

Emigration and retention of *Palinurus elephas* (Fabricius, 1787) in a central western Mediterranean marine protected area

MARIA CRISTINA FOLLESA, DANILA CUCCU, RITA CANNAS,
ANDREA SABATINI and ANGELO CAU

Department of Animal Biology and Ecology, University of Cagliari, Viale Poetto 1, 09126 Cagliari, Italy.
E-mail: follesac@unica.it

SUMMARY: This study describes the results obtained by applying the Arnason Schwartz multistate mark-recapture model to eight years of data collected in and around a small no-fishing marine protected area (MPA; 4 km²) in the central western Mediterranean. From 1997 to 2004, a total of 4044 specimens of *Palinurus elephas* (Fabr., 1787) were tagged and 317 recaptured. The most parsimonious model which best explained the data variability was that of a temporally constant rate of apparent survival and movement in each of the two strata. The absence of any temporal influence in the apparent survival rate inside the no-take area suggested that spillover and mortality are constant for each period of the study. The lower apparent survival rate in surrounding zones than inside the MPA (0.26 ± 0.04 (SE) vs 0.94 ± 0.03 (SE)) is presumed to be a function of fishing effort. A continuous movement of *P. elephas* across the boundary of the small MPA was also tested. This information on retention of lobsters in the MPA contributes to our understanding of the effect of introducing MPAs into a managed commercial fishery system.

Keywords: multistate models, survival estimation, movements, spiny lobster, central western Mediterranean.

RESUMEN: EMIGRACIÓN Y RETENCIÓN DE *PALINURUS ELEPHAS* (FABRICIUS, 1787) EN UN ÁREA MARINA PROTEGIDA DEL MEDITERRÁNEO CENTRAL OCCIDENTAL. – Este estudio presenta los resultados de aplicar el modelo multiestado de marcado y recaptura de Arnason Schwartz a una serie de ocho años de datos recolectados en el interior y alrededor de una pequeña área marina protegida (AMP) vedada a la pesca (4 km²) del Mediterráneo central occidental. Desde 1997 a 2004, un total de 4044 ejemplares de *Palinurus elephas* (Fabr., 1787) fueron marcados, de los cuales 317 fueron recapturados. El modelo más parsimonioso que explicó mejor la variabilidad de los datos fue aquel con una tasa temporal constante de aparente supervivencia y movimiento entre los dos estratos. La ausencia de influencia temporal sobre la tasa de supervivencia aparente en el interior del área protegida, sugirió que el “spillover” y la mortalidad son constantes para cada periodo del estudio. La menor tasa aparente de supervivencia en zonas alrededor de la reserva respecto al interior de la misma (0.26 ± 0.04 (SE) vs 0.94 ± 0.03 (SE)) se considera que es una función del esfuerzo pesquero. Un movimiento continuo de *P. elephas* a través de los límites de la pequeña AMP fue evaluado. Esta información sobre la retención de langostas en el AMP contribuye a comprender el efecto de la introducción de AMPs en un sistema regulado de pesquería comercial.

Palabras clave: modelos multiestado, estimación de supervivencia, movimientos, langosta, Mediterráneo central occidental.

INTRODUCTION

During the last century a large number of marine reserves were established around the world (Jones *et al.*, 1993) in an attempt to halt further deterioration of sensitive habitats or to offer an alternative to tradi-

tional management options (Sanchez Lizaso *et al.*, 2000). In the last decade a few efforts have been made to show that the reserves (also called marine protected areas (MPAs) or no-take areas, where all forms of fishing are prohibited) promote an increase in abundance as well as in the mean size of the pro-

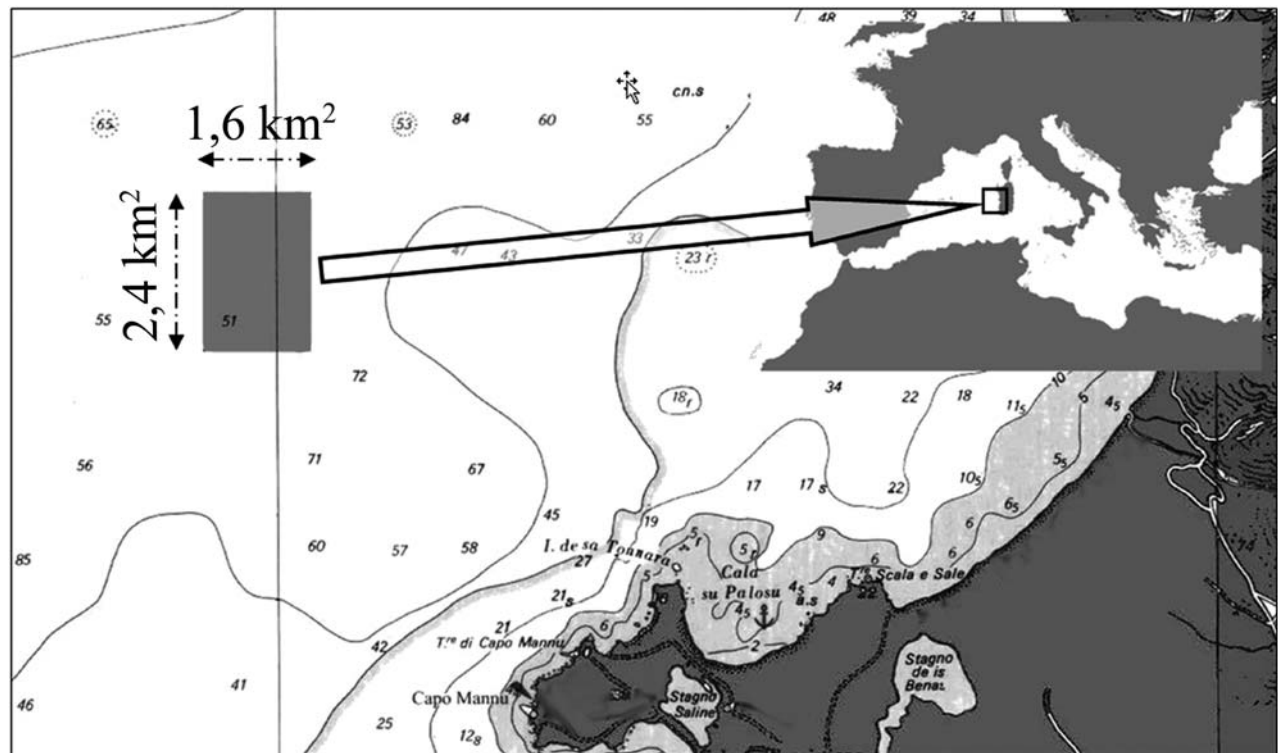


Fig. 1. – Map of the Sardinian protected area and surrounding coastline.

tected populations. The effect of a reduction of fishing on density and biomass of fish populations has been thoroughly investigated both in the Mediterranean and in other marine regions (Sánchez Lizaso *et al.*, 2000). Most studies conclude that fishery reserves can increase the fish stocks in neighbouring areas, especially through migration of adults (Dugan and Davis, 1993; Roberts and Polunin, 1993; Rakitin and Kramer, 1996; Guenette *et al.*, 1998).

At present, it is not possible to establish from the published data whether the exporting of specimens from the “source” population to fished areas is a response to resource limitation inside the protected area or only of random movements of adult individuals across the MPA boundaries (Beverthson and Holt, 1957; Kramer and Chapman, 1999). Some studies have only demonstrated that fish or invertebrates tagged and released inside MPAs may be caught outside them (Davis and Dodrill, 1980, 1989; Gitschlag, 1986; Yamasaki and Kuwahara, 1990; Hunt *et al.*, 1991; MacDiarmid and Breen, 1993; Attwood and Bennett, 1994; Bohnsack, 1998; Goñi *et al.*, 2006). Some authors reported emigration from reserves to adjacent fished areas (Attwood and Bennett, 1994; Zeller *et al.*, 1998; Johnson *et al.*, 1999; Cole *et al.*, 2000; Martell *et al.*, 2000), while others described bidirectional movements with con-

trasting results (Davis and Dodrill, 1989; Rowe, 2001; Zeller *et al.*, 2003; Kelly and MacDiarmid, 2003; Tremain *et al.*, 2004) depending on the species and their lifestage, and on the size of the MPAs (Goñi *et al.*, 2006). Recently, Goñi *et al.* (2006) used a combination of tag recapture methods, fishing surveys and commercial fishery data to demonstrate the existence of a negative gradient of lobster density up to 4.5 km from the Columbretes Islands Marine Reserve.

The movement of protected species from marine areas, although predicted by theory and modelling (DeMartini, 1993; Man *et al.*, 1995), has rarely been tested and assessed (Russ and Alcalá, 1989; McClanahan and Kaunda-Arara, 1996; Hobday *et al.*, 2005; Goñi *et al.*, 2006). Effective tests of the movements are hampered by the difficulty of achieving a good study design and also the lack of a tagged-fish catch time series and fish recovery data (Roberts and Polunin, 1993; McClanahan and Kaunda-Arara, 1996).

The present paper describes an eight-year study, using mark recapture techniques, designed to assess the survival, resighting and movement rate of the spiny lobster, *Palinurus elephas*, in an MPA and its adjacent fished zone located in the central western Mediterranean.

MATERIALS AND METHODS

Field methods

The study was carried out in an area of central-western Sardinia (central-western Mediterranean) at a depth of 50 to 100 m (Fig. 1).

This area, first identified in 1997, was chosen as an MPA on account of its geomorphological and bionomic characteristics. It is characterised by formations comparable to coastal pre-coraligenous and coraligenous detritus (Peres and Picard, 1964). Beginning from 1998, fishing was prohibited in the ca. 4-km² area (Regional Law No. 776 of 6-5-1998) (Secci *et al.*, 1999).

From 1997 to 2004, in the period from May to September, an average of 10 fishing samples were carried out each year (except for 2004, when there were only four), following a sampling plan with transects set up in such way as to enable the whole study area to be investigated. These samples were conducted using trammel nets of 1000 m length (nominal mesh from 50 to 73 mm). All the specimens caught inside the area (total 529) and a sample of 3515 individuals (mean carapace length (CL) of 65.17 mm ± 7.31 (SD) for females and 66.22 ± 9.04 (SD) for males, respectively) caught by local fishermen in commercial areas in every year of the experiment (except for 2002 and 2003) were tagged with plastic T-bar-type tags. These were inserted dorso-laterally, using a tagging gun, between the first and second abdominal segments (Campillo *et al.*, 1979). The following parameters were recorded for each specimen: carapace length (CL) in mm, measured along the median line from the top of the rostrum to the posterior edge of the cephalothorax, total length (TL) in cm, measured along the median line from the infraorbital spine to the posterior edge of the telson, total weight (TW) in grams, and sex. After about three days in tanks in order to assess tagging stress (Secci *et al.*, 1999), the tagged specimens were released in the centre of the MPA. On recapture, whenever possible, the same biometric parameters as those recorded at release were noted for each specimen. A distinction was made between recaptures caught inside the area (IN) and those in the neighbouring fished zone (OUT) (the zone around the MPA within a radius <5 km from the centre of the area), on the basis of reports from professional fishermen. In this neighbouring area, commercial

fishing was carried out mainly by the same boats as those involved in the sampling inside the area. All these boats belong to the fishermen of "Coop. Su Pallosu".

As few data were available, in the following analysis they were processed as a whole, without distinguishing their original site of capture (i.e. IN or OUT).

Modelling procedure

Recapture histories of the tagged spiny lobsters were analysed using Arnason-Schwartz (AS) mark-recapture models (Arnason, 1973; Schwartz *et al.*, 1993), a multistate generalisation of Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965). The CJS model focuses on "typical" open-sea population mark-recapture models in which the probability of an individual being seen is defined by two parameters: the probability of the animal surviving and remaining in the sample area (Φ) (this is an "apparent survival" since it is not possible to distinguish between losses due to death and those due to permanent emigration), and the probability of the animal being encountered (p), conditional on it being alive and in the sample area. The multistate model adds a further level of biological realism by incorporating movement data (Ψ) (Brownie *et al.*, 1993). Models were fitted using the MARK program (White and Burnham, 1999).

The fully parametrised AS model can be represented by $\Phi(t,s)p(t,s)\Psi(t,s)$. Thus, the likelihood of survival, resighting and movement is a function of time (t) and strata (IN = inside MPA; OUT = neighbouring fished zone). With 7 encounter occasions, 1 group, and 2 strata, the unconstrained saturated model had 42 parameters. All models were initially structured using the identity design matrix and sink function.

Model selection was guided primarily by the knowledge of the biology of the marked lobsters' population. The aim of the model selection is to identify the biologically meaningful model that explains the significant variability in the data but excludes unnecessary parameters (the principle of parsimony), i.e. additional parameters that cannot be justified on the basis of actual data (cf. Burnham *et al.*, 1987). Parsimony was assessed using the adjusted form of the Akaike Information Criteria (AICc), incorporating an adjustment for lesser lack of fit of the saturated model (Burnham *et al.*, 1995; Anderson *et al.*, 1998), $\Delta AICc$, i.e. the difference

TABLE 1. – Number of specimens tagged each year (total, males and females).

Year of tagging	No. tagged come from		Number tagged		Number Total tagged
	IN	OUT	Males	Females	
1997	116	0	47	69	116
1998	15	1021	555	481	1036
1999	184	675	459	400	859
2000	161	923	574	510	1084
2001	137	370	292	215	507
2002	-	-	-	-	-
2003	-	-	-	-	-
2004	32	410	229	213	442
Total	645	3399	2156	1888	4044

in AICc between two models and the normalised AICc weights which provide a relative weight of evidence for a particular model that best describes the data (Burnham and Anderson, 1998). Finally, the most parsimonious model was tested for the most important biological question by comparing it with neighbouring ones using the likelihood ratio test (LRT) (Lebreton *et al.*, 1992).

TABLE 2. – Breakdown of the recaptures recorded inside (IN) and outside (OUT) the MPA in the years of experimentation (no data available for 1997).

	1998		1999		2000		2001		2002		2003		2004	
	IN	OUT	IN	OUT	IN	OUT	IN	OUT	IN	OUT	IN	OUT	IN	OUT
Tagged 1997		5	4	2		1								
Tagged 1998		6	10	16	15	5	4	7	2	3				1
Tagged 1999			12	1	16	9	9	11	5	7	1	1		
Tagged 2000					5	4	26	32	14	34	2	9		2
Tagged 2001							5		16	5	1	2		1
Tagged 2004														2
No. of recaptures come from IN		0	5	5	4	1	7	6	12	2	3	1	1	0
Total		11	26	19	36	19	44	50	37	49	4	12	6	4

TABLE 3. – Multistate model reduction process.

Model No.	Hypothesis	Model description	AICc	Δ AICc	AICc weight	Parameters
1	Saturated model	$\Phi(t,s)p(t,s)\Psi(t,s)$	1403.88	19.88	0.00004	42
2	Survival and movement vary with strata but not time	$\Phi(s)p(t,s)\Psi(s)$	1384.00	0.00	0.75817	18
3	Survival varies in fished areas over time; no time effect of movement	$\Phi IN(.)\Phi OUT(t)p(t,s)\Psi(s)$	1386.922	2.92	0.17484	23
4	Survival constant; movements vary only over time	$\Phi(.)p(t,s)\Psi(t)$	1389.992	5.99	0.03767	22
5	Survival constant in both strata	$\Phi(.)p(t,s)\Psi(t,s)$	1391.776	7.61	0.0205	28
6	Survival varies in MPA in 2002 and 2003	$\Phi IN(.)exp_{2003}\Phi OUT(t)p(t,s)\Psi(t,s)$	1391.910	13.90	0.00072	38
7	Survival varies only in fished areas over time	$\Phi IN(.)\Phi OUT(t)p(t,s)\Psi(t,s)$	1392.44	8.43	0.0109	32
8	Survival varies only in MPA over time. No time effect of movement rate	$\Phi IN(t)\Phi OUT(.)p(t,s)\Psi(s)$	1398.92	14.92	0.00043	29
9	Survival constant and movement do not vary over time	$\Phi(.)p(t,s)\Psi(s)$	1520.10	136.08	0.00000	17
10	Survival constant; resighting varies only over time	$\Phi(.)p(t)\Psi(s)$	1415.96	31.96	0.00000	11

RESULTS

During the eight years of experimentation (1997-2004), a total of 4044 specimens were tagged, of which 317 were recaptured, with proportionally more males. Altogether, 153 tagged lobsters were caught inside the MPA and 164 in the neighbouring areas from 1998 to 2004 (Tables 1 and 2). The number of recaptures from IN and OUT zones was substantial during the survey years except in the last two years, when it began to decrease.

The recapture data do not appear to indicate fidelity to the site of original capture (Table 2). Given the limited number of data, the following model was thus applied to all the data, without making any distinction according to the site of original capture.

Model selection

The model which best explains the variation in the data while using the fewest parameters is Model 2 with 18 parameters (Table 3), which is approxi-

mately 4.5 times better supported by the data than the next best model, Model 3.

The best model shows the apparent survival to be constant over time in each stratum (in the no-take area and its surrounding areas it is 0.94 ± 0.03 (SE) and 0.26 ± 0.04 (SE), respectively) although the next best model could lead one to presume that there are temporal changes of survival in the neighbouring fished zone. The likelihood ratio test (LRT) indeed shows the absence of a particularly significant difference in the fit between the two models ($\chi^2 = 7.908$ $df = 5$ $P = 0.1614$).

The most parsimonious model shows that the resighting probability varies during the sampling years in the two strata. The values registered in the OUT zone are greater than those in the IN zone, where the values ranged from 0.06 ± 0.03 SE to 0.308 ± 0.05 SE, and from 0.13 ± 0.06 SE to 0.96 ± 0.15 SE, respectively. In both strata the values decreased in the last two years (Fig. 2). These data confirm the recapture trend of tagged specimens observed during the eight annual samples.

The probability of movement from the MPA to the neighbouring fished zone and vice versa appears constant over the years, showing mean values of 0.28 ± 0.03 and 0.31 ± 0.12 , respectively.

DISCUSSION

Tagging and recapture methods, such as the Cornack-Jolly-Seber (CJS), have always been considered basic elements for assessing the probability

of a population surviving (Williams *et al.*, 2002). However, recent developments of the CJS have shown that the capture and survival rates of an open-sea population can be affected by a certain amount of individual variability (Williams *et al.*, 2002). Thus, statisticians and ecologists have attempted, in recent years, to widen the CJS model by introducing “multistate models”, in which, in addition to environmental and temporal factors, capture, survival rates and movements of specimens are considered in relation to the individual variability inherent in a population (Bonner and Schwarz, 2006).

The present study describes the results of applying the Arnason Schwartz multistate mark-recapture model (Arnason, 1973; Schwartz *et al.*, 1993) to a temporal series of data covering eight years of experimentation. This method allowed us to examine the apparent survival rate and movement trends of *P. elephas* in an MPA of the central-western Mediterranean and in the fished areas surrounding it.

The most parsimonious model which best explains the data variability is that of temporally constant rates of apparent survival and movement in each of the two strata, together with an abruptly decreasing trend in the probability of encountering tagged specimens, which was observed in the last two years of experimentation.

The absence of any temporal influence in the apparent survival rate inside the no-take area suggests that spillover and mortality are constant for each period of study. The high value could be also linked to the fact that the introduced specimens, aged between 3 and 4 years (Marin, 1987; Follesa *et*

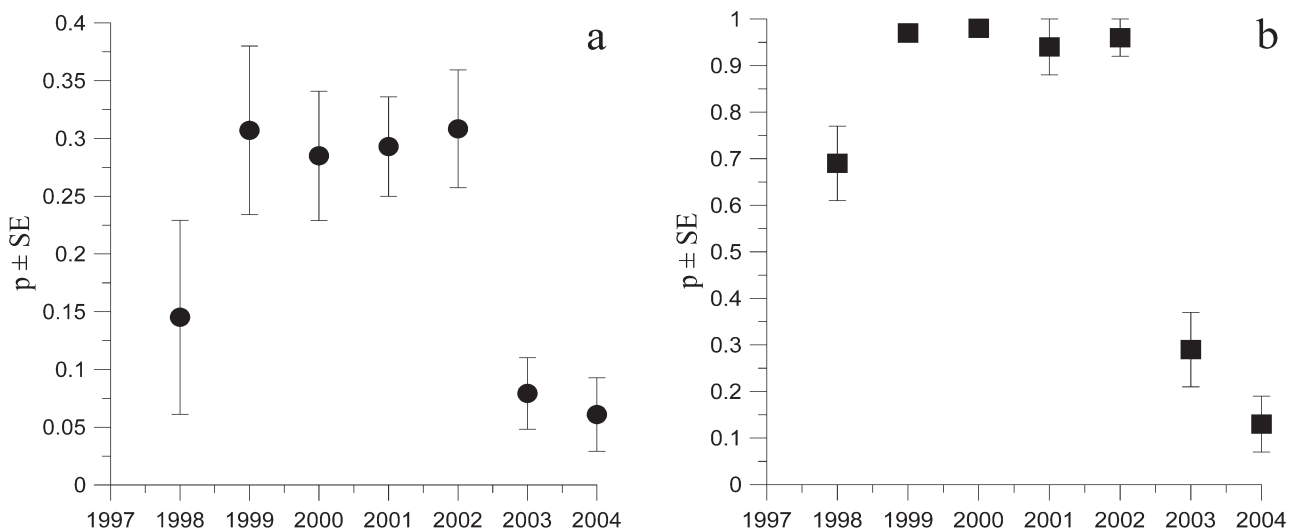


FIG. 2. – Probability of resighting (p) of spiny lobsters in the restocking area (a) and the neighboring fishing zone (b).

al., 2003), do not represent the main prey of certain species, such as *Scorpaena scrofa*, *Scorpaena porcus*, *Diplodus sargus* and the cephalopod *Octopus vulgaris*, which are present in the area. These predators prey mainly on recently settled juvenile *P. elephas* (Diaz *et al.*, 2005). The apparent survival rate also remained practically constant over the years in the fished zone surrounding the MPA, although with a value lower than in the MPA. This datum confirms the continuous emigration of *P. elephas* across the boundary of the small MPA. The lobsters move from inside the MPA to the outside regions, where they are liable to be caught by a small number of fishermen mainly belonging to the same cooperative. Despite this, from the first year of experimentation their fishing effort probably had an effect on the survival of the animals in the OUT zones. Also, the variations in the resighting rate values were correlated with the various degrees of fishing effort and with the reporting rate in the IN and OUT areas.

For the immediate and substantial spillover of a species with a medium-low mobility, like *P. elephas*, into the surrounding fished zone to occur, the protected area needs to be on about the same spatial scale as the annual movement of individuals (Childress, 1977; Sánchez Lizaso *et al.*, 2000; Kelly *et al.*, 2002). In a reserve substantially greater than the scale of lobster movement, the majority of lobsters will be retained within the boundaries, thus limiting spillover.

The small size of our study area (4 km²) seems to have ensured, even in the first few years of experimentation, the movement of lobsters from the IN zone to the OUT ones, at a rate that appeared to be constant throughout the eight-year period. Considering, in fact, that all the lobsters recaptured had covered a mean distance of ca. 1.8 km/yr and that the distance a specimen would have to cover in order to move outside the area (calculated as a straight line from the centre of the area) would be between 1.4 and 1.6 km, it appears clear that the spillover of adult specimens outside the area proved to be consistent after one year of the area being set up.

The results of the present study are encouraging for the potential enhancement of spiny lobster populations. This is the first time that CSJ modelling has been applied to an adult population of lobsters. The relatively small standard errors associated with apparent survival, resighting and also movement rates show that even with a small sample size tests can be powerful. Robust and quantitative informa-

tion on the movements of lobsters across the MPA boundary has been acquired. However, the lower survival rate estimated in the surrounding fished areas than in the MPA ones could indicate that the imposition of MPAs should be associated with a controlled fishery pressure in the adjacent fished areas, depending on the state of depletion in the fishery before their introduction.

Hence, even if our results cannot be extended as a generalisation to other protected areas, we hope that this information will make a useful and important contribution to the wider debate on the effect of introducing MPAs into a managed commercial fishery of rock lobsters.

ACKNOWLEDGEMENTS

The authors wish to express their gratitude to Pere Abelló, Caleb Gardner and one anonymous reviewer for their useful advice and comments on the manuscript.

REFERENCES

- Anderson, D.R., K.P. Burnham and G.C. White. – 1998. Comparison of Akaike Information Criterion and consistent Akaike Information Criterion for model selection and statistical inference from capture-recapture studies *J. Appl. Stat.*, 25: 263-282.
- Arnason, A.N. – 1973. The estimation of population size, migration rates and survival in a stratified population. *Res. Pop. Ecol.*, 15: 1-8.
- Attwood, C.G. and B.A. Bennett. – 1994. Variation in dispersal of Galjoen (*Coracias capensis*) (Teleostei: Coraciidae) from a marine reserve. *Can. J. Fish. Aquat. Sci.*, 51: 1247-1257.
- Beverton, R.J.H. and S. J. Holt. – 1957. On the dynamics of exploited fish populations. *UK Ministry of Agriculture fisheries and food Investigation Series*, 2: 19.
- Bohnsack, J.A. – 1998. Marine reserves: lessons from Florida, In: M.M. Yoklavich (eds.), *Marine Harvest Refugia for West Coast Rockfish: A workshop*. pp. 89-99. NOAA technical Memorandum National Marine Fisheries Service-S.W. Fisheries Science Center 255.
- Bonner, S.J. and C.J. Schwarz. – 2006. An extension of the Cormack-Jolly-Seber model for continuous covariates with application to *Microtus pennsylvanicus*. *Biometrics*, 62: 142-149.
- Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock and J.B. Hestbeck. – 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics*, 51: 888-898.
- Burnham, K.P. and D.R. Anderson. – 1998. *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Burnham, K.P., D.R. Anderson, G.C. White, C. Brownie and K.H. Pollock. – 1987. Design and analysis methods for fish survival experiments based on release-recapture. *Am. Fish. Soc. Monogr.*, 5.
- Burnham, K.P., G.C. White and D.R. Anderson. – 1995. Model selection in the analysis of capture-recapture data. *Biometrics*, 51: 888-898.
- Campillo, A., L. De Reynal and J. Amadei. – 1979. Premières observations sur la reproduction de la langouste rouge *Palinurus elephas* Fabr. de Méditerranée. *Rapp. Comm. Int.*

- Mer Médit.*, 25/26: 4.
- Childress, M.J. – 1977. Marine reserves and their effects on lobster populations: report from workshop. *Mar. Freshw. Res.*, 48, 1111-14.
- Cole, R.G., E. Villouta and R.J. Davidson. – 2000. Direct evidence of limited dispersal of the reef fish *Parapercis colias* (Pinguipedidae) within a marine reserve and adjacent fished areas. *Aquatic. Conserv. Mar. Freshw. Ecosyst.*, 10: 421-436.
- Cormack, R.M. – 1964. Estimates of survival from the sighting of marked animals. *Biometrika*, 51: 429-438.
- Davis, G.E. and J.W. Dodrill. – 1980. Marine parks and sanctuaries for spiny lobsters fisheries management. *Proc. Gulf Caribbean Fish. Inst.*, 32: 194-207.
- Davis, G.E. and J.W. Dodrill. – 1989. Recreational fishery and population dynamics of spiny lobsters *Panulirus argus* in Florida Bay, Everglades National Park, 1977-1980. *Bull. Mar. Sci.*, 44(1): 78-88.
- DeMartini, D.M.E., D.M. Ellis and V.A. Honda. – 1993. Comparisons of spiny lobster *Palinurus marginatus* fecundity, egg size, and spawning frequency before and after exploitation. *Fish. Bull.*, 91: 1-7.
- Díaz, D., M. Zabala, C. Linares, B. Hereu and P. Abelló. – 2005. Increased predation of juvenile European spiny lobster (*Palinurus elephas*) in a marine protected area. *N.Z. J. Mar. Freshw. Res.*, 39: 447-453.
- Dugan, J.E. and G.F. Davis. – 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.*, 50: 2029-2042.
- Follesa M.C., D. Cuccu, F. Damele, A. Sabatini and A. Cau. – 2003. Valutazioni sull'accrescimento di *Palinurus elephas* (Fabr., 1877) tramite marcatura e ricattura nei mari sardi. *Biol. Mar. Médit.*, 10 (2): 253-256.
- Gitschlag, G.R. – 1986. Movement of pink shrimp in relation to the Tortugas sanctuary. *North Am. J. Fish. Manag.*, 6: 328-38.
- Goñi, R., A. Quetglas and O. Reñones. – 2006. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar. Ecol. Prog. Ser.*, 306: 207-219.
- Guenette, S., T. Lauck and C. Clark. – 1998. Marine reserve: from Beverton and Holt to the present. *Rev. Fish. Biol. Fish.*, 8: 251-272.
- Hobday, D., A.E. Punt and D.C. Smith. – 2005. Modelling the effects of Marine Protected Areas (MPAs) on the southern rock lobster (*Jasus edwardsii*) fishery of Victoria, Australia. *N. Z. J. Mar. Freshw. Res.*, 39: 675-686.
- Hunt, J.H., T.R. Matthews, D. Forcucci, B.S. Hedin and R.D. Bertelsen. – 1991. Management implications of the trends in the population dynamics of the Caribbean spiny lobster, *Panulirus argus*, at Looe Key National Marine Sanctuary. NOAA Contract N. 50-DGNC-6-0093, Final Report
- Johnson, D.R., N.A. Funicelli and J.A. Bohnsack. – 1999. Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. *North. Am. J. Fish. Manag.*, 19: 436-453.
- Jolly, G.M. – 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, 52: 225-247.
- Jones, G.P., R.C. Cole and C.N. Battershill. – 1993. Marine reserves: do they work? In: C.N. Battershill, D.R. Schiel, G.P. Jones, R.G. Creese and A.B. MacDiarmid (eds.) *Proceedings of the Second international temperate Reef Symposium*, 7-10 January, 1992., pp. 29-45 Wellington New Zealand: NIWA Marine.
- Kelly, S., D. Scott and A.B. MacDiarmid. – 2002. The value of a spillover fishery for spiny lobsters around a marine reserve in New Zealand. *Coast. Manag.*, 30: 153-166.
- Kelly, S. and A.B. MacDiarmid. – 2003. Movements patterns of mature spiny lobsters, *Jasus edwardsii*, from a marine reserve. *N. Z. J. Mar. Freshw. Res.*, 37: 149-158.
- Kramer, D.L. and M.R. Chapman – 1999. Implication of fish home range size and relocation for marine reserve function. *Env. Biol. Fish.*, 55: 65-79.
- Lebreton, J.D., K.P. Burnham, J. Clobert and D.R. Anderson. – 1992. Modelling survival and testing biological hypothesis using marked animals: unified approach with case studies. *Ecol. Monogr.*, 62: 67-118.
- MacDiarmid, A.B. and P.A. Breen. – 1993. Spiny lobster population change in a marine reserve. In: C.N. Battershill, D.R. Schiel, G.P. Jones, R.G. Creese and A.B. MacDiarmid (eds.) *Proceedings of the Second international temperate Reef Symposium*, 7-10. January, 1992, pp. 29-45. Wellington New Zealand: NIWA Marine.
- Man, A.R.L. and N.V.C. Polunin. – 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. *Biol. Conserv.*, 71: 197-204.
- Marin, J. – 1987. *Exploitation, biologie et dynamique du stock de langouste rouge de Corse. Palinurus elephas Fabricius*. Thèse Univ. Aix-Marseille. Faculté Sciences Luminy.
- Martell, S.J., C.J. Walters and S.W. Wallace. – 2000. The use of marine protected areas for conservation of lingcod (*Ophiodon elongates*). *Bull. Mar. Sci.*, 66(3): 729-743.
- McClanahan, T.R. and B. Kaunda-Arara. – 1996. Fishery recovery in a coral reef marine park and its effects on the adjacent fishery. *Conserv. Biol.*, 10(4): 1187-1199.
- Pérès, J.M. and J. Picard. – 1964. Nouveau manuel de bionomie benthique der la Méditerranée. *Rec. Trav. Stat. Mar. Endoume*, 31(47): 1-37.
- Rakitin, A. and D.L. Kramer. – 1996. Effect of marine reserve on the distribution of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.*, 131: 97-113.
- Roberts, C.M. and N.V.C. Polunin. – 1993. Effects of marine reserve protection on Northern Red Sea fish populations *Proceedings of the 7th International Coral Reef Symposium*, 2: 979-87.
- Rowe, S. – 2001. Movement and harvesting mortality of American lobsters (*Homarus americanus*) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Can. J. Fish. Aquat. Sci.*, 58: 1336-1346.
- Russ, G.R. and A.C. Alcala. – 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser.*, 56: 13-27.
- Sánchez Lisazo, J.L., R. Goñi, O. Renones, J.A. García Charton, R. Galzin, J.T. Bayle, P. Sánchez Jerez, A. Pérez Ruzafa and A.A. Ramos. – 2000. Density dependence in marine protected populations: a review. *Environ. Conserv.*, 27(2): 144-158.
- Schwartz, C.J., J.F. Schweigert and A.N. Arnason. – 1993. Estimation migration rates using tag- recovery data. *Biometrics*, 49: 177-193.
- Seber, J.A.F. – 1965. A note on the multiple recapture census. *Biometrika*, 52: 249-259.
- Secchi, E., D. Cuccu, M.C. Follesa and A. Cau. – 1999. Fishery and tagging of *Palinurus elephas* in Sardinian seas. In: J.C. Von Vaupel Klein and F.R. Schram (eds.), *The Biodiversity Crisis and Crustacea: Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20-24, 1998*, pp. 665-672.
- Tremain, D.M., C.W. Harnden and D.H. Adams. – 2004. Multidirectional movements of sportfish species between an estuarine no-take zone and surrounding waters of the Indian River Lagoon, Florida. *Fish. Bull.*, 102: 533-544.
- Yamasaki, A. and A. Kuwahara. – 1990. Preserved area to effect recovery of overfished Zuwai crab stocks off Kyoto Prefecture. In: *Proceedings of the International Symposium on King and Tanner Crabs*, pp. 575-85. Alaska Sea Grant College Program, University of Alaska.
- White, G.C. and K.P. Burnham. – 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46 (suppl.): 120-139.
- Williams, B.K., J.D. Nichols and M.J. Conroy. – 2002. *Analysis and management of animal populations*. San Diego, California, Academic Press.
- Zeller, D.C., S.L. Stoute and G.R. Russ. – 2003. Movements of reef fishes across marine reserve boundaries: effects of manipulating a density gradient. *Mar. Ecol. Prog. Ser.*, 254: 269-280.

Scient. ed.: P. Abelló.

Received July 27, 2006. February 23, 2007.

Published online May 21, 2007.

