united nations
educational, scientific
and cultural
organization

international atomic
energy agency

the
abdus salam
international centre for theoretical physics

SMR/1108 - 11

COURSE ON
"MEDITERRANEAN SEA(S) CIRCULATION & ECOSYSTEM FUNCTIONING"
2 - 20 November 1998

Trieste, Italy

"Causes of Increase in a Jellyfish Population"

T. LEGOVIĆ
R. Bošković Institute
Zagreb, Croatia

Please note: These are preliminary notes intended for internal distribution only.

strada costiera 11 - 34014

ne
nt.
nd
of
's
d
s

Elsevier Science Publishers B.V., Amsterdam – Printed in The Netherlands

A RECENT INCREASE IN JELLYFISH POPULATIONS: A PREDATOR–PREY MODEL AND ITS IMPLICATIONS

TARZAN LEGOVIĆ

Center for Marine Research, 'Rudjer Bošković' Institute, 41001 Zagreb (Yugoslavia)

(Accepted 2 October 1986)

ABSTRACT

Legović, T., 1987. A recent increase in jellyfish populations: a predator–prey model and its implications. *Ecol. Modelling*, 38: 243–256.

Factors that might have caused a recent increase of jellyfish populations in the Mediterranean sea are investigated using a simple predator–prey model. Higher nutrient inflow causes an increase in the steady state of a jellyfish population and no change in the steady state of jellyfish prey. Qualitatively the same change is obtained if the population of predators competing for jellyfish prey is decreased. A decrease of predators on the jellyfish population causes an increase in jellyfish prey. Sufficiently high nutrient enrichment, or a decrease in jellyfish competitors or predators, may cause the appearance of a stable limit cycle, i.e., asymptotically periodic fluctuations of both the jellyfish population and its prey. If persistent periodic fluctuations of jellyfish and their prey are a natural phenomenon, then the above ecological changes will increase the amplitude of the periodic fluctuations.

INTRODUCTION

Since 1977 it has been observed that populations of jellyfish *Pelagia noctiluca* (Forskål) have increased considerably in the Adriatic Sea (Malej, 1980) and the whole of the Northern Mediterranean. The phenomenon has aroused much interest in the Mediterranean countries because of its negative effects on tourism and fisheries.

The following three hypotheses have been put forth to account for the observed massive appearance of jellyfish:

(1) Nutrient enrichment induces growth of jellyfish population since the jellyfish are able to indirectly utilize the nutrient pool (Wilkerson and Dugdale, 1983)

(2) An unusually strong entrance (ingression) of Mediterranean waters brings to and maintains in the Adriatic Sea a higher population (Vučetić, 1983). Field measurements have shown that indeed during the recent ingres-

0304-3800/87/$03.50

sion jellyfish appeared in masses. However, during most of the earlier recorded ingressions, jellyfish have not been observed.

(3) In laboratory experiments it has been found that the swimming ability of young jellyfish (ephyrae) of species *Pelagia noctiluca* ceases around 8° C. If temperature is further decreased, then after a subsequent rise in temperature, the swimming ability cannot be restored (Rottini-Sandrini, 1982) and ephyrae die.

The hypothesis put forth by Stravisi (1983) is that the minimum temperature of the sea water has been sufficiently high during recent years to allow ephyrae to survive through the winter in the North Adriatic Sea. A larger starting population in spring then produces a larger population during early summer. Indeed, a positive correlation between population of jellyfish and winter sea water temperature has been found. Furthermore, there exists a significant positive correlation between winter sea water temperature and frequency of blowing of Jugo, a warm south wind. This hypothesis as well as the second one suggested a favourable climatic condition to be, if not the complete cause, then at least the triggering factor. However, they consider only the massive appearance of jellyfish in the Adriatic Sea and not in the rest of the Mediterranean.

In addition to the above, the effect of the change in abundance of jellyfish competitors and jellyfish predators (Legović et al., 1987) will be investigated. First, a simple predator–prey model is introduced and its steady state and dynamic properties are summarized. Then the effects of possible ecological changes are investigated. Finally, an example is given and analyzed with the help of computer simulations.

A MODEL OF JELLYFISH POPULATION AND ITS PREY

It is known that jellyfish consume mainly zooplankton and fish eggs. Malej (1982) has found the diet of jellyfish *Pelagia noctiluca* includes Appendicularia, *Noctiluca scintilans*, Hydromedusae, Siphonophora, *Penilia avirostris, Evadne*, Copepoda, *Doliolum, Clupea* eggs and *Engraulis eucrasicholus* (anchovy) eggs. In turn, jellyfish are preyed upon by predators such as mackerel, sea turtle (A. Benović, Institute of Biology, Dubrovnik, Yugoslavia, personal communication, 1985), bogue, black bream and saddle bream (Axiak, 1983), and tuna (Vučetić, 1985).

In what follows we shall assume the jellyfish have a logistically growing prey. This assumption is not as restrictive as it may look at first sight, since similar qualitative dynamics would be observed if some other form of prey growth is assumed. In addition, it will be assumed that the feeding behaviour of jellyfish conforms to the Michaelis–Menten function. This form has been used to represent uptake of nutrients by phytoplankton (Dugdale and MacIsaacs, 1971) and feeding of herbivorous and carnivorous zooplankton (Canale et al., 1976). However, it has been found (Reeve et al., 1978) that ingestion by ctenophores may be linearly related to prey density in a fairly large range. At high densities, found in some copepod aggregations, the experiments have shown that the ingestion rate of ctenophores begins to deviate from the linear dependence. The Michaelis–Menten function with a high half-saturation constant easily represents feeding at both small concentrations, where almost linear dependence is obtained, and at high concentrations where a clear deviation from linear dependence has been noted.

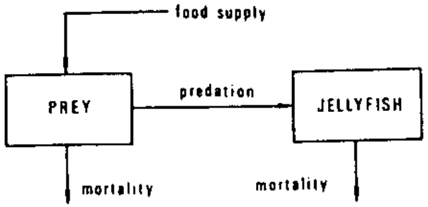

Fig. 1. Diagram of biomass flux in the jellyfish–prey model.

Using a diagram where arrows indicate material flow and boxes denote populations (in terms of numbers of organisms or biomass density), the prey and jellyfish populations may be represented as in Fig. 1. The unit in which biomass density will be expressed is mg m^{-3}. One may rightly argue that there is a cycle of matter which is being closed by decomposition of jellyfish by-products that become available to phytoplankton and finally to jellyfish prey. While this is true, it certainly has a very small or negligible effect on the budget of jellyfish prey.

Balance equations for the prey and jellyfish population are:

— prey:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \left(r(1 - P/K) - c - vM/(k_s + P)\right)P \tag{1}$$

— jellyfish:

$$\frac{\mathrm{d}M}{\mathrm{d}t} = \left(avP/(k_s + P) - b\right)M \tag{2}$$

where P is biomass density of prey (mg C m^{-3}), M biomass density of jellyfish (mg C m^{-3}), r intrinsic growth rate of prey (day^{-1}), K carrying capacity for the prey population (mg m^{-3}), c specific mortality rate by other predators and other factors (day^{-1}), v maximum specific predation rate of jellyfish (day^{-1}), k_s half-saturation constant (mg C m^{-3}), a conversion of prey biomass into jellyfish biomass (unitless), and b specific mortality rate of jellyfish (day^{-1}). By definition, all the parameters are non-negative.

When a jellyfish population is not present, the prey population exhibits the usual logistic growth. The reason for including two predatory terms in equation (1) is that prey is consumed by jellyfish and another group of predators such as carnivorous zooplankton and fish. In addition, by explicitly including parameter c, we will later be able to investigate the effect of a change of c on both the prey and the jellyfish.

The above model is a variant of a class of predator–prey models for which a nominal behaviour is well known; hence, the main results will be summarized briefly and attention will be focused on how an ecological change can modify the nominal behaviour.

From equations (1) and (2) the three steady states are:

(1) Total extinction:

$$P^{(t)} = 0; \qquad M^{(t)} = 0$$

(2) Jellyfish extinction:

$$P^{(e)} = K(1 - c/r); \qquad M^{(e)} = 0$$

In order that $P^{(e)} > 0$, the restriction on c is:

$$c < r \tag{3}$$

(3) Nonextinction state $(P^{(n)}, M^{(n)})$:

$$P^{(n)} = dk_s/(v - d) \tag{4}$$

where $d = b/a$, and:

$$M^{(n)} = \big(r(1 - P^{(n)}/K) - c\big)\big(k_s + P^{(n)}\big)/v \tag{5}$$

In order that $P^{(n)} > 0$ and $M^{(n)} > 0$, the condition on v is:

$$v > d(1 + rk_s/K(r - c)) \tag{6}$$

which means:

$$P^{(e)} > P^{(n)} \tag{7}$$

The ecological intepretation of the conditions (3) and (7) is obvious.

Stability in the neighborhood of each steady state (local stability) is readily analyzed by linearizing equations (1) and (2) around each steady state. One finds that $(P^{(t)}, M^{(t)})$ is an unstable saddle point. In the P, M coordinate system, the two axes are the separatrices. Along the P axis the solution is going out from, and along the M axis it is approaching $(P^{(t)}, M^{(t)})$. Similarly, $(P^{(e)}, M^{(e)})$ behaves as a saddle point in its neighborhood. The first separatrix is the P axis. The second separatrix has a negative slope in the vicinity of the steady state and is directed into the positive quadrant (see Svirezhev and Logofet, 1983).

The stability in the neighborhood of $(P^{(n)}, M^{(n)})$ is determined from the roots of the following characteristic equation:

$$\begin{vmatrix} \alpha - \lambda & -d \\ \beta & -\lambda \end{vmatrix} = 0 \tag{8}$$

where

$$\alpha = r(1 - 2P^{(n)}/K) - c - x \tag{9}$$

$$\beta = ax \tag{10}$$

$$x = (v - d)\big(r(1 - P^{(n)}/K) - c\big)/v \tag{11}$$

From conditions (6) and (7) it follows that $\beta > 0$.

The necessary and sufficient condition for local stability of $(P^{(n)}, M^{(n)})$ is that:

$$\alpha < 0 \tag{12}$$

If in addition to (12):

$$\gamma = \alpha^2 - 4; \qquad d > 0 \tag{13}$$

then $(P^{(n)}, M^{(n)})$ is a stable node. In case $\gamma < 0$ and $\alpha < 0$, then the steady state is a stable focus. Whenever the steady state is locally stable, it is also globally stable with regard to perturbations in initial conditions, since the solutions are bounded and both P and M axes are separatrices to the other unstable saddles.

Finally, in case condition (12) does not hold, the limit cycle is formed around $(P^{(n)}, M^{(n)})$. This follows directly from the Kolmogorov theorem. The limit cycle is orbitally stable (i.e. it is stable from the outside and inside).

EFFECT OF A CHANGE IN ECOLOGICAL FACTORS

A change in an ecological factor may be a consequence of either an anthropogenic or natural action. From the class of anthropogenic changes, we shall analyze the effects arising from nutrient enrichment (an increase in carrying capacity, K), a decrease in predator populations that feed on jellyfish prey (a decrease in specific mortality rate, c) and a decrease in predator populations that feed on medusae (a decrease in specific mortality of jellyfish, b). Among natural fluctuations, only the effects of variation in temperature will be presented since it most directly determines the feeding ability of medusae and thus changes the maximum specific predation rate, v.

Nutrient enrichment

An increase of food supply to prey results in an increase of carrying capacity K. From expressions (3) and (4) it follows that the non-extinction steady-state concentration of the prey will not change, while the steady-state concentration of jellyfish will increase along a hyperbola with the asymptote at $M_a = (t - c)P^{(n)}/d$.

When carrying capacity increases, α increases as well, so that finally for $K > rP^{(n)}(1 + v/d)/(r - c)$ the non-extinction steady state becomes unstable and a limit cycle appears around it. Further increase in food supply to prey increases the amplitude of fluctuations of both prey and jellyfish population. If we adopt the practical stability concept (Brauer and Soudack, 1978), we may say that sufficiently large K practically destabilizes the prey–jellyfish system since there exists a time instant $t_1 > t_0$ at which $P(t_1) < \epsilon_1$ or $M(t_2) < \epsilon_2$, where ϵ_1 and ϵ_2 are small constants.

A decrease of jellyfish competitors. Jellyfish competitors are the species which consume the same prey as medusae do. Common competitors are other carnivorous zooplankton and fishes. If the fishing of these species is increased, their standing stock decreases and consequently more prey is available to jellyfish. In the model this will be reflected as a decrease in parameter c.

A decrease in the specific mortality, c, will not cause a change in the steady state of prey population. It will, however, linearly increase jellyfish population. The coefficient of linear increase is $k_s/(v - d)$.

As long as $\alpha < 0$ this means that $c > r - (r + v/d)P^{(e)}/k = c_{cr}$. If $c_{cr} > 0$, then as c decreases below c_{cr} the limit cycle appears. In case c_{cr} is negative, $(P^{(n)}, M^{(n)})$ remains stable even if competitors vanish.

A decrease in predators on jellyfish population. The most important jellyfish predators are mackerel, bogue and saddle bream. All the predators feed on oral arms of the jellyfish; the jellyfish without oral arms dies. An increase in commercial fishery on these species causes their standing stock to decrease. Indeed, the only reason for not increasing the fishing effort in an area further is that populations of these fish have already been reduced to an uneconomical level.

A reduction of predator populations causes an increase in the steady state of jellyfish population and a decrease in the prey populations.

When $\alpha < 0$, then $d > v(K(r - c) - rk_s)/(rk_s + K(r - c) = d_{cr}$. As d decreases, the steady state point is being destabilized so that for $d < d_{cr}$ a limit cycle is formed around $(P^{(n)}, M^{(n)})$. If d decreases further, the limit cycle enlarges, and hence higher amplitudes of population fluctuations are expected.

A change in maximum specific predation of jellyfish. When sea water temperature rises from suboptimal toward optimal conditions, at least two processes consequently change: maximum specific predation by jellyfish is increased, and their mortality is decreased. However, above a temperature of 10 °C, specific mortality does not change much, while maximum specific predation rises until optimal temperature, which is in the range of 17–19 °C, is reached. Above this temperature, the maximum specific predation decreases (Rottini-Sandrini et al., 1987) and mortality probably increases.

When v increases from low values, the steady-state population of prey, $P^{(n)}$, decreases along the hyperbola with asymptotes $v_a = d(1 + rk_s/K(r - c))$ and $P^{(n)} = 0$. When $v = v_a$ the stable steady-state of jellyfish population is the extinction state. Above the value of v_a, the steady state of the jellyfish population increases until a maximum is reached: $M^{(n)} = K(r - c)/4rd$ at the value of $v_{opt} = d(1 + 2rk_s/K(r - c))$. The corresponding steady-state prey population is $P_{opt} = P^{(e)}/2$. Beyond v_{opt}, steady-state populations of both prey and jellyfish decrease.

At $v = v_{opt}$, steady-state populations are always stable. Furthermore, if:

$$1/k_s + 1/P_{opt} > a^2r/4bK \tag{14}$$

the point (P_{opt}, M_{max}) is a stable focus. If, instead, the right hand side of (14) is greater than the left side, the point is a stable node.

As v is increased above v_{opt}, α increases; hence, the nonextinction steady-state is less stable. Furthermore, $M^{(n)}$ decreases. For large values of v, the steady state is less stable in the sense that $P(t)$, $M(t)$ tends slower to it. Furthermore, according to the practical stability concept, the system is destabilized if either $P^{(n)} < \epsilon_1$ or $M^{(n)} < \epsilon_2$, where ϵ_1 and ϵ_2 are small constants.

NUMERICAL EXAMPLE

Data needed in the model are obtained by averaging rates of predation by jellyfish *Pelagia noctiluca* on different prey types and considering concentrations of these scyphomedusae in the Adriatic Sea.

Caloric content of zooplankton that consitutes jellyfish prey in the bay of Trieste (north Adriatic) is 370 J m^{-3} in spring, and 290 J m^{-3} in summer (Malej, 1984). Using the factor of 45 kJ g^{-1} C (Jørgensen, 1979) one finds that zooplankton concentration is approximately 6.4–8.2 mg C m^{-3}. These values may be larger if averaged for the whole Adriatic. Since these values are actual concentrations, they are substantially smaller than carrying capacity. Carrying capacity is probably in the range of 10–50 mg C^{-3} m.

The instantaneous growth rate of zooplankton is anywhere between 0.1–1 day^{-1}. Copepods which can become a major food source when present in

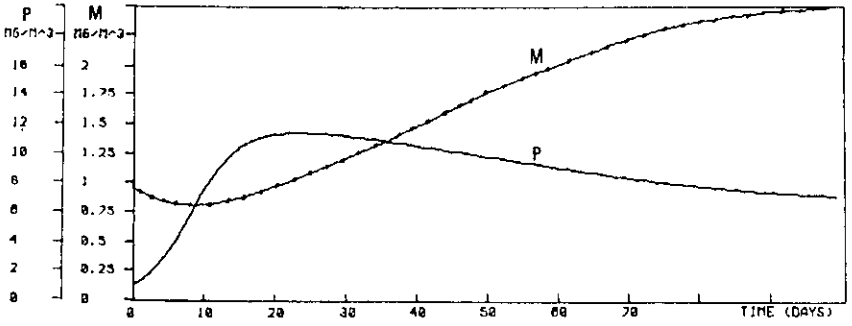

Fig. 2. Simulation of the nominal behaviour. Initial conditions: $P(t=0)=5$, $M(t=0)=5$ (mg C m^{-3}). Parameter values: $r=0.5$, $K=20$, $c=0.15$, $k_s=20$, $a=0.1$, $b=0.05$.

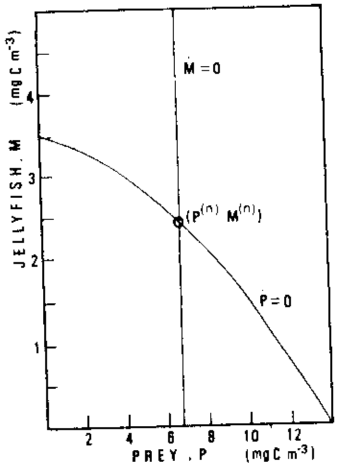

Fig. 3. Prey and jellyfish isoclines for the nominal behaviour. $P^{(n)}$, $M^{(n)}$ is the non-extinction steady state.

high abundance may have an instantaneous growth rate of 0.3 day^{-1} (Reeve et al., 1978)

The value for the specific mortality rate of jellyfish must be estimated indirectly. Given carrying capacity K, if other predators alone reduce prey to $0.5K$ or $0.75K$, then c corresponding to these values is $c=0.25$ and 0.125.

In order to estimate the maximum specific predation rate v, we ask the following question: Given the highest value of prey, how fast can jellyfish feed? Although we have no data for *Pelagia noctiluca* data from ctenophore predation, Reeve and Waltman (1978) suggest values in excess of 20 mg C of prey per mg C of predator per day. This value is probably unattainable by *P. noctiluca* but values from 1 to 3 mg C prey mg^{-1} C predator day^{-1} may be reasonable based on direct observations (L. Rottini-Sandrini, Department of Zoology, University of Trieste, Italy, personal communication, 1985) and may be expected based on observed metabolism (Malej, 1984).

The model describes the sizes of prey and jellyfish populations starting from initial values $P(t=0)>0$, $M(t=0)>0$ and using parameters given in Fig. 2. Non-extinction steady-state is $P(t=0)=6.66$, $M(t=0)=2.4$ mg C m^{-3}.

Prey and jellyfish isoclines and the non-extinction steady-state ($P^{(n)}$, $M^{(n)}$) are shown in Fig. 3.

In order that $M^{(n)}>0$ it follows form the condition (6) that $r>0.223$. Figure 4 shows that ($P^{(n)}$, $M^{(n)}$) is a stable node for $0.223<r<0.3$. An increase in r is followed by a linear increase in jellyfish steady-state density. Also, α decreases linearly which means that r greatly determines the return rate to the steady state. Larger r means higher degree of stability. For $r>0.3$, the steady state is a stable focus.

The constraint on carrying capacity is $K>9.524$ mg C m^{-3}. For small values of K ($9.524<K<18$) the steady state is a stable node but as K increases the node becomes first a stable focus ($18<K<45$) and for $K>45$ mg C m^{-3} an unstable focus (Fig. 5). Around the unstable focus a limit cycle exists, first with a small period T and a small amplitude. As K is further increased, the maximum distance δ_{max} between ($P^{(n)}$, $M^{(n)}$) and the

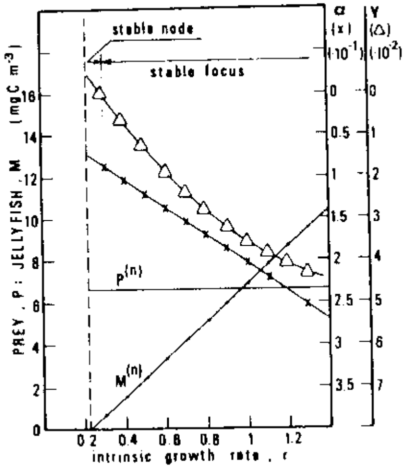

Fig. 4. Effect of change in the inristic growth rate, r, of the prey on the nonextinction state and its stability.

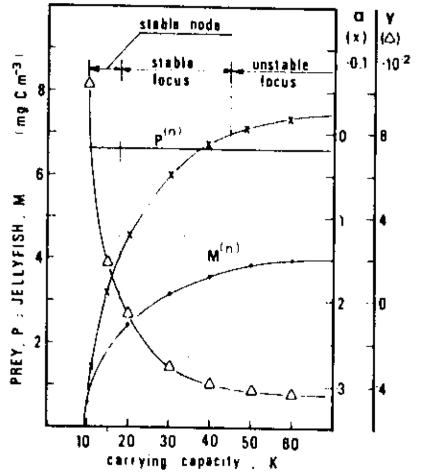

Fig. 5. Effect of change in the carrying cappacity, K, of the prey on the non-extinxtion steady state and its stability.

limit cycle is decreased, which can intuitively be judged from the raise in α and a relatively constant negative γ. The precise information can, however, be obtained through computer simulation for varying K. The distance may be defined as:

$$\delta_{\max} = \max_{t\in(t_1,t_1+T)} \left(\left(P^{(n)} - P(t)\right)^2 + \left(M^{(n)} - M(t)\right)^2 \right)^{1/2}$$

where $P(t)$, $M(t)$ are values from the limit cycle, and T is the period of the cycle. For example, let $K = 70$ mg C m^{-3}. The steady-state populations are $P^{(n)} = 6.66$, $M^{(n)} = 4.03$ mg C m^{-3}. The actual computer simulation (Fig. 6) reveals that $P_{\max} = 33.4$, $P_{\min} \doteq 0.2$, $M_{\max} \doteq 7.5$, $M_{\min} \doteq 1.35$. From the simulation results, one easily calculates $\delta \doteq 27$. The period of the cycle is approximately $T \doteq 75$ days.

In order that $M^{(n)} > 0$, a condition on c is $c < 0.33$. When c decreases from $c = 0.33$ to zero, the steady state is changed from a stable node to a stable focus (Fig. 7). Since c_{cr} is negative, even if jellyfish competitors vanish, a limit cycle cannot appear. However, for some other choice or parameters instead of those in Fig. 2, this may have been possible.

Following a change in maximum specific predation rate υ, changes in steady state of prey and jellyfish populations are shown in Fig. 8. A constraint on υ is that $\upsilon > 1.215$. A vary narrow range of υ corresponds to a stable node ($1.215 < \upsilon < 1.8$). The rest of the range corresponds to a stable focus.

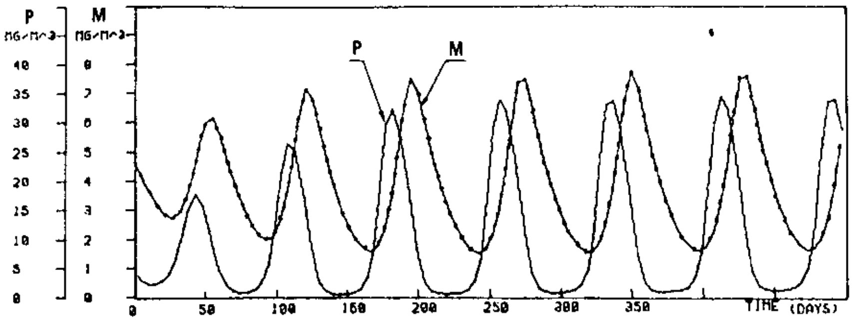

Fig. 6. Simulation of the jellyfish–prey model when carrying capacity is increased to $K = 70$ (mg C m^{-3}). The steady state is unstable and the limit cycle is formed around it.

From expressions (1) and (2) it is clear that if υ is slightly lowered from $\upsilon = 2$, the jellyfish isocline is also lowered with the net result that M increases to a maximum. In fact, the maximum value is $M_{\max} = 2.45$ at $\upsilon = 1.93$ (Fig. 8). The corresponding steady-state prey population is $P = P^{(e)}/2 = 7$. At this point the jellyfish utilizes its prey at the maximum rate. Both α and γ are negative, hence (P_{opt}, $M_{\max}$) is a stable focus.

The critical value of b below which $M^{(n)} > 0$, is $b = 0.0824$. As b is decreased from b_{cr} the non-extinction steady state passes from a stable node

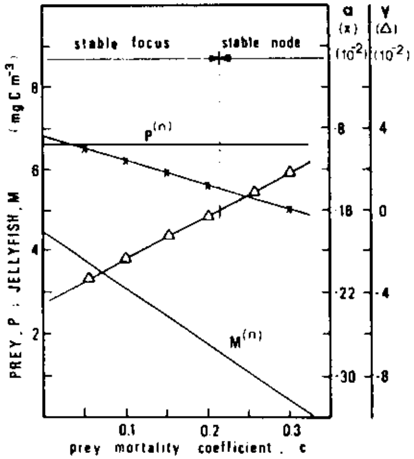

Fig. 7. The effect of change in predation rate of the prey by other predators, c, on the nonextinction state and its stability.

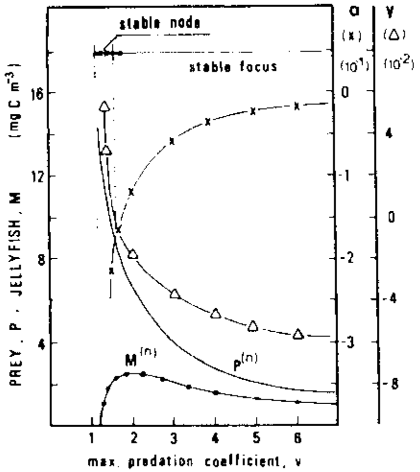

Fig. 8. Effect of change in the maximum specific rate of predation, v, by jellyfish on the non-extinction state and its stability.

to a stable focus (Fig. 9). Since the requirement for the appearance of a limit cycle is:

$b < av(K(r-c) - rk_s)/(K(r-c) + rk_s) = -0.0353$

the limit cycle can not be formed even if all the predators of jellyfish disappear. As it is seen from the above expression, the limit cycle may be formed if k_s value is smaller. In order to have a cycle for $b > 0$, k_s would need to be smaller than 14 mg C m^3. This may well be the case in the sea.

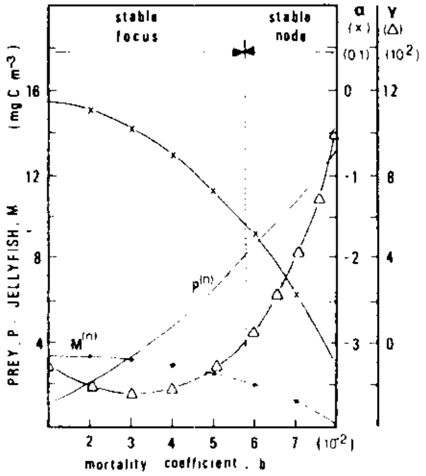

Fig. 9. Effect of change in specific mortality, b, of jellyfish on the non-extinction steady state and its stability.

A decrease in b corresponds to a decrease in the mortality of jellyfish due to a reduction of predatory fish or an increase in winter temperature. The reduction of standing stock of predatory fish is a consequence of increase in fishing efforts. Since increase in fishing on predators of jellyfish is evident from fishing records, even if a limiting cycle is not formed, one may expect greater fluctuations in stocks of jellyfish.

CONCLUSIONS

Using a very simple predator-prey model, we have demonstrated that steady-state density and, hence, standing jellyfish population increases if either of the following holds: (a) the food source to jellyfish prey is increased (nutrient enrichment); (b) the standing stock of jellyfish competitors is decreased (intensive fishing); (c) the standing stock of of the jellyfish predator population is decreased (intensive fishing); (d) the jellyfish mortality is significantly decreased due to a rise in winter sea water temperature in the suboptimal range.

Furthermore, in the all four cases an increase in jellyfish populations corresponds to a less stable prey-jellyfish system and hence larger fluctuations may be expected.

ACNOWLEDGEMENT

This research has been supported by the Self-Management Community for Scientific Research of SR Croatia, Yugoslavia and UNEP (Mediterranean Trust Fund).

REFERENCES

Axiak, V., 1983. A brief note on the occurrence of *Pelagia noctiluca* around Maltese Islands. In: Proc. Workshop Medusa in the Mediterranean, Athens, 3-8 June, Ministry of Physical Planning, Housing and Environment, Athens, pp. 1-9.

Brauer, F. and Soudack, A.C., 1978. Response of predator-prey nutrient enrichment and proportional harvesting. Int. J. Control, 27: 65-86.

Canale, R.P., De Palma, L.M. and Vogel, A.H., 1976. A plankton based food web model for lake Michigan. In: R.P. Canale (Editor), Modelling Biochemical Processes in Aquatic Ecosystems. Ann Arbor Science, Ann Arbor, MI, pp. 33-74.

Dugdale, R.C. and MacIsaacs, J.J., 1971. A computation model for the uptake of nitrate in the Peru upwelling region. Invest. Pesq., 35: 299-308.

Jørgensen, S.E. (Editor), 1979. Handbook of Environmental Data and Ecological Parameters, Pergamon, Oxford, 1162 pp.

Legović, T., Avian, M. and Rottini-Sandrini, L., 1987. Causes of massive occurrence o jellyfish *Pelagia noctiluca* in the Mediterranean Sea (submitted).

Malej, A., 1980. Preliminary report on ephyrae of *Pelagia noctiluca* (Forskål) from the bay of Trieste, North Adriatic. Proc. of the CIESM, Calgiari, 27: 149–150.

Malej, A., 1982. Some notes on the biology of *Pelagia noctiluca* in the gulf of Trieste. Acta Adriat., 23: 97–102.

Malej, A., 1984. Metabolism of *Pelagia noctiluca* in the gulf of Trieste. In: Proc. Workshop Jellyfish Blooms in the Mediterranean, Trieste, 3–4 September 1984, 8 pp.

Reeve, M.R., Walter, M.A. and Ikeda, T., 1978. Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. Limnol. Oceanogr., 23: 740–751.

Rottini-Sandrini, L., 1982. Effect of water temperature on the motility of *Pelagia noctiluca* (Forskål). Experimentia, 38: 453–454.

Rottini-Sandrini, L., Avian, M. and Zanelli, 1987. Water temperature and pulsating rate-motility of *Pelagia noctiluca* (Forskål). Schyphosoa, Semaeostomeae (submitted).

Stravisi, F., 1983. Meteoclimatic influence on the blooms in the Mediterranean Northern Adriatic. Rep. Workshop Jellyfish Blooms in the Mediterranean. UNEP, Athens, pp 179–184.

Svirezhev, Yu.M. and Logofet, D.O., 1983. Stability of Biological Communities. Mir, Moscow 319 pp.

Vučetić, T., 1983. Fluctuation in the distribution of schyphomedusa *Pelagia noctiluca* (Forskål) in the Adriatic. Oceanol. Acta, Proc. 17th European Marine Biol. Symp., Brest, France, 17 September–1 October 1982, pp. 207–211.

Vučetić, T., 1985. Changes in the distribution and size of the population of *Pelagia noctiluca* in the Mediterranean. UNEP, Athens, 37 pp.

Wilkerson, F.P. and Dugdale, R., 1983. Possible connections between sewage effluent, nitrogen levels and jellyfish blooms. Rep. Workshop Jellyfish Blooms in the Mediterranean. UNEP, Athens, pp. 195–201.