon* is 6.0/year. Turn-over values for benthic species, as far as they are known, vary between 0.5 and 20.0/year (VOROBEV, 1949 and SHORYGIN, 1952 in WINBERG, 1970). The turn-over of *Crangon* seems to be in good agreement with these findings.

5.2. Production of eggs.

The egg-production was calculated from

(1) the mean density of fertile females in the population,

(2) the mean number of eggs per oviposition (HAVINGA, 1930 ; MEYER, 1937 ; JENSEN, 1958),

(3) the mean number of ovipositions per female per year (HAVINGA, 1930 ; TIEWS, 1954) and

(4) the chemical composition of eggs (PANDIAN, 1967).

The yearly egg-production (P_e) averages 2015 eggs/m^2 or 6.7 ± 4.2 mg C/m^2 (figure 4).

The total number of larvae produced per year (P_{el}) was computed in analogy to the total egg-production. In this case however the calculations started from the mean density of ovigerous females with well-developed abdominal eggs (dark-blue or black coloured eggs). The production of larvae was estimated at 560 larvae/m^2/year with an initial egg-weight of 1.9 mg C/m^2/year (figure 4). Thus only 27.8 % of the eggs produced yearly develop into planktonic larvae while 72.2 % are lost during the embryonic phase (P_{em}).

5.3. Total production.

The total production by the population, excluding the production of exuvae, amounts to 640 ± 376 mg C/m^2/year ($P_g + P_e$). From this 1.9 mg C/m^2/year ends up, as larvae, in the plankton. The remaining part, 638 ± 376 mg C/m^2/year, is available for emigration (M_e), natural mortality (P_{om}), fishery (P_{fi}), predation by demersal predators (P_{dp}) and by the *Laridae* (P_{la}) (figure 4).

6. Mortality.

The production of the *Crangon* population is "consumed" by higher trophic levels (demersal predators, man, *Laridae*) or is returned into the ecosystem by natural, non-predatory mortality. The investigations concentrated on fishing- and predation mortality because these could be expected to be the main mortality causes of postlarval shrimp. Moreover our knowledge on natural mortality of shrimp (e.g. due to disease, moulting or pollution) is rather scarce, making any reliable estimation of these mortality factors impossible.

6.1. Predation mortality.

The ichthyofauna of the coastal area comprises about 60 fish species. These were classified according to their abundance in the coastal waters and to their food preference for postlarval shrimp.

Quantitative research of predation mortality focused on the most important predators : *Odontogadus merlangus*, *Trisopterus luscus*, *Gadus morhua*, *Ciliata mustela*, *Pomatoschistus species*, *Trigla species*, *Agonus cataphractus* and *Liparis liparis*.

Predation mortality of postlarval *Crangon* was computed from
(1) the average yearly abundance and biomass of the predators,
(2) the results of quantitative stomach analyses on these predators and
(3) bibliographic data on digestion time and daily food uptake of fishes.

These investigations are discussed in C.M.1980/K:33.

Total predation mortality, *expressed in numbers* of *Crangon* amounts to 14.12 ± 5.66 *Crangon*/m^2/year. This value should be considered as a minimal estimate of the real yearly predation mortality since only the eight most important vertebrate and none of the invertebrate predators (e.g. *Macropipus*) were taken into account. The greatest mortality is caused by *Pomatoschistus*, followed by *Odontogadus*, *Trisopterus*, *Trigla*, *Agonus*, *Liparis*, *Gadus* and *Ciliata* (table 3).

Total predation mortality, *expressed in weight units* of *Crangon* (P_{dp}) is minimally 126 ± 40 and maximally 789 ± 236 mg C/m^2/year (figure 4). *Odontogadus* is the most important predator, followed by *Trisopterus*, *Trigla*, *Gadus*, *Liparis*, *Pomatoschistus*, *Agonus* and *Ciliata* (table 3).

6.2. Fishing mortality.

Fishing mortality was deduced from national landing statistics. During the period 07.1973 - 06.1976 yearly 1702 ± 455 tons of cooked shrimp, corresponding to 1975 ± 527 tons live weight, were landed in Belgian harbours. Fishing mortality then is 1.14 ± 0.30 individuals/m^2/year or 100 ± 27 mg C/m^2/year (P_{fi}) (figure 4), assuming that the complete catch originates from the area defined as "Belgian coastal waters" (see section 2).

A comparison of these data with the yearly production of larvae (560 Larvae/m^2) shows that only 0.20 % of the larvae grow into shrimp of commercial size (larger than 50 mm). This proportion is in good agreement with the findings for the Dutch shrimp stock, where 0.17 % of the larvae reach a commercial size (BODDEKE and BECKER, 1976).

Predation mortality of postlarval Crangon is on average 12.4 times greater than fishing mortality (both expressed in numbers of Crangon). This relation is clearly higher than in the German Bight where the ratio predation/fishing mortality was found to vary between 1.7 and 12.9 (TIEWS, 1965). It should however be noted that predation mortality of shrimp in the German Bight is to some extent underestimated, due to the lack of data on predation during winter (ICES, 1979). The real magnitude of predation mortality in the German waters and consequently also the ratio predation/fishing mortality, are higher than the estimates which have been published (TIEWS, 1965, 1975). The difference between the values of this ratio for the shrimp populations in the Belgian and German waters gets smaller when this underestimation is taken into account.

Fishing activities also cause casualties among juvenile, undersized shrimp. Analyses showed that the unsorted catches of Belgian shrimp vessels consist for 70.7 % of undersized shrimp. Maximally 25 % of them do not survive the manipulation of the catch (MISTAKIDIS, 1958), mainly as a consequence of desiccation (ICES, 1979). The resulting "indirect" fishing mortality was estimated at 0.69 ± 0.18 Crangon/m^2/year or 19 ± 5 mg C/m^2/year. Part of the discarded, undersized shrimp, alive or dead, are eaten by Laridae. The importance of this output still remains unknown. The others sink or swimm to the bottom. Indications were found that demersal fishes may feed on dead, discarded shrimps. A certain degree of overlapping between predation mortality and "indirect" fishing mortality may thus not be excluded.

7. Quantitative model.

The estimates of biomass, consumption, production by growth, production of eggs and larvae, fishing- and predation mortality were assembled into a quantitative consumption-production-model of the Crangon population (figure 4). The carbon fluxes for respiration, excretion, defecation, production of exuvae, natural mortality, predation by Laridae and migration still remain unestimated. Most of them refer to physiological processes of Crangon, upon which our knowledge is ultimately scarce.

The sum of predation - and fishing mortality (minimally 226 ± 48 and maximally 889 ± 238 mg C/m^2/year) is in good agreement with the estimate of the part of the production which is available for higher trophic levels or for natural mortality (638 ± 376 mg C/m^2/year). This proves that at least the estimates of the production of the population are reliable.

The results of this study confirm the concurrential relationship between predation and shrimp fishery and the vulnerable situation of the latter. They also indicate that regulatory measures for the shrimp fishery should be considered with criticism. Indeed, the eventual positive effects of such measures may easily be annihilated by predation.

From the larvae which are produced yearly by Crangon only 2.7 % on average end up in the stomachs of predators or in the commercial catches. Mortality during the larval and early postlarval stages may be of major importance. This mortality may be caused by pelagic carnivores as well as by lethal physico-chemical conditions. These findings indicate that the yearly fluctuations in the catches of commercial shrimp should be attributed mainly to fluctuations in broodsize and in survival of the larvae.

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Table 1 - Estimates of the correction factors for the sampling efficiency of the trawl for postlarval Crangon crangon.

Length class - mm -	a	b	c	d	e
11-15	2.00	1.27	200.00	254.00	508.00
16-20	2.00	1.27	200.00	254.00	508.00
21-25	2.00	1.27	66.67	84.67	169.34
26-30	2.00	1.27	16.67	21.17	42.34
31-35	2.00	1.27	6.25	7.94	15.88
36-40	2.00	1.27	2.63	3.34	6.68
41-45	2.00	1.27	1.49	1.89	3.78
46-50	2.00	1.27	1.18	1.50	3.00
51-55	2.00	1.11	1.06	1.18	2.36
56-60	2.00	1.11	1.02	1.13	2.26
61-65	2.00	1.11	1.00	1.11	2.22
66-70	2.00	1.11	1.00	1.11	2.22
71-75	2.00	1.11	1.00	1.11	2.22
76-80	2.00	1.11	1.00	1.11	2.22
81-85	2.00	1.11	1.00	1.11	2.22

a : correction factors for the "collecting efficiency" of the trawl
b : correction factors for the selectivity in the large-meshed anterior part of the net
c : correction factors for the selectivity in the small-meshed codend
d : correction factors for the selectivity of the trawl (d = b.c)
e : gross correction factors for the sampling efficiency of the trawl (e = a.d)

Table 2 - Daily food uptake of postlarval Crangon crangon.

L_0	L_1	L_2	C_{0-2}	C_{1-2}	A_1	A_2	dA	$C_{d,I}$	$\bar{W}$	$C_{d,W}$	$C_{d,p}$
mm	mm	mm	mg dw	mg dw	days	days	days	mg dw/day/ individual	g ww	mg dw/day/g dw	mgC/day/mg C
						Females					
10.5	10.5	20.0	19.4	19.4	18	110	92	0.21	0.02	36.36	0.032
	20.5	30.0	106.9	87.5	110	168	58	1.51	0.10	52.02	
	30.5	40.0	223.8	116.9	168	200	32	3.65	0.27	46.66	
	40.5	50.0	378.4	154.6	200	245	45	3.44	0.59	20.08	
	50.5	55.0	600.7	222.3	245	289	44	5.05	0.96	18.15	
						Males					
10.5	10.5	20.0	21.2	21.2	18	118	100	0.21	0.02	36.55	
	20.5	30.0	130.9	109.7	118	175	57	1.92	0.10	66.36	
	30.5	40.0	252.4	121.5	175	212	37	3.28	0.27	41.94	
	40.5	50.0	447.1	194.7	212	278	66	2.95	0.59	17.24	
	50.5	55.0	770.5	323.4	278	352	74	4.37	0.96	15.70	

ww : wet weight
dw : dry weight

explanation of symbols : see section 4.1

Table 3 - Predation mortality of postlarval Crangon crangon caused by demersal fishes.

Predator species	n/m^2/year	mg C/m^2/year	
		minimum	maximum
Odontogadus merlangus	1.48 ± 1.20	84.2 ± 36.5	421.1 ± 182.6
Trisopterus luscus	0.89 ± 0.40	24.4 ± 14.8	244.2 ± 148.3
Gadus morhua	0.06 ± 0.02	7.6 ± 2.0	38.0 ± 10.0
Ciliata mustela	0.03 ± 0.02	0.2 ± 0.1	2.2 ± 1.0
Pomatoschistus species	10.86 ± 5.51	2.1 ± 1.1	4.2 ± 2.2
Trigla species	0.41 ± 0.23	6.5 ± 1.1	64.9 ± 11.0
Agonus cataphractus	0.25 ± 0.19	0.5 ± 0.3	4.8 ± 2.6
Liparis liparis	0.14 ± 0.08	1.0 ± 0.8	9.9 ± 7.7
Total	14.12 ± 5.66	126.5 ± 39.5	789.3 ± 235.9

all figures refer to the period 07.1973-06.1976

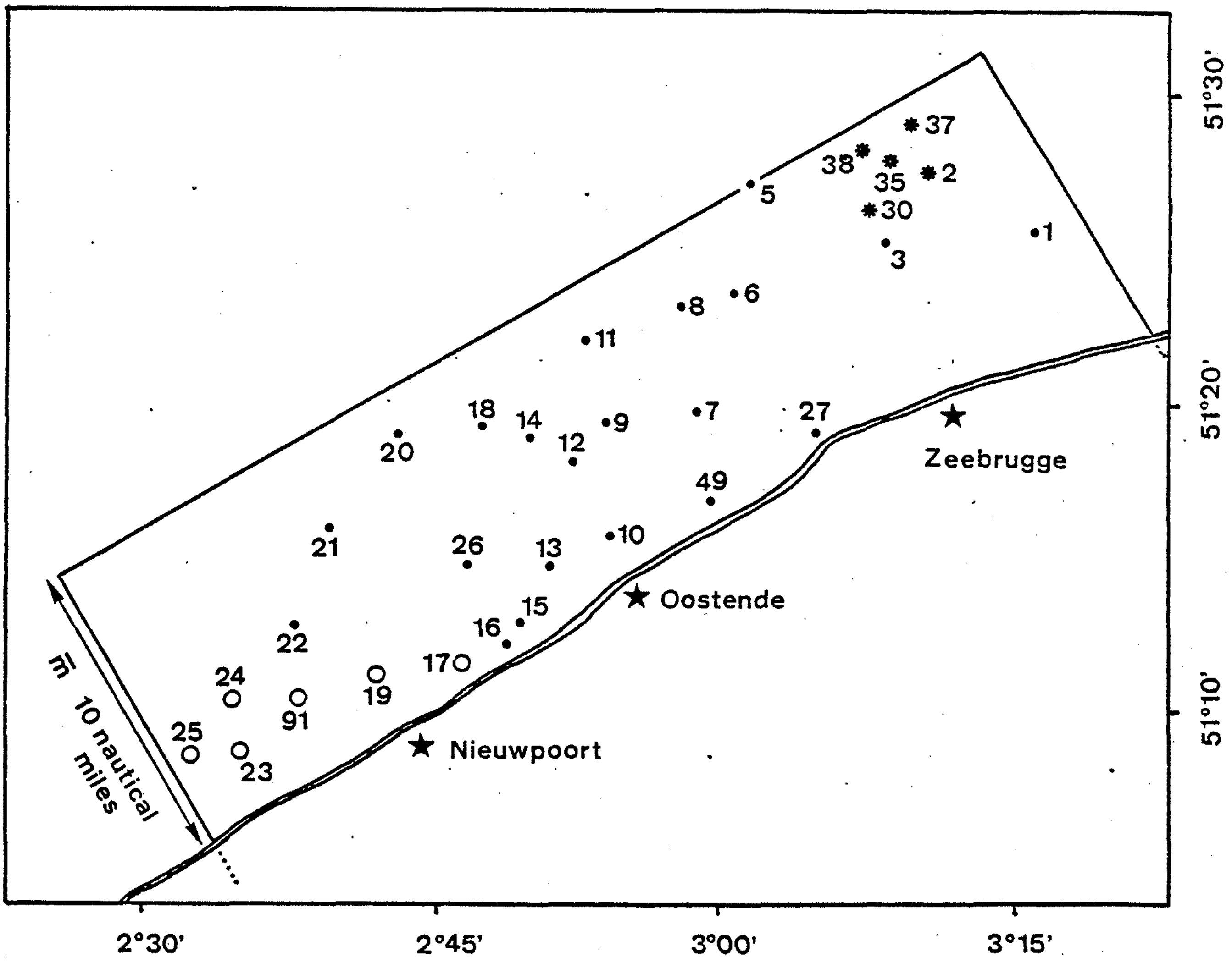

Figure 1 - Positions of the sampling stations in the Belgian coastal waters :

○ W-coast inshore, monthly samplings,
✱ E-coast offshore, monthly samplings,
• spring- and autumn surveys.

The boundaries of the area defined as "Belgian coastal waters" are also indicated in this figure.

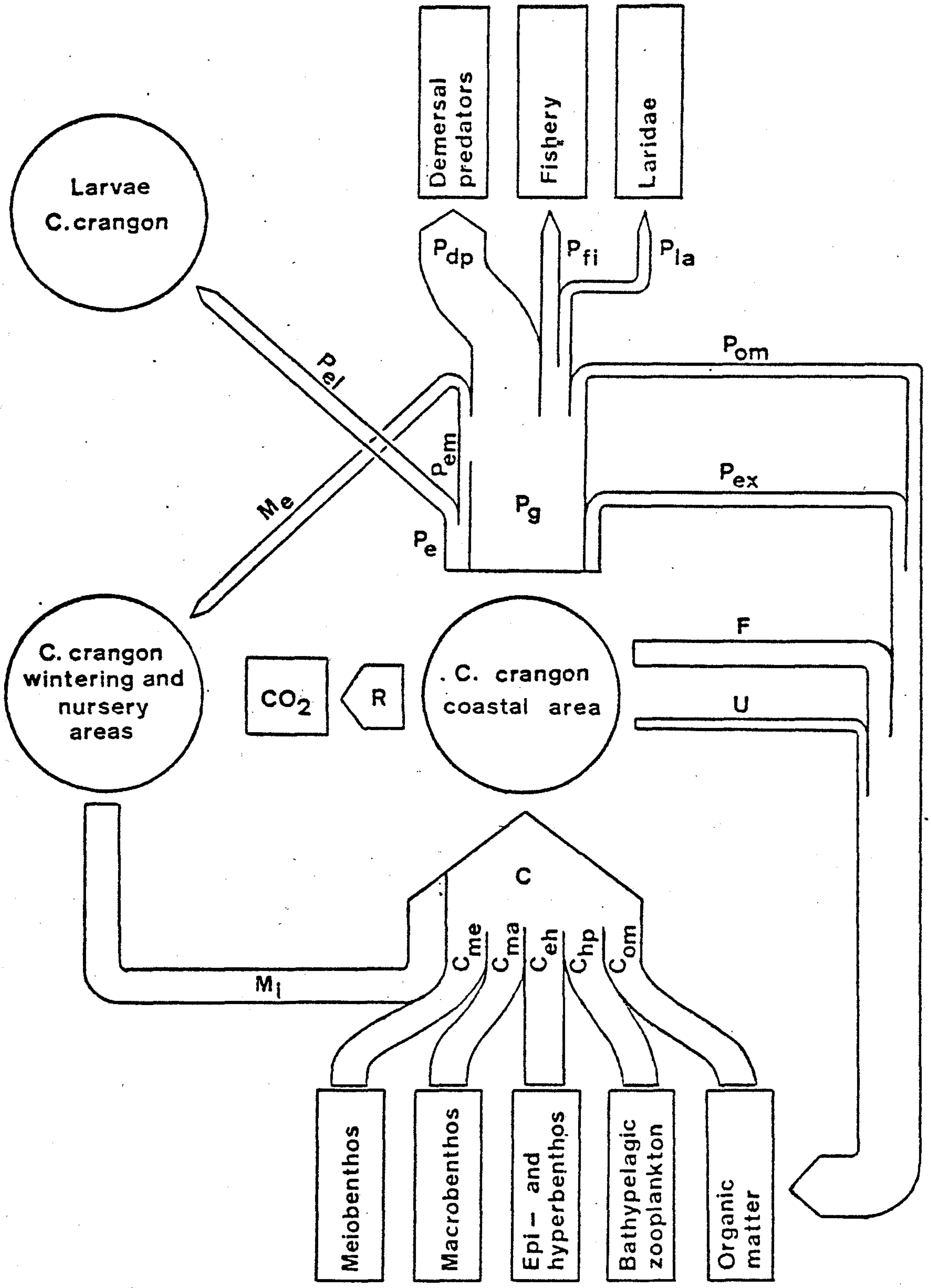

Figure 2 - Review of the fluxes connecting the population of postlarval brown shrimp with the other compartments of the ecosystem. Explanation of symbols cfr. par. 2.

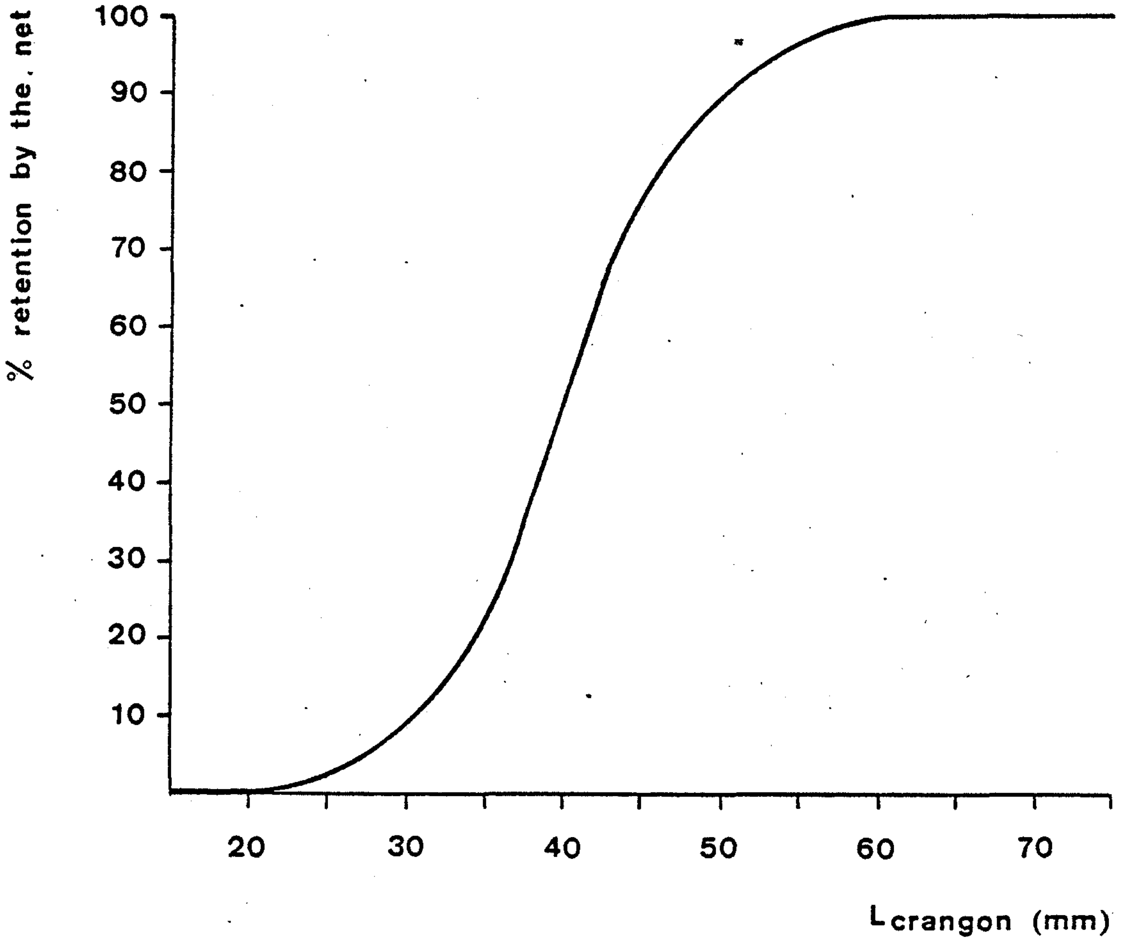

Figure 3 - Hypothetical selectivity curve of the 18 mm trawl codend for postlarval brown shrimp.

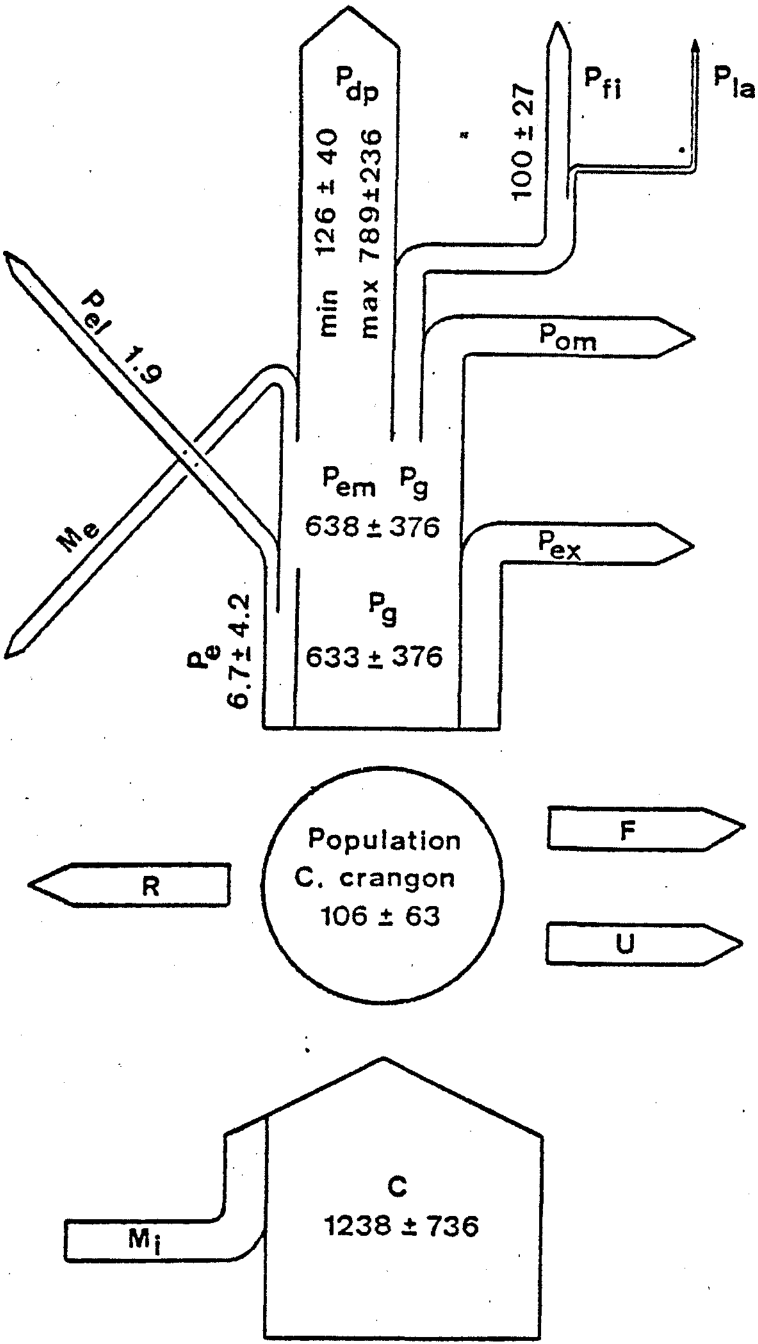

Figure 4 - Quantitative consumption-production model of the population of postlarval brown shrimp in the Belgian coastal waters.

Biomass in mg C/m^2, fluxes in mg C/m^2/year. All figures refer to the period 07.1973-06.1976.

Explanation of symbols cfr. par. 2.