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Biology, ecology, fisheries and effects of protection on the spiny lobster *Palinurus elephas* (Fabricius, 1787) in the Western Mediterranean

Biología, ecología, pesquerías y efectos de la protección sobre la langosta espinosa *Palinurus elephas* (Fabricius, 1787) en el Mediterráneo Occidental

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RAQUEL GOÑI BELTRÁN DE GARIZURIETA
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TESIS DOCTORAL

Biology, ecology, fisheries and effects of protection on the spiny lobster *Palinurus elephas* (Fabricius, 1787) in the Western Mediterranean

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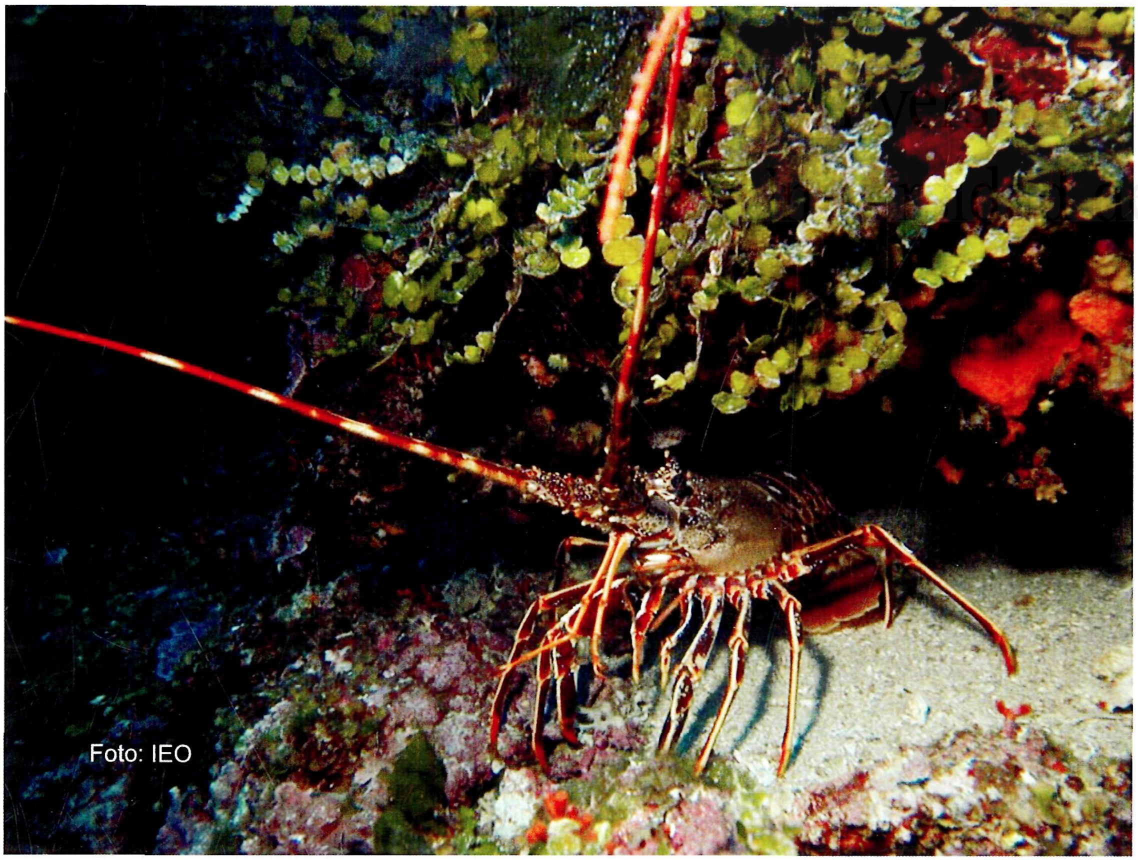
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RESUMEN

INTRODUCCIÓN GENERAL

Antecedentes

La langosta *Palinurus elephas* (Fabricius 1787) es la especie de langosta espinosa de mayor importancia comercial en el Mediterráneo y Atlántico nororiental. Se trata de un crustáceo decápodo de gran talla que habita en fondos rocosos y coralígenos desde la costa hasta aproximadamente 200 m de profundidad. *P. elephas* ha sido tradicionalmente explotada por flotas artesanales en toda su área de distribución, principalmente en el Mediterráneo Occidental. Su alto valor comercial (hasta 60 euros por kilo en 2003) permite que la pesca continúe produciendo beneficios incluso con bajos rendimientos. Por ello, la mayor parte de los stocks atlánticos han colapsado y los del Mediterráneo se consideran sobre-explotados (Latrouite y Noel 1997, Goñi y Latrouite 2005).

En el Mediterráneo español más de 600 barcas y 1100 pescadores pescan langosta cada año durante toda o parte de la temporada de pesca (Alarcón 2001). La pesquería está regulada por una veda de 6 meses durante el periodo de incubación de huevos (Septiembre a Febrero), una talla mínima (80 mm LC) y la prohibición de descargar hembras ovadas. El alto valor unitario y la escasez relativa de *P. elephas* han sido obstáculos importantes para su estudio y hasta hace poco el conocimiento de su biología, ecología y pesquerías era escaso, al tiempo que la mayoría de los estudios existentes estaban contenidos en documentos no publicados de diversos institutos de investigación o universidades.

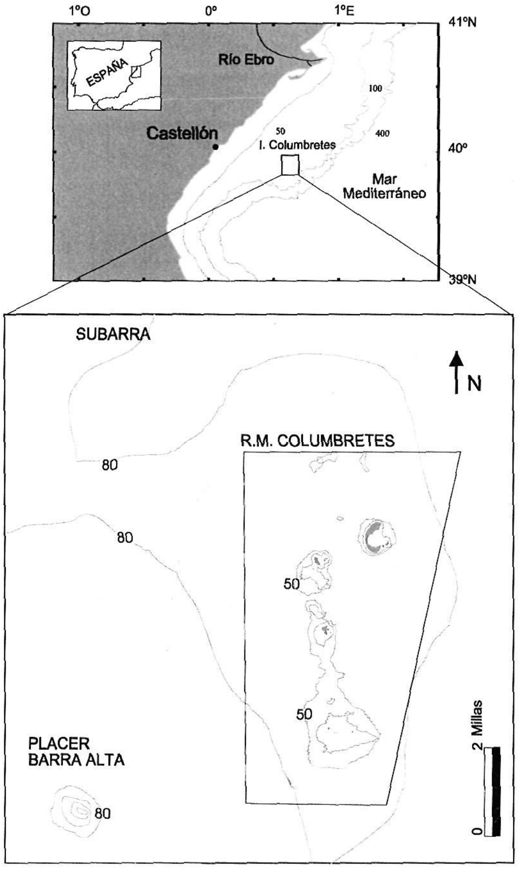
En 1997 el Centro Oceanográfico de Baleares (Instituto Español de Oceanografía) inició un proyecto de investigación dirigido a desarrollar una base sólida de conocimientos sobre la biología, la ecología y las pesquerías de *P. elephas* en el Mediterráneo español. Con anterioridad, solo se habían realizado dos estudios en profundidad de la especie, uno sobre la biología y ecología de las poblaciones en aguas de Irlanda (Mercer 1977) y otro sobre las pesquerías, dinámica y biología de la especie en aguas de Córcega (Marin 1987). Además, hay una serie de estudios de menor magnitud realizados principalmente durante los años 70 y 80 sobre aspectos diversos de la biología y pesquerías de *P. elephas* del Atlántico (Bouvier 1914, Vasconcellos 1960, Gibson y O'Riordan 1965, Hepper 1967 1970 1977, Ansell y Robb 1977, Latrouite y Alfama 1996, Latrouite y Noël 1997) y Mediterráneo (Santucci 1926 1928, Gamulin 1955, Campillo y Amadei 1978, Campillo *et al.* 1979, Campillo 1982, Cuccu *et al.* 1999, Hunter 1996, Diaz *et al.* 2001, Soldo *et al.* 2001). Más tarde, Hunter *et al.* (1999) realizaron una revisión sucinta de la especie. En años recientes, Goñi y colegas (Goñi *et al.* 2000, Goñi *et al.* 2001a, b, Goñi *et al.* 2003a, b, c, Quetglas *et al.* 2005) han realizado en el marco del proyecto arriba mencionado una serie de estudios sobre la población de *P. elephas* en la Reserva Marina de las Islas Columbretes (RMIC o la Reserva) y en las pesquerías más importantes del Mediterráneo español. Además, el conocimiento disponible hasta la fecha sobre la especie ha sido examinado y recogido en un artículo de revisión publicado recientemente (Goñi y Latrouite 2005) y en el capítulo de un libro dedicado a las especies del genero Palinurus (Groeneveld *et al.*, en prensa).

El primer capítulo de está tesis es una introducción general, el segundo contiene una revisión exhaustiva y actual del conocimiento de la especie que es un extracto del artículo mencionado anteriormente (Goñi y Latrouite 2005). El tercer, cuarto y quinto capítulos presentan tres estudios, dos de ellos publicados (Goñi *et al.* 2001b, Goñi *et al.* 2003a) y uno enviado, que constituyen un esfuerzo coherente para evaluar los efectos del cese de la pesca sobre la población de *P. elephas* en la Reserva Marina de las Islas Columbretes. El Capítulo 3 estudia la dinámica espacio-temporal de la abundancia de langosta con el fin de evaluar la recuperación de la población de langosta en la RMIC; el estudio también examina la dinámica estacional de la población en la Reserva. El Capítulo 4 está dedicado a la biología reproductiva de la especie en la Reserva, estudiada por primera vez en el Mediterráneo español. En este estudio también se estima el potencial reproductivo de una población no explotada y se evalúa el potencial de puesta de huevos por unidad de área de la Reserva con relación al de áreas explotadas. El Capítulo 5 estudia el potencial de exportación de adultos de la Reserva a la pesquería adyacente examinando la distribución espacial del esfuerzo de pesca y de la captura en función de la distancia a la reserva marina. Para este estudio se utilizan también resultados parciales de un estudio de marcado y recaptura iniciado en 1997. Finalmente, el Capítulo 6 contiene una sucinta discusión general que resume las discusiones contenidas en los capítulos anteriores, seguido de las conclusiones y referencias.

La Reserva Marina de las Islas Columbretes

El grupo de islas que conforman el archipiélago conocido como Islas Columbretes está situado a 30 millas náuticas de la costa de Castellón (Levante de la península Ibérica) entre los paralelos 39º 51' y 39º 55' de latitud N y los meridianos 0º 40' y 0º 42' de longitud E de Greenwich, Datum Europeo (Figuras R.1 y R.2).

Figura R.1: Mapa del Mediterráneo Occidental indicando la situación de la Reserva Marina de las Islas Columbretes.



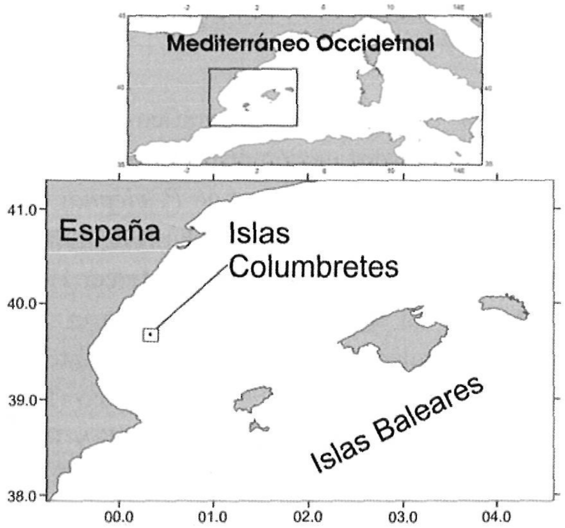


Figura R.2: Situación de la Reserva Marina de las Islas Columbretes indicando el perímetro de la misma y los dos caladeros explotados usados como referencia para a comparación espacial de índices de abundancia: Placer de la Barra Alta (PLA) y Subarra (SUB).

Las Islas Columbretes se formaron en el periodo cuaternario y constituyen la parte emergida de un extenso campo volcánico situado al borde de la gran plataforma continental al sur de la desembocadura del río Ebro (Templado y Calvo 2002). La parte emergida del archipiélago ocupa una extensión de 19 ha y está constituida por cuatro grupos de islas y algunos afloramientos rocosos. La parte sumergida consta principalmente de substratos rocosos verticales o subverticales de origen volcánico desde la costa hasta 30-40 m de profundidad, a la base de los cuales se encuentran grandes rocas y bloques desprendidos de los mismos. A continuación se encuentra un estrato detrítico alternando con zonas de fango de origen continental (Templado y Calvo 2002).

La gran distancia que separa Columbretes de la costa junto a la ausencia de fuentes contaminantes en las islas determina la alta calidad de las aguas marinas. La transparencia del agua permite la presencia de algas erectas (ej. *Laminaria*) a profundidad considerable (80 m) (Templado y Calvo 2002). Otra característica notoria de la comunidades bentónicas del archipiélago es la ausencia de *Posidonia oceánica* y la presencia de praderas de *Cymodocea nodosa* y de una exuberante comunidad de algas fotófilas (Templado y Calvo 2002). Algunas especies animales son también inusualmente abundantes en Columbretes, especialmente desde que la pesca fue prohibida. En este contexto, la langosta europea *Palinurus elephas* es quizás la especie más emblemática del archipiélago.

Las primeras iniciativas de conservación del archipiélago datan de finales de los años 70. Diez años más tarde el archipiélago fue declarado Parque Natural mediante el decreto 15/88 del Consell de la Generalitat Valenciana el 25 de Enero de 1988 y poco después fue creada una Reserva Marina en el entorno marino del mismo mediante la orden ministerial del 19 de Abril de 1990 por el Ministerio de Agricultura y Pesca del gobierno nacional. El objetivo de creación de la Reserva Marina fue 'crear áreas de reserva integral y de acceso restringido para la pesca marítima y la protección de los recursos pesqueros autóctonos'.

La RMIC cubre 4400 ha con un rango batimétrico que va desde la costa hasta 90 m de profundidad. Cuando fue creada contaba con dos reservas integrales que sumaban un área de 540 ha donde no se permitían actividades extractivas. En la actualidad la Reserva cuenta con 1883 ha cerradas a toda actividad humana excepto la investigación y educación: el Murall del Cementeri (270 ha), L'Illa (269 ha), la Horadada (367 ha) y el Carallot (68 ha) (Figura R.3). Fuera de estas áreas todas las modalidades de pesca están prohibidas excepto algunas modalidades de pesca artesanal con caña, curricán y potera, además de cerco para pequeños pelágicos. Estas actividades están circunscritas a las embarcaciones incluidas en el censo de la RMIC en el momento de su creación. La pesca recreativa también está permitida previa autorización y sin fondear. La pesca de la langosta está prohibida en toda la Reserva. Este estatus conlleva, de acuerdo con la clasificación de áreas marinas protegidas de la Unión Internacional para la Conservación de la Naturaleza, conservación por medio de una gestión activa y el uso sostenible de sus recursos marinos (Templado y Calvo 2002). Las prohibiciones pesqueras entraron en vigor en 1991 cuando se construyó una casa para los guardas. El grado de cumplimiento de las restricciones pesqueras es muy alto aunque no se descarta que exista algo de pesca furtiva.

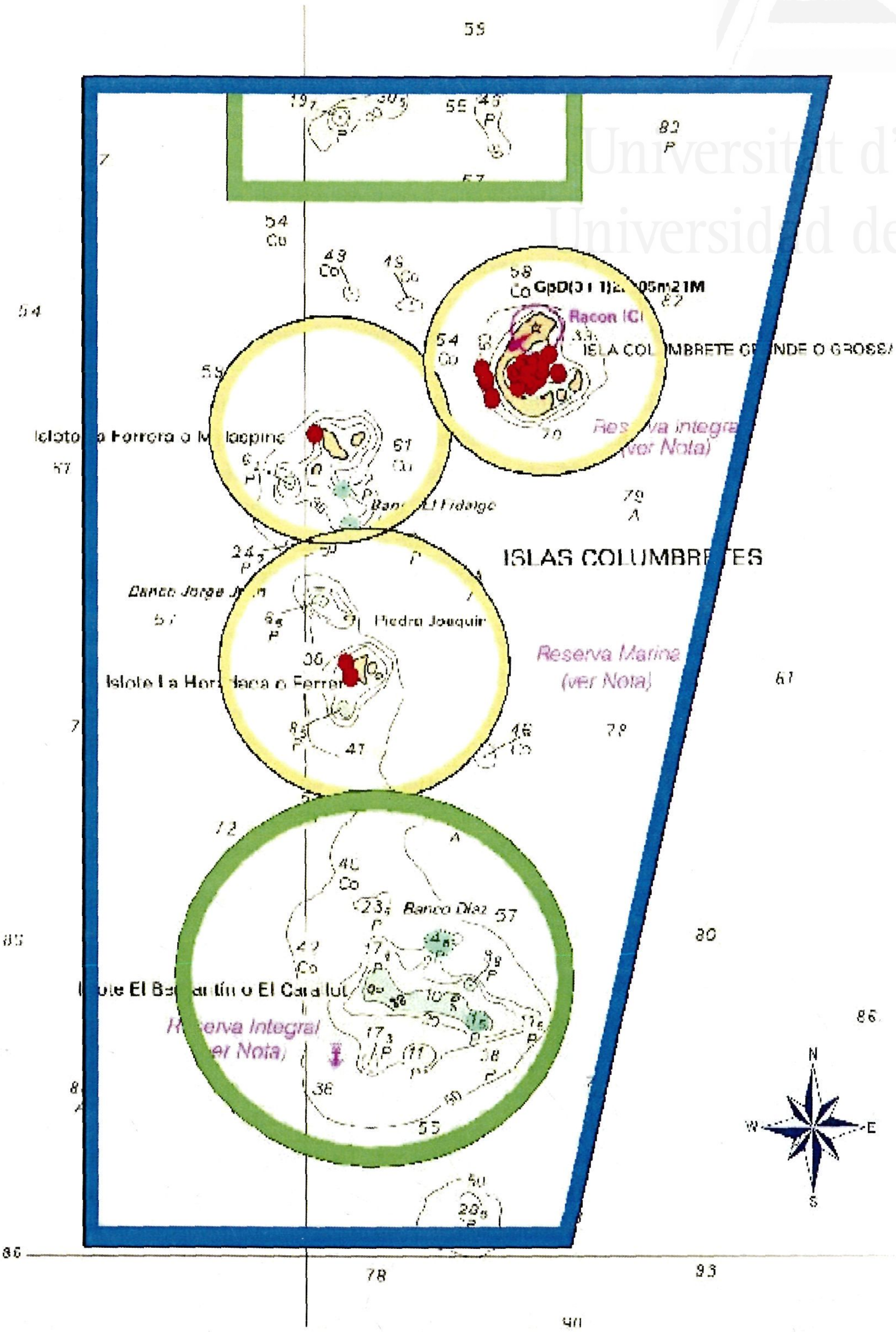


Figura R.3: Zonación de la Reserva Marina de las Islas Columbretes. Verde: actividades humanas prohibidas; Amarillo: buceo recreativo permitido; Azul: pesca permitida con restricciones (ver texto).

En aguas del archipiélago de Columbretes la langostas adultas habitan fondos rocosos y detríticos en el estrato circalitoral desde 30 hasta 90 m de profundidad, aunque ocasionalmente se pueden observar especimenes en fondos someros generalmente por debajo de la termoclina estival (15-25 m). Las post-larvas y los juveniles pueden asentarse en fondos muy someros (>10m) aunque son más abundantes a profundidades superiores a 20 m.

La langosta *Palinurus elephas*, junto con la centolla *Maja squinado*, ahora ausente en está zona, ha sido uno de los recursos pesqueros tradicionales de mayor valor en el archipiélago y noticias de su explotación datan de finales del siglo XIX (Von Salvador 1895). Los pescadores usaban trasmallos y nasas para capturar langostas hasta que el desarrollo de nuevos materiales y técnicas de halado condujeron a la expansión del trasmallo para la captura de langosta en los años 70 y 80. A partir de entonces el esfuerzo de pesca aumentó, alimentado por el creciente mercado turístico a lo largo de la costa mediterránea. Desde el establecimiento de la RMIC, el esfuerzo de pesca se concentra a lo largo de sus límites y en caladeros tradicionales principalmente al oeste y norte del archipiélago (Figura R.4).

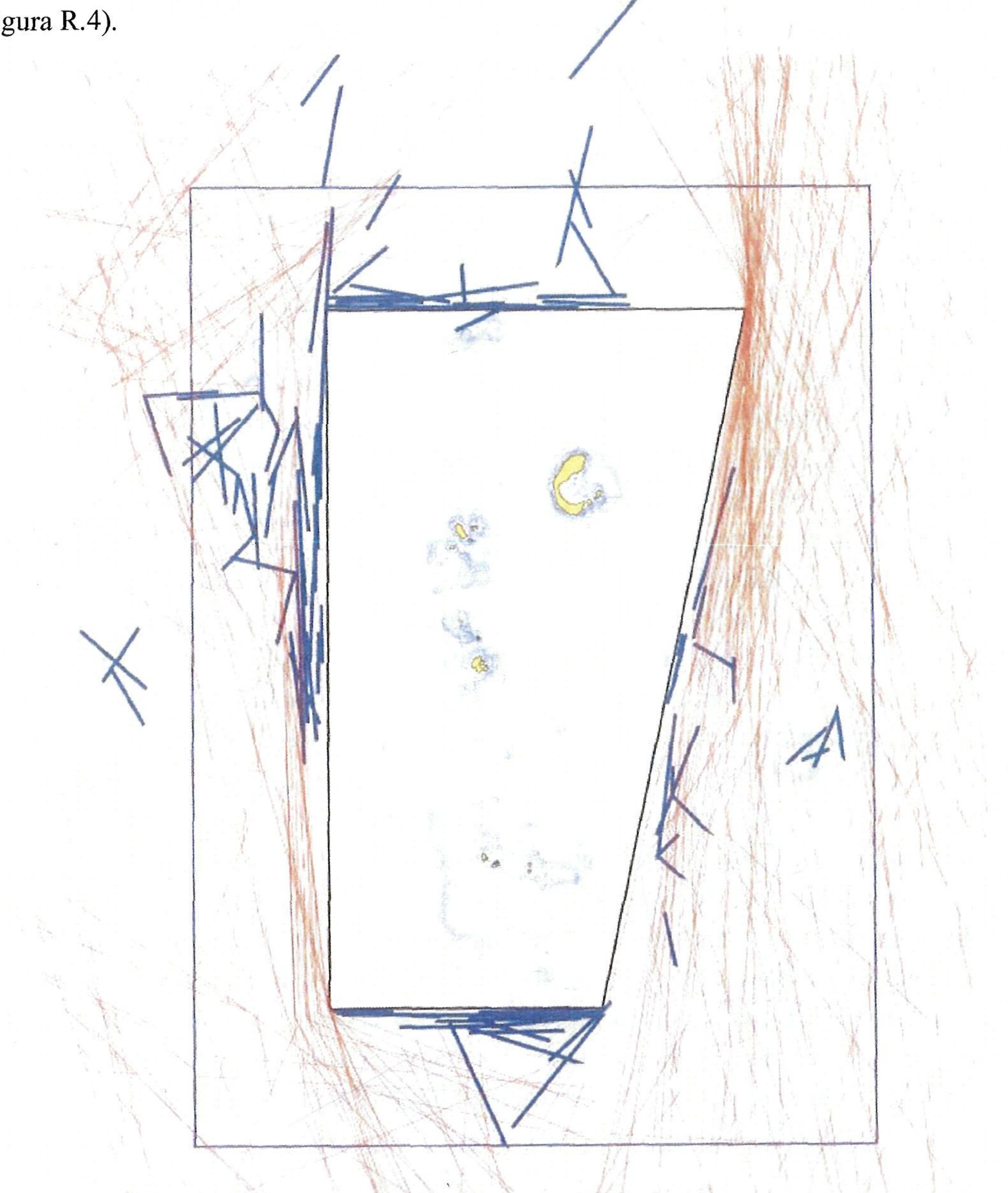


Figura R.4: Distribución espacial de la pesca de arrastre (líneas rojas) y de artes menores (líneas azules) en el entorno de la Reserva Marina de las Islas Columbretes. El cuadrado señala los límites de la ampliación prevista de la RMIC. Fuente: Datos recogidos por los guardas de la Reserva en 2003.

Efectos de la protección sobre las poblaciones de langostas espinosas

De todos los mares europeos, el Mediterráneo alberga el mayor número de reservas marinas; aproximadamente 50 eran operativas en 1999 (Boudouresque 2000). De estas, la RMIC es la única en la que *Palinurus elephas* es una especie clave del ecosistema bentónico y que protege caladeros tradicionales de la especie.

Cuando se creó la RMIC no se prestó atención en determinar las características tales como le tamaño o las medidas de protección necesarias para alcanzar una protección efectiva de ninguna de las especies marinas residentes de especial interés comercial o ecológico. Sólo en 1997, siete años después de la creación de la Reserva, se inició un estudio encaminado al estudio de la dinámica y las respuestas al cese de la pesca de la población protegida de *P. elephas*. Hasta entonces, en el Mediterráneo no se habían realizado estudios para evaluar la efectividad de las áreas marinas protegidas (AMPs) sobre las langostas espinosas y solamente un estudio había tenido como objetivo la dinámica de poblaciones en el Mediterráneo (Marin 1987, Córcega).

Las respuestas de las poblaciones de langostas espinosas a la protección han sido evaluadas en una serie de AMPs alrededor del mundo. Las especies mejor estudiadas son *Panulirus argus* en Florida (USA) (ej., Davis 1977, Davis y Dodrill 1980, Hunt *et al.* 1991) and *Jasus edwardsii* en Nueva Zelanda (ej., Cole *et al.* 1990, MacDiarmid y Breen 1993, Babcock *et al.* 1999, Kelly *et al.* 2000 2002). Desde el punto de vista de una población explotada, se esperan una serie de respuestas cuando la pesca cesa en una reserva marina (ver revisiones en Dugan y Davis 1993, Sánchez-Lizaso *et al.* 2000, Mosquera *et al.* 2000, Halpern y Warner 2002, Russ 2002). La consecuencia más inmediata es que la mortalidad desciende y el la densidad de población aumenta. Al aumentar la supervivencia de los organismos en la AMP, la talla media individual de la población aumenta. Como la fecundidad aumenta con la talla, la consecuencia del efecto combinado de la mayor densidad y talla individual es un aumento del potencial reproductivo de la población. El incremento del potencial reproductivo de una población protegida de langosta puede resultar no sólo del mayor número talla de las hembras adultas sino también de aumento tanto de oportunidades de acoplamiento como de la fecundidad efectiva proporcionada por el mayor número y talla de los machos adultos disponibles. Los efectos descritos hasta aquí se circunscriben a la AMP. Además, la mayor densidad de las especies explotadas en reservas marinas puede resultar en un aumento de los rendimientos pesqueros en las pesquerías adyacentes a través de la exportación de huevos y larvas y de la emigración de post reclutas (ver revisiones en Dugan y Davis 1993, Roberts y Polunin 1993, Guenette *et al.* 1998, Gell y Roberts 2002, Russ 2002). Sin embargo, a pesar de que muchos estudios han corroborado la recuperación de poblaciones explotadas dentro de AMPs, estudios recientes señalan la escasa evidencia disponible de efectos en el exterior de las mismas (Russ 2002). Los beneficios pesqueros de las AMPs han sido difíciles de evaluar en parte por que la mayoría de las reservas marinas son pequeñas y no han sido diseñadas con objetivos pesqueros específicos, pero también debido a la falta de datos pesqueros antes de que su creación (Dugan y Davis 1993). La falta de replicación espacial es también un problema común en estudios de los efectos de las AMPs (Palumbi 2001).

Para algunas langostas espinosas se ha observado mayor abundancia y talla media dentro de AMPs en comparación con áreas explotadas (ej. Cole *et al.* 1990, Hunt *et al.* 1991, MacDiarmid y Breen 1993, Babcock *et al.* 1999, Kelly *et al.* 2000), mientras que en otros casos no se encontraron diferencias entre poblaciones protegidas y explotadas (ej. Hunt *et al.* 1991, MacDiarmid and Breen 1993). En estos casos, el pequeño tamaño de las AMPs en relación con la movilidad de las especies parece ser la causa de la falta de efectividad de las AMPs. La biología reproductiva de poblaciones protegidas de langostas espinosas ha sido estudiada en *J. edwardsii* (MacDiarmid 1989 a, b) y *P.argus* (Davis 1975, Bertelsen y Mathews 2001) y el aumento del potencial reproductivo de poblaciones protegidas ha sido documentado en ambas (*J. edwardsii*: Annala 199, Kelly *et al.* 2000, *P. argus*: Bertelsen y Cox 2001).

Finalmente, sólo dos estudios hasta la fecha han evaluado los efectos de la protección de especies de langostas espinosas en AMPs sobre las pesquerías adyacentes comparando los rendimientos cerca y lejos de la AMP (Kelly *et al.* 2002) y midiendo el gradiente de abundancia del borde hacia el centro de la AMP (Davidson *et al.* 2002). Ambos sugieren exportación de biomasa explotable del interior a exterior de las AMPs. Una deficiencia general de los estudios encaminados a evaluar exportación es la falta de datos para evaluar tasas de movimiento neto dentro-fuera.

Los efectos de la protección sobre poblaciones de *P. elephas* han sido estudiados por primera vez en los tres estudios contenidos en los Capítulos 3, 4 y 5 que se realizaron en la RMIC durante el periodo 1997-2002. De las respuestas esperadas antes descritas, estos trabajos combinan el estudio de aspectos de la biología, dinámica y pesquerías de *P. elephas* en la población protegida y en poblaciones explotadas para evaluar los efectos de la protección sobre la abundancia relativa y el potencial reproductivo y de exportación de la población en la RMIC. Los Capítulos 2 a 4 de está tesis son independientes y cada uno contiene introducción, métodos, resultados y discusión específicos. A continuación se resumen los métodos utilizados en estos trabajos.

MATERIAL y MÉTODOS

Estimación de índices de abundancia de langosta

Para estudiar poblaciones de langostas de profundidad, como *P. elephas*, se suele recurrir a la pesca ya que la observación directa subacuática está muy limitada por su distribución batimétrica (Miller 1990). Sin embargo las capturas de langosta pueden estar determinadas, además de por la abundancia, por otros factores, tales como factores fisiológicos, de comportamiento o medioambientales que provocan cambios en la capturabilidad (o probabilidad de que un animal sea capturado por una unidad de esfuerzo aplicada al azar; Morgan 1974) (Krouse 1989, Miller 1990, MacDiarmid 1991, Addison 1995). Así mismo las capturas pueden estar influidas por la selectividad (Krouse 1989, Miller 1990) o saturación del aparejo de pesca (Miller 1990, Fogarty y Addison 1997). Además, la capturabilidad de los decápodos puede variar enormemente entre individuos (por ejemplo por razones de sexo y talla) (Krouse 1989, Miller 1990).

Las nasas son usadas para capturar langostas y otros crustáceos en muchas pesquerías del mundo (Krouse 1989). En la mayor parte de las pesquerías del Mediterráneo occidental se usaban nasas con cebo para capturar la langosta roja hasta que el desarrollo de nuevos materiales y técnicas de pesca en los años 19760 llevó a la introducción de las expansión de las redes de trasmallo, que prácticamente eliminaron el uso de las nasas. Sin embargo las nasas presentan características deseables como aparejos de pesca y como herramientas para muestrear poblaciones en reservas marinas porque producen pocas capturas no deseadas, la captura normalmente está viva (Miller 1990) y tienen un impacto mínimo sobre las comunidades bentónicas (Eno *et al.* 2001). Por ello se escogió la nasa como herramienta de muestreo en la serie de campañas experimentales para estimar la abundancia y estructura de la población de langosta protegida en la RMIC. Sin embargo, pronto quedó patente que por ser la nasa un aparejo de pesca bastante selectivo, era necesario determinar la selectividad de las mismas usando simultáneamente un muestreador más efectivo. Por ello en cada campaña se simultaneó un cierto número de pescas de nasas con pescas de trasmallo – aparejo muy poco selectivo para la langosta - con el fin de poder evaluar la selectividad de las nasas para langosta y el posible sesgo de las estimaciones de abundancia y estructura de la población derivadas de las capturas de nasas (Figura R.5). Los resultados de dicho estudio han sido ya publicados en 2003 (Goñi *et al.* 2003b) y aunque no se presentan como parte de está tesis por ser temáticamente independientes de la misma, se utilizan en la interpretación de algunos de los resultados de los estudios contenidos en ella.

Figura R.5: Buque oceanográfico Odón de Buen con nasas utilizadas en el estudio y barca artesanal encargada de las pescas experimentales con trasmallo en la RMIC.

Las nasas empleadas en el estudio son nasas comerciales, con malla cuadrada de plástico, anillos de acero y una abertura lateral cuando la nasa yace en el lecho marino. El tamaño de la malla es de 2 cm y el diámetro del embudo de 21 cm (Figuras R.6 y R.7). La forma cilíndrica de las nasas permite su disposición paralela a la corriente con la abertura del embudo y la pluma de olor del cebo corriente abajo. Las nasas se dispusieron en líneas con 40 unidades espaciadas a intervalos de 12 m, midiendo cada l unos 480 m de longitud. Las redes de trasmallo usadas en el estudio son de 1.7 m de altura y estaban confeccionadas con tres paños hechos de filamentos de redes de poliamida (Figura R.8). Los paños exteriores son dos redes de 300 mm de tamaño de malla estirada y el paño interior es una red de 80 mm de tamaño de malla estirada. Las piezas del trasmallo miden 50 m y se montaron en hileras de 10 piezas, midiendo cada hilera de redes de trasmallo 500 m de longitud.

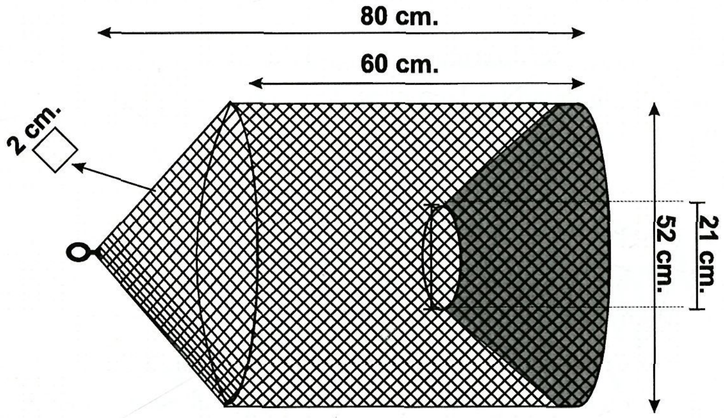


Figura R.6: Nasa utilizada en las campañas de pescas experimentales.

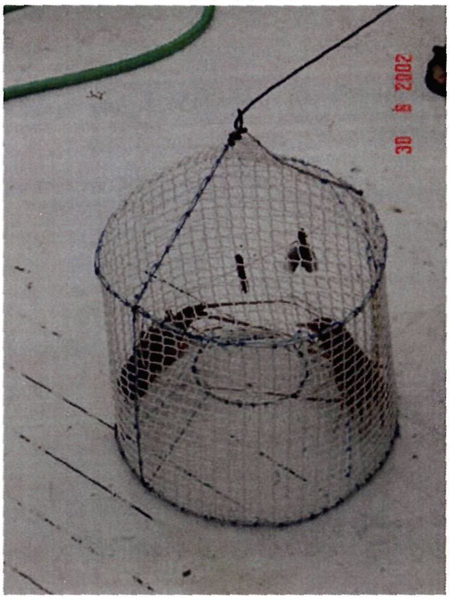


Figura R.7: Nasa y captura de langostas durante la campaña de pescas experimentales en la RMIC.

De los factores que podían afectar la captura de langostas en las nasas (Miller 1990), el tiempo de calada, la saturación del aparejo, los ciclos lunares y el tipo de cebo se controlaron en el diseño de la campaña. Se estandarizó el tiempo de calada de los aparejos a una noche. El resultado de un pequeño número de lances de nasas caladas durante 2 y 3 noches produjo rendimientos por debajo de la media (Goñi *et al.*, datos no publicados), sugiriendo más escape que entrada (Miller 1990, Cockcroft *et al.* 1995). Estos mismos datos mostraron que en las nasas la captura máxima se alcanzaba con caladas de aproximadamente 24 h, indicando que la saturación de los aparejos no ocurría antes. Por el contrario, la captura en redes de trasmallo aumentaba con el tiempo de calada (Goñi *et al.*, datos no publicados). La estandarización del tiempo de calada también fue necesaria para controlar la estructura de tallas de la captura en las nasas (Miller 1990). Debido a que en algunos palinúridos las tasas de captura pueden depender de la fase del ciclo lunar (Miller 1990), las campañas se desarrollaron siempre durante las mismas fases del ciclo lunar (cuarto creciente a cuarto menguante). Finalmente, se utilizó el mismo cebo, la pintarroja (*Scyliorhinus canicula*) para todas las campañas con nasas.

Las hileras de redes de trasmallo y los palangres de nasas se calaron al azar sobre fondos rocosos o coralígenos donde se sabe que habitan las langostas. Las pescas se realizaron en fondos de 25 a 80 m de profundidad (máxima profundidad en la reserva).

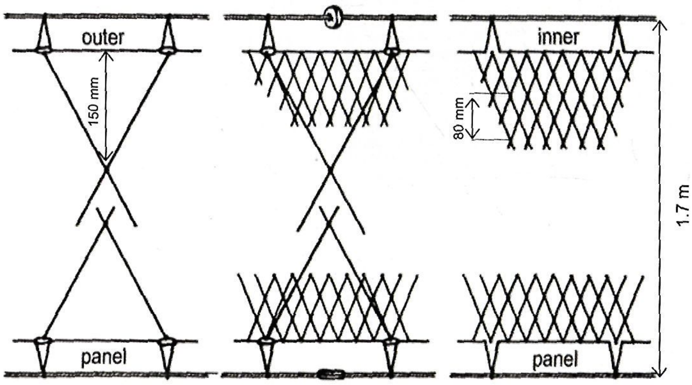


Figura R.8: Detalle del arte de trasmallo utilizado en las campañas de pecas experimentales en la RMIC.

Experiencias de marcado y recaptura

Las langotas capturadas durante las campañas de pescas experimentales en la RMIC se marcaron con marcas externas Hallprint de tipo t-bar en posición dorsolateral entre el 1er y 2^{o} segmentos abdominales (Figura R.9). Entre 1997 y 2002 se marcaron 10683 langostas y hasta septiembre de 2002 se habían recuperado 2177. Las langostas se capturaron y marcaron en la reserva marina y se liberaron en la misma localidad en que fueron capturadas o en puntos pre-definidos de la Reserva. Aproximadamente el 60% de las recapturas obtenidas hasta la fecha fueron realizadas en operaciones de pesca comercial fuera de la reserva (en caladeros del entorno de Columbretes) y el resto en campañas subsiguientes dentro de la RMIC.

Antes de la liberación y en el momento de la recaptura se tomaron los siguientes datos: Talla (longitud del cefalotórax, LC, en mm), sexo, profundidad, posición y fecha de captura o recaptura. El programa de marcado y recaptura se publicitó entre los pescadores que faenan en el entorno de Columbretes y en las cofradías y lonjas afectadas y se ofreció una recompensa económica de 12 euros por cada marca recuperada. Se proveyó a los pescadores de calibres para tomar medidas y de estadillos para anotar los datos de las langostas recapturadas.

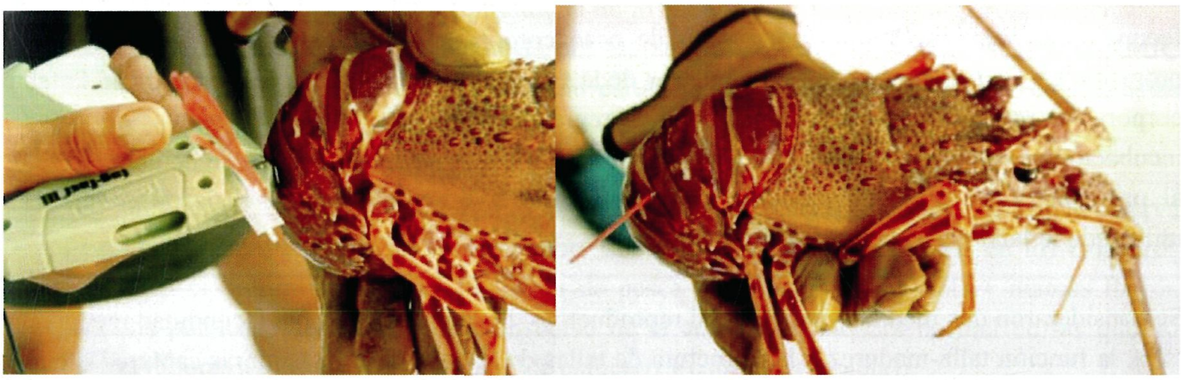


Figura R.9: Pistola y marcas utilizadas para marcar las langostas.

Estudio de la reproducción y del potencial reproductivo en la población protegida

Las muestras para el estudio de la biología reproductiva se obtuvieron de la captura de las pescas experimentales con trasmallo realizadas en la RMIC en agosto-septiembre de 1998 (agosto), febrero-marzo de 1999 (febrero), septiembre-octubre de 1999 (septiembre) y junio de 2000 (junio). Para cada langosta se registró la longitud del caparazón (LC, mm) y el peso (w, gramos). La presencia de huevos externos y de espermatóforos en las hembras y de esperma en los orificios genitales de los machos también fue anotada. En cada campaña se seleccionó una muestra de un mínimo de 5 langostas por sexo y clase de talla de 5 mm LC para su posterior disección. En estos muestreos biológicos se anotó el estado de madurez de los ovarios (de acuerdo con la escala de Marin (1987) consistente en 7 estados) en las hembras y el peso de las gónadas en machos y hembras.

El período de reproducción se estudió a partir del desarrollo temporal de los ovarios en las hembras y de la evolución del índice gonadosomático en machos y hembras. La presencia de espermatóforos en las hembras y de esperma en los machos también fue usada como indicador de actividad reproductiva. Se estimó la talla de madurez fisiológica (o talla a la cual los ovarios alcanzan la madurez) y la talla de madurez funcional (talla a la cual las hembras participan en la reproducción y ponen huevos). Las tallas a las cuales el 50% de las hembras estaban maduras o portaban huevos (L50%) fueron utilizadas para definir las tallas medias de madurez fisiológica y funcional respectivamente. La talla de primera madurez de las hembras también se estimó por la relación obtenida entre el peso de las gónadas (GW) y la talla corporal (LC) durante el período de freza. En los machos de langosta no es posible determinar la madurez fisiológica a partir de caracteres externos o por la apariencia macroscópica de las gónadas. Por consiguiente se estimó la talla de primera madurez por medio de la relación entre el peso de las gónadas y la talla corporal estimada durante el período de freza (como se ha descrito para las hembras). También se utilizó la presencia de esperma en los orificios genitales como evidencia de madurez fisiológica.

La fecundidad se definió como el número de huevos unidos a los pereiópodos de las hembras inmediatamente después de la puesta. Se extrajeron los huevos de los pereiópodos por disección, se pesaron y se congelaron para almacenarlos. Se separaron y pesaron tres submuestras de cómo mínimo el 0.5 % (en peso) de la masa total de cada puesta. Las tres réplicas de cada puesta fueron utilizadas para estimar el error de muestreo en las determinaciones de fecundidad. Las fecundidades relativa (huevos por gramo de peso corporal) y absoluta se estimaron usando el promedio de los tres conteos. Los parámetros de la función que relaciona la fecundidad con la talla corporal se estimaron mediante un análisis de regresión lineal. La pérdida de huevos durante la incubación se calculó comparando las ecuaciones talla-fecundidad en muestras de hembras ovadas al principio y al final del período de incubación. Para ello se usó el análisis de covarianza utilizando la talla de las langostas como covariable.

Se consideraron dos medidas de potencial reproductivo. La primera utiliza la fecundidad media por talla, la función talla-madurez y la estructura de tallas de la población de hembras capturadas en la campaña de junio para calcular el potencial reproductivo relativo (RRPi) por clase de tallas de la población de *P. elephas* en la reserva. En la segunda se utilizó una modificación del índice de puesta potencial de Morgan *et al.* (1982) para evaluar diferencias de potencial reproductivo en poblaciones de *P. elephas* explotadas y no explotadas. El índice de puesta potencial (IPP) se estimó mediante el producto de la CPUE de hembras maduras como índice de abundancia y la fecundidad media individual de la población. Mientras que el RRP depende de la estructura de tallas de la población de hembras, el IPP también depende de la abundancia de hembras maduras. Por lo tanto, el IPP da una medida más apropiada de potencial reproductor que el RRP al comparar poblaciones explotadas y no explotadas.

Estudio de los efectos sobre la pesquería adyacente a la RMIC

El estudio de la influencia de la RMIC sobre la pesquería de langosta en el entorno de la misma se ha evaluado mediante la hipótesis exportación de biomasa (adultos) de la reserva hacia caladeros adyacentes. Para ello se ha estudiado la distribución espacial de las capturas y del esfuerzo de la flota comercial en relación con la distancia al límite de la reserva marina. Los datos de la actividad pesquera se recogieron en el periodo 1999-2002 mediante en embarques realizados una semana por mes durante la temporada de pesca (Marzo-Agosto) en barcas colaboradoras que faenan en los caladeros del entorno de la reserva marina. Para obtener información de la distribución espacial del esfuerzo que fuera representativa de la distribución real de la pesquería se muestrearon todos los lances realizados en esa semana sin dirigir el esfuerzo de muestreo o de la actividad pesquera.

En está pesquería las langostas son capturadas con trasmallos como los utilizados en las pescas experimentales realizadas en el interior de la RMIC (ver descripción más arriba). Las redes se calan sobre fondos de roca, cascajo o maërl y se dejan caladas durante varios días (media 4-5 días), dependiendo de las condiciones meteorológicas y del mar. En cada lance se tomaron los siguientes datos: longitud de la red calada, tiempo de calada, posición, profundidad, y número de langostas capturadas con y sin marca (recapturas). Durante 1999-2002 se muestrearon 214 lances a menos de 5 Km. del límite de la reserva marina. La ausencia de actividad pesquera a distancias entre 5 y 10 Km. de la RMIC indica una clara discontinuidad de los hábitats de langosta en la zona. Además, 4 Km. es la distancia media máxima recorrida por las langostas marcadas y liberadas en la RMIC (Goñi *et al.* 2003d). La captura por unidad de esfuerzo se estimó por el número de langostas capturadas en 600 m de red por día.

De las 10683 langostas marcadas durante 1997-2001, 726 fueron recapturadas dentro de la reserva marina en campañas sucesivas hasta Septiembre 2002 y 85 fueron recapturadas en los caladeros adyacentes en el transcurso de los 214 lances de pesca muestreados. Otras 600+ marcas fueron recapturadas por los pescadores en el transcurso de la actividad pesquera normal en las que no había observadores abordo (no información de esfuerzo y captura completa).

Las distancias desde cada lance de pesca a la reserva fueron medidas en línea recta desde la posición del punto central del lance hasta el límite de la RMIC más cercano. Para cada lance se calculó, al igual que la CPUE, el número de marcas por unidad de esfuerzo (TPUE) y la proporción de langostas marcadas en cada lance (POT). El área de estudio donde opera la pesquería se dividió en celdas de 1x1 Km. y la distancia de cada celda al borde de la reserva se midió por la distancia en línea recta desde el centro de la celda (o de la porción de celda que queda fuera de la Reserva en aquellas que cruzan el límite la misma) hasta el límite de la RMIC más cercano. Para cada celda se calculó la CPUE media, el número de lances de pesca (esfuerzo por unidad de área) y la captura por unidad de área (CPUA). Modelos generales aditivos (GAM) y lineares (GLM) se utilizaron para explorar y describir las relaciones entre la CPUE, CPUA, TPUE y POT y la distancia a la reserva.

DISCUSIÓN GENERAL

P. elephas es una especie de crecimiento lento, vida larga y baja fecundidad en comparación con otras especies de langostas espinosas de interés comercial. Además, la amplitud de movimientos de los adultos es pequeña (Capítulo 2). Estas características ecológicas y biológicas, unidas a su alto precio, hacen que la especie sea muy vulnerable a la sobrepesca. No se conoce la relación stock-reclutamiento de *P. elephas*, pero su fase pelágica es larga y por tanto la dispersión por corrientes oceánicas puede ser extensiva. Por ello, si el reclutamiento ocurre lejos del stock parental, puede no existir relación entre la abundancia de reproductores y el reclutamiento local.

El que las pesquerías dirigidas a *P. elephas* en el Atlántico hayan desaparecido, junto al estado de sobre-explotación de las pesquerías del Mediterráneo, apoyan la idea de la vulnerabilidad de la especie. El inicio de la decadencia de las pesquerías de *P. elephas* parece encontrarse en los años 70 y 80 cuando el esfuerzo de pesca aumentó mucho con la substitución de métodos de pesca selectivos y poco eficientes como las nasas o el buceo por las redes con la introducción del nylon, haladores y de otros avances tecnológicos. El problema está exacerbado por la captura de langosta como bycatch en pesquerías de enmalle para peces (ej. rape). Sin embargo, la carencia de series históricas de datos de captura y esfuerzo impide evaluar está hipótesis. Un estudio reciente (Goñi *et al.* 2003b, c) indica que los trasmallos capturan una mayor proporción de langostas grandes que las nasas y que su impacto sobre los hábitats de langosta y las comunidades bentónicas donde operan es mucho mayor.

La langosta *P. elephas* es capturada por un gran numero de barcos pertenecientes a muchos puertos distribuidos a lo largo de la costa. Por ello, el control del esfuerzo pesquero en el mar es impracticable y en general los límites de longitud de redes son ampliamente excedidos. Además, mientras que las nasas tienen que ser recogidas cada día para reponer el cebo, las redes suelen dejarse en el agua dos o más días. Las malas condiciones meteorológicas hacen que a menudo las redes permanezcan en el agua durante períodos más largos con la consiguiente pérdida de captura y la devolución al mar de ejemplares inmaduros en mal estado.

La falta de datos impide discriminar el impacto relativo del aumento de mortalidad por pesca (resultante del aumento del esfuerzo de pesca) y del cambio en el patrón de explotación asociado al uso de trasmallos. Por su alto valor unitario, la explotación de *P. elephas* prosigue a pesar de los bajos rendimientos ya que el continuo aumento de los precios sostiene pesquerías económicamente viables. En muchas zonas los pescadores están presionando a los gestores para que impongan restricciones que permitan recuperar las poblaciones (Hunter 1996) y medidas adicionales, tales como áreas cerradas a la pesca, áreas abiertas sólo a la pesca con nasas, y programas para la reintroducción de las nasas están siendo consideradas en algunas regiones (ej. Islas Baleares).

En este contexto, es de gran importancia poder evaluar la efectividad de las reservas marinas para mejorar el estado de las poblaciones de *P. elephas* y su potencial para recuperar las pesquerías. La RMIC ha proporcionado está oportunidad única ya que alberga fondos de pesca de langosta tradicionales donde las tasas de explotación eran muy altas. La primera consecuencia esperada de la reducción de la mortalidad pesquera en poblaciones protegidas en reservas marinas es que la abundancia de la población aumenta (Russ 2002). Para evaluar la esperada recuperación de la abundancia de langosta en la RMIC se compararon índices de abundancia en la Reserva y en zonas explotadas de características similares. La comparación se hizo al final de la primavera, en otoño y en invierno con el fin de evaluar variaciones estacionales. Los resultados indican que entre siete y diez años después de la creación de la Reserva, la abundancia de langosta era de 5 a 20 veces superior en la RMIC que en las áreas explotadas dependiendo de la época del año. Está respuesta era de esperar dadas las altas tasas de explotación observadas en las pesquerías de *P. elephas* (Pereiro y Fernandez 1974, Marin 1987, Goñi y Latrouite 2005) así como en pesquerías de otras langostas espinosas (Childress 1997). Respuestas positivas al cese de la pesca han sido observadas en otras especies de langostas espinosas (Hunt *et al.* 1991, Cole *et al.* 1990, MacDiarmid y Breen 1993). La falta de efectividad de algunas AMPs para recuperar poblaciones de langostas se ha achacado a migraciones ontogénicas o a movimientos en busca de alimento de gran amplitud en relación con el tamaño de las AMPs (Hunt *et al.* 1991, MacDiarmid y Breen 1993). Así mismo se han observado respuestas desiguales según el sexo debido a diferencias en los patrones de movimiento (MacDiarmid y Breen 1993). Los datos de la RMIC indican que *P. elephas* tiene movilidad limitada (desplazamiento medio máximo – machos grandes < 5 Km.) y que por lo tanto el tamaño de la RMIC (9 x 4.5 Km.) es adecuada para recuperar la población local de *P. elephas* (Capítulo 5).

La población de langosta en la RMIC sufre notables variaciones estacionales de abundancia y estructura poblacional (tallas y sexo) (Capítulo 3) aunque, en conjunto, la abundancia parece estabilizada mientras que la talla media individual continúa aumentando. Esto sugiere que la recuperación de la población en cuanto a número de individuos puede haber alcanzado un límite, posiblemente relacionado con la capacidad de carga de la RMIC. Una explicación complementaria sería que la densidad de población ha llegado a un punto tal que cualquier aumento se traduce en la emigración de individuos al exterior de la Reserva donde son capturados por la pesquería. Las variaciones estacionales observadas parecen relacionadas con migraciones batimétricas que llevarían a ciertos componentes de la población hacia dentro y hacia fuera de la Reserva (Capítulo 3). Estas conclusiones deben ser consideradas con precaución ya que cambios estacionales en el comportamiento de las langostas asociadas a la reproducción y la muda, especialmente en machos, pueden afectar las estimaciones del tamaño y estructura de la población de *P. elephas* (Goñi *et al.* 2003b).

La mayor densidad de población dentro de la RMIC se traduce en un gradiente negativo de captura por unidad de área en la pesquería comercial adyacente según aumenta la distancia a la Reserva (Capítulo 5). Este efecto es muy pronunciado en el primer kilómetro pero se extiende hasta 4.5 Km. La información obtenida de langostas marcadas y liberadas en la RMIC y recapturadas en la pesquería adyacente sugiere que la RMIC está actuando como fuente de langostas a la pesquería adyacente (Capítulo 5). Este proceso de exportación (o rebosamiento) podría ser causado por procesos denso-dependientes o podría ser el resultado de movimientos aleatorios o estacionales entre areas de alta y baja densidad (Sanchez-Lizaso *et al.* 2000, Jennings 2001, Russ 2002). Parece que las migraciones estacionales juegan un papel en está exportación; los cambios de abundancia de machos y hembras en los fondos someros de la RMIC son consistentes con movimientos cíclicos en profundidad observados en *P. elephas* del Atlántico (Mercer 1973, Ansell y Robb 1977) y que son comunes en poblaciones de otras langostas espinosas de aguas templadas (Hernkind 1980).

La CPUE comercial declina abruptamente cerca del límite de la reserva en consonancia con la concentración de esfuerzo en los bordes de la RMIC, la alta capturabilidad (Goñi *et al.* 2003b) y tasa de explotación en la pesquería cercana (Goñi *et al.* 2000), y la movilidad limitada de la especie (Goñi *et al.* 2003d). La bajada de CPUE es seguida por una plataforma que sugiere que la exportación es suficiente para mantener tasas de captura constantes hasta 1.5 Km. del borde de la Reserva (Capítulo 5). Una característica del esfuerzo de pesca que se ejerce en los límites de la Reserva, que contribuye a la depresión local de CPUE observada, es la estrategia de los pescadores de ocupar esos deseados lugares de pesca a lo largo de la temporada con independencia de los rendimientos. Muchos estudios de pesquerías cercanas a reservas marinas documentan la concentración de esfuerzo en los bordes de AMPs (Yamasaki y Kuwahara 1989, Johnson *et al.* 1999, Murawski *et al.* 2004, Kelly *et al.* 2002, Ashworth y Ormond 2005). En caladeros no asociados a AMPs los pescadores tienden a recolocar sus redes cuando los rendimientos bajan. La alta efectividad de los barcos en la pesquería comercial asociada a la eficacia del trasmallo para la captura de langosta, inducen altas tasas de explotación local y agotan el área rápidamente. En el extremo, si los barcos pescasen siempre en el mismo sitio y ejercieran una alta tasa de mortalidad pesquera local, podrían capturar (en cada intervalo de tiempo) todas las langostas que saliesen de la Reserva (Maury y Gascuel 2001).

En general la evidencia de exportación de langostas desde reservas marinas es escasa. Kelly *et al.* (2002) consideraron evidencia de exportación el que la CPUE media de langosta *Jasus edwardsii* alrededor de una AMP en Nueva Zelanda fuera similar a la de caladeros explotados a pesar de no poder acceder a los arrecifes costeros más productivos. La alta variabilidad de las capturas cerca de la reserva y el patrón de movimientos de la especie derivados de estudios de marcado-recaptura (Kelly 2001, Kelly y MacDiarmid 2003) avalaban esa conclusión. Por otra parte Davidson *et al.* (2002) dedujeron que se producía exportación a partir de la observación de un gradiente negativo de densidad de la misma especie del centro al borde de la AMP. Entre los crustáceos la evidencia más convincente la constituye el gradiente negativo de CPUE del cangrejo *Chionectes opilio* que se extiende hasta 13 Km. de una reserva marina en Japón (Yamasaki y Kuwahara 1989).

Por primera vez en el Mediterráneo español se ha determinado el periodo de reproducción, la talla de primera madurez, la fecundidad y, lo que es más importante en el contexto de reservas marinas, el potencial reproductivo de una población no explotada de *P. elephas*. En las Islas Columbretes *P. elephas* se reproduce entre Junio y Octubre, con un pico de puesta en Septiembre. La incubación de los huevos se prolonga durante unos 5 meses y los huevos eclosionan entre Diciembre y Febrero. La madurez sexual tiene lugar a la misma edad (4 años, Marin 1987) pero a talla ligeramente distinta en hembras (77 cm LC) que en machos (82 cm LC) (Capítulo 4). La fecundidad de *P. elephas* en la población protegida aumenta linealmente con la talla hasta la talla máxima de las hembras. Esto es importante en el contexto de una población protegida ya que se ha sugerido que podría darse senectud reproductiva en las hembras más longevas (Chubb 2000). Sin embargo, el máximo rendimiento reproductivo (número de huevos por gramo) se alcanza a tallas intermedias, como observó Bertelsen y Matthews (2001) en *Panulirus argus*. También se observó que el diámetro de los huevos aumenta con la talla de la hembra, lo que sugiere que, al igual que en otras especies (*J. edwardsii*, MacDiarmi, comunicación personal), huevos de mayor tamaño podrían dar lugar a larvas más grandes capaces de sobrevivir en condiciones de poco alimento durante periodos más largos.

A lo largo de la mayor parte del rango de tallas de las hembras maduras, la fecundidad individual en la Reserva es mayor que en otras poblaciones Mediterráneas estudiadas (Córcega) (Capítulo 4). Esto puede resultar de la mayor disponibilidad de machos grandes en la población protegida junto con su mayor contribución potencial a la reproducción en comparación con los machos pequeños (MacDiarmid y Buttler 1999). Es interesante notar que la relación talla-fecundidad de la población protegida coincide con la estimada para una población poco explotada de Irlanda (Mercer 1973). El estudio de la fecundidad de la población protegida ha proporcionado una oportunidad única para evaluar hipótesis convencionales tales como la denso-dependencia de la fecundidad de las langostas (Chittleborough 1976) o la mayor fecundidad a la talla como resultado de la explotación (DeMartini *et al.* 1993). Los resultados del estudio de *P. elephas* en la RMIC no apoyan estas hipótesis.

Un resultado útil de este trabajo indica que la TML (80 mm LC) de *P. elephas* en las pesquerías mediterráneas, que es sólo ligeramente superior a la talla de madurez sexual, contribuye únicamente el 1% del potencial de producción de huevos de la población protegida (Capítulo 4). La superior contribución de las hembras grandes al potencial reproductivo de la población ha sido observado en poblaciones de otras especies de langostas espinosa (*P. argus* and *Panulirus homarus*, Kanciruk 1980). Jamieson (1993) propuso que la TML, de *P. elephas* en este caso, debería establecerse en una talla que permitiese a los individuos reproducirse al menos una o dos veces antes de ser susceptibles a la pesca. En todo caso, el aumento de la TML por si sola no parece haber sido capaz de evitar la sobrepesca de poblaciones de *P. elephas* de la Bretaña (Latrouite y Noel 1997) y Croacia (Soldo *et al.* 2001). Por ello, el aumento de la TML puede considerarse una medida necesaria pero insuficiente para asegurar la continuidad de pesquerías de *P. elephas* viables.

Las poblaciones protegidas están caracterizadas no sólo por su superior abundancia y producción relativa de huevos pero también por una mayor proporción de individuos grandes (naturalización de la estructura poblacional) y por tanto por su mayor potencial reproductivo (Russ 2002). Por ello, la comparación de los índices de potencial de puesta (número de huevos por unidad de área) en poblaciones explotadas y protegidas permite evaluar como la producción de huevos de *P. elephas* puede estar influida por la explotación. Los resultados del estudio indican que, tomando la población de la Reserva como referencia y asumiendo similar productividad en todas las áreas, el potencial de puesta en la Reserva puede haber aumentado entre 6 y 20 veces en una década (Capítulo 4). Este resultado es comparable a las estimaciones de número de huevos por recluta obtenidas por Annala (1991) en poblaciones explotadas y no explotadas de *J. edwarsii* (1.2% a 36.8% dependiendo del área; media = 20.1%), y es superior a la tasa de incremento medio de 6.6% estimado por Kelly *et al.* (2000) para la misma especie en tres AMPs. El aumento del potencial de puesta de huevos en la RMIC parece deberse principalmente al mayor número de hembras maduras disponibles (más que a la ligeramente mayor talla media de las mismas) y a su mayor fecundidad (Capítulo 4).

En resumen, la densidad, talla media y potencial de puesta de *P. elephas* son superiores en la RMIC que en las áreas explotadas estudiadas y sugieren que son el resultado del cese de la pesca en la Reserva. Además, la distribución espacial de la captura y el esfuerzo en la pesquería adyacente indica que se produce una emigración de langostas de la Reserva que alimenta la pesquería adyacente. Sin embargo, la falta de otros lugares comparables y de datos recogidos antes de que las medidas de protección entrasen en vigor, impiden una evaluación verdadera de las respuestas de *P. elephas* en la RMIC (Underwood 1992). Esto es un problema común agravado por el hecho de que muchas reservas se establecen en áreas singulares (see, *e.g.*, Cole *et al.* 1990, Carr y Reed 1993, Jones *et al.* 1993, MacDiarmid y Breen 1993). Desgraciadamente este problema no tiene solución y el dilema subraya la importancia de realizar estudios que sirvan de referencia antes de que las AMPs sean establecidas. Finalmente, a pesar de ser crucial para una completa comprensión de la efectividad de la RMIC, el estudio del patrón de dispersión de huevos y larvas a partir de la Reserva y de la relación entre la producción de huevos y el reclutamiento resultante no ha sido acometido debido a los formidables problemas logísticos que impone.

CONCLUSIONES

- Las características biológicas y ecológicas de *P. elephas* – crecimiento lento, vida larga (> 15 años), fecundidad baja y movimientos restringidos – la hacen muy vulnerable a la explotación.

- Los altos precios de *P. elephas* hacen que su explotación sea provechosa incluso a niveles de abundancia bajos. En la actualidad, la mayoría de las pesquerías en el Atlántico han desaparecido y las poblaciones en el Mediterráneo se consideran sobre-pescadas. Pesquerías viables existen principalmente en archipiélagos e islas.

- Entre siete y nueve años después de la creación de la Reserva Marina de las Islas Columbretes (RMIC), la abundancia de *P. elephas* era de 5 a 20 veces superior que en fondos explotados cercanos, dependiendo de la estación del año.

- Los cambios temporales de abundancia de langosta siguen patrones diferentes en la Reserva y en los fondos explotados estudiados. En la Reserva la abundancia era superior al principio del verano antes de la reproducción; esto está asociado con la migración reproductiva hacia fondos someros. En las áreas explotadas, la abundancia máxima se registró al final del periodo de veda, en Febrero, indicando que las vedas temporales son efectivas para recuperar poblaciones explotadas de langosta.

- La variabilidad temporal y batimétrica de la estructura de tallas y sexos de la población protegida en la RMIC es coherente con migraciones anuales en profundidad observadas en poblaciones atlánticas de *P. elephas*, así como en poblaciones de otras especies de langosta espinosa de aguas templadas.

- Al igual que en otras áreas, en la Reserva *P. elephas* realiza una sola puesta de huevos anual entre Junio y Octubre. Las hembras grandes copulan y ponen huevos antes que las hembras pequeñas mientras que los machos copulan y recargan las gónadas repetidamente a lo largo del periodo reproductivo. La incubación de los huevos dura alrededor de cinco meses.

- La madurez fisiológica y funcional de las hembras en la RMIC tiene lugar con 76-77 mm LC. Los machos alcanzan la madurez fisiológica a mayor talla – 82 mm LC - pero a la misma edad que las hembras.

- La fecundidad individual de *P. elephas* en la población protegida aumenta linealmente con la talla hasta la máxima talla observada, lo que contradice la hipótesis de infertilidad de las hembras de mayor edad.

- La fecundidad relativa máxima – huevos por gramo - se alcanza a tallas intermedias (105-110 mm LC).

- El tamaño del huevo aumenta con la talla de la hembra. De acuerdo con observaciones realizadas en otras especies, huevos de mayor tamaño podrían dar lugar a larvas más grandes capaces de sobrevivir en condiciones de poco alimento durante periodos más largos.

- A lo largo de la mayor parte del rango de tallas de las hembras maduras la fecundidad individual en la población protegida es más alta que en las poblaciones explotadas del Mediterráneo. Se propone que la diferencia podría deberse a la mayor disponibilidad de machos grandes en la población protegida junto a su mayor contribución potencial a la reproducción en relación con los machos de pequeños. Este resultado no apoya la hipótesis de denso-dependencia de la fecundidad de las langostas espinosas ni la de mayor fecundidad relativa como resultado de la explotación.

- En la población no explotada de la Reserva la clase de talla de hembras maduras que contribuyen mas a la producción de huevos es 105-110 mm LC (que corresponde a unos 7-8 años), que es muy superior a la talla mínima legal (TML, 80 mm LC) y edad (unos 3-4 años).

- Las hembras maduras jóvenes que están protegidas por la TML proporcionarían tan solo el 1% del potencial de producción de huevos de una población no pescada y son 20 veces menos productivas que las hembras en la clase 105-110 mm LC.

- Tomando la RMIC como referencia y asumiendo similar productividad de los caladeros estudiados, el potencial de puesta en la reserva puede haber aumentado entre 6 y 20 veces en diez años.

- Alrededor del 75% de los lances de pesca en la pesquería comercial adyacente a la Reserva (en un radio de 5 Km.) se realizan a menos de 1 Km. del borde de la misma.

- La CPUE comercial muestra una relación negativa con la distancia a la CIMR. El gradiente de CPUE tiene una caída brusca muy cerca del borde que está seguida de una meseta y un declive gradual a medida que aumenta la distancia. La caída brusca de CPUE está asociada a la concentración del esfuerzo pesquero cerca de la Reserva que causa sobrepesca local. La meseta que sigue a la caída sugiere que la exportación de langostas de

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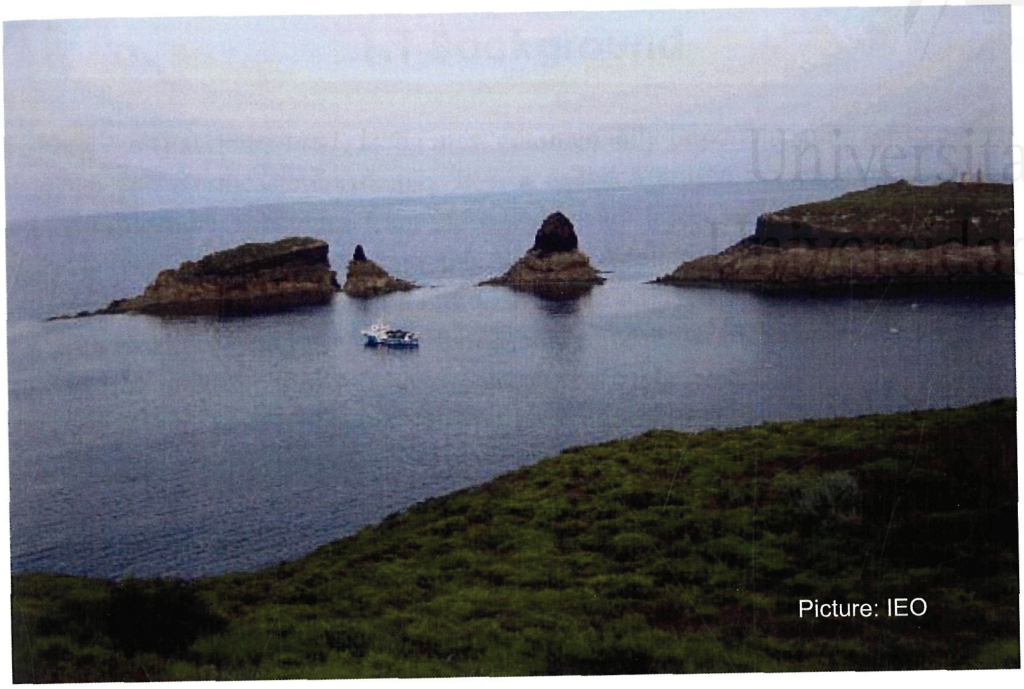
la RMIC es suficiente para mantener tasas de captura estables hasta una distancia de 1000 m del borde.

- La captura por unidad de área en la pesquería comercial adyacente disminuye linealmente con la distancia al borde.

- Tanto el gradiente negativo de CPUE como la concentración de esfuerzo pesquero en los límites de la RMIC pueden ser explicados por un proceso de exportación de adultos. Datos de marcado y recaptura también indican que la RMIC está suministrando langostas a la pesquería adyacente.

- Tanto la falta de datos anteriores a la creación de la Reserva como réplicas de la Reserva impiden una evaluación verdadera de los efectos de la protección sobre *P. elephas* en la RMIC y en las pesquerías cercanas.



Picture: IEO

Picture: Animal's House

CHAPTER 1: GENERAL INTRODUCTION

1.1 Background

Palinurus elephas (Fabricius 1787) is the most commercially important spiny lobster species in the Mediterranean and Northeastern Atlantic. It is a decapod crustacean of large size that inhabits rocky and coralligenous substrates from close inshore to depths of over 160 m (Holthuis 1991). Commonly known as "red lobster" in the Western Mediterranean and as "crayfish" in the Northeastern Atlantic, *P. elephas* has traditionally been targeted by artisanal fisheries throughout its range, with most occurring in the Western Mediterranean. Its high commercial value (up to 60 euros/kg first sale in 2003) allows fishing to go on profitably even at low yields. Because of that, most Atlantic stocks have collapsed (Latrouite & Noel 1997, Goñi & Latrouite 2005) and Mediterranean ones are overfished.

In the Spanish Mediterranean, over six hundred artisanal vessels and some 1100 fishermen engage in lobster fishing every year (Alarcón 2001). The fishery is regulated by an annual 6-month closure during the egg-bearing period (September to February), a minimum landing size (MLS) (80 mm CL) and a ban on catching berried females. The high unit value and the relative scarcity of *P. elephas* have been important obstacles to research and, until recently, knowledge of the biology, ecology and fisheries of the species was scarce while most studies were contained in unpublished documents from universities or research institutes.

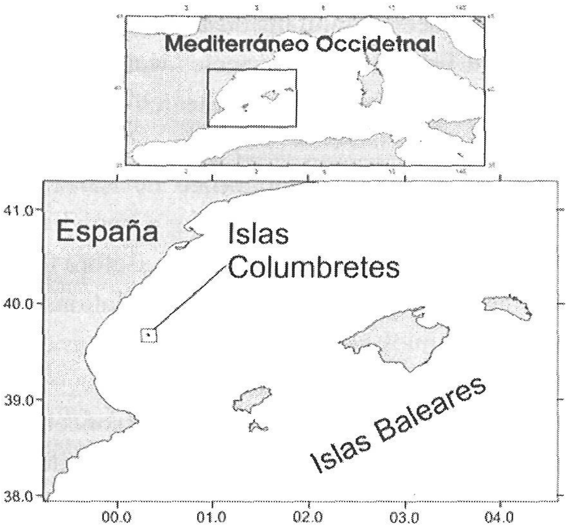
In 1997, the Centro Oceanográfico de Baleares (Instituto Español de Oceanografía) initiated a research project aimed at developing a knowledge base of the biology, ecology and fisheries of *P. elephas* in the Spanish Mediterranean. Before then, only two in depth studies of *P. elephas* existed, one on the biology and ecology of populations off Ireland (Mercer, 1977) and another one on the fisheries, dynamics and biology of *P. elephas* off Corsica (Marin, 1987). In addition, a number of specific studies were available from the 1970s and 1980s on various aspects of the biology and fisheries of Atlantic (Bouvier 1914, Vasconcellos 1960, Gibson & O'Riordan 1965, Hepper 1967, 1970, 1977, Ansell & Robb 1977, Latrouite & Alfama 1996, Latrouite & Noël 1997) and Mediterranean (Santucci 1926, 1928, Gamulin 1955, Campillo & Amadei 1978, Campillo *et al.* 1979, Campillo 1982, Cuccu *et al.* 1999, Hunter 1996, Díaz *et al.* 2001, Soldo *et al.* 2001) populations. Later, Hunter *et al.* (1999) published a short review of the species. In recent years Goñi *et al.* (Goñi *et al.* 2000, Goñi *et al.* 2001a,b, Goñi *et al.* 2003a,b,c, Quetglas *et al.* 2005) have conducted in the framework of the above-mentioned project a number of studies on the population of the Columbretes Islands Marine Reserve and in the most important Spanish lobster fisheries. Furthermore, all the knowledge available on the species has been appraised and summarized in a recent review article (Goñi & Latrouite 2005).

In this Thesis Chapter 1 constitutes an up-to-date, comprehensive appraisal of the knowledge of the biology, ecology and fisheries *of P. elephas* available to date and is an extract of the above-mentioned article (Goñi & Latrouite, 2005). Chapters 2 to 4 contain three studies, two of them published (Goñi *et al.* 2001b, Goñi *et al.* 2003a) and one submitted, that constitute a coherent effort to assess the effects of the cessation of fishing in the Marine Reserve of the Columbretes Islands on the *P. elephas* population. Chapter 2 studies the spatial dynamics of the protected population in order to infer the rebuilding of the population in the Reserve; it also assesses the temporal dynamics of the population inside the Reserve. Chapter 3 covers the reproductive biology of the species in the Reserve, estimates the relative reproductive potential of the unfished population and assesses the spawning potential per unit area in the Reserve relative to that of exploited Mediterranean populations. Chapter 4 studies the spillover potential of lobsters by examining the influence of the Reserve on the spatial distribution of catches and effort in the adjacent lobster fishery with the help of some specific results of a tag-release programme conducted in the Reserve since 1997.

1.2. The Columbretes Islands Marine Reserve

The group of islands that form the archipelago known as Columbretes Islands is located 30 nm off the coast of Castellón (Eastern Iberian Peninsula) between the parallels 39º 51' and 39º 55' latitude N and the meridians 0º 40' and 0º 42' longitude E from Greenwich, European datum (Figures 1.1 and 1.2).

Figure 1.1: Map of the Western Mediterranean indicating the location of the Marine Reserve of the Columbretes Islands.



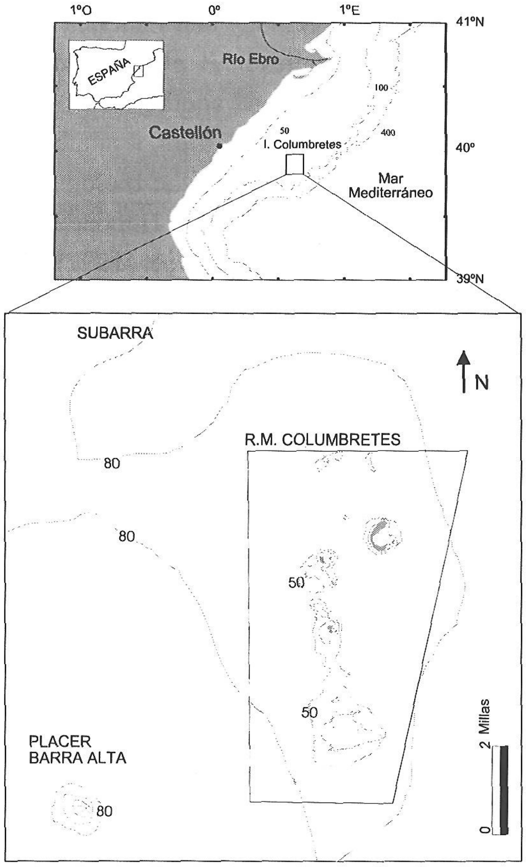


Figure 1.2: Location of the Marine Reserve of the Columbretes Islands indicating the boundary and the two reference areas used for the spatial comparison of abundante indices, Placer de la Barra Alta (PLA) y Subarra (SUB) (depth in meters).

The Columbretes Islands were formed in the Quaternary and are the emerged part of an extensive, submerged volcanic field situated at the edge of the huge platform located south of the mouth of the Ebro River (Templado & Calvo 2002). Four island groups and a few rocky outcrops that cover 19 ha constitute the emerged part of the archipelago. The seabed is made up of vertical or sub-vertical rocky substrates of volcanic origin from the surface to 30-40 meters of depth at the base of which lay blocks and boulders collapsed from the cliffs. A detritic stratum alternating with areas of mud of continental origin follows.

The great distance that separates Columbretes from the coast, together with the lack of contaminant sources in the islands, determine the high quality of their marine waters. The transparency of the water allows the presence of erected algae (e.g., *Laminaria,*) at considerable depth (80 m) (Templado & Calvo 2002). Another notorious characteristic of the benthic communities of the archipelago is the absence of the seagrass *Posidonia oceanica* and the presence of the sea grass *Cymodocea nodosa* and of an exuberant community of photofilic algae (Templado & Calvo 2002). Some animal species are also unusually abundant in Columbretes, and especially since fishing was banned. In this context, the spiny lobster *Palinurus elephas* has become, perhaps, the most emblematic species of the archipelago.

The first initiatives for the conservation of the archipelago date from the late 1970s. However, it took over ten years to establish the Columbretes Islands Archipelago as a Natural Park (Parque Natural) by decree 15/88 of the Consell de la Generalitat Valenciana on 25 January 1988. Around the Park, a Marine Reserve (Reserva Marina) was soon created by ministerial order of 19 April 1990 by the Ministerio de Agricultura y Pesca of the national government. The stated objectives of the the establishment of the Reserve were '*to create areas of integral reserve and of restricted access for maritime fishing and the protection of the local marine resources*'.

The Columbretes Islands Marine Reserve (CIMR) covers 4400 ha and extends from the shore up to 90 m depth. At the time of its creation had two integral reserves encompassing 540 ha where no extractive activities were allowed. Now there are five integral reserves encompasing 1882.6 Ha closed to all human activities except research and education: around the Murall del Cementeri in the north (270 ha), L'Illa (269 ha), La Ferrera, (269 ha), La Horadada (367 ha) and El Carallot (688 ha) (Figure 1.3). Outside these areas, all fishing is forbidden except for limited professional artisanal fishing with hand-line, troll-line and squid-jig and purse seining for small pelagic fishes. Only boats listed in the CIMR census at the time of its creation are allowed to fish. Limited recreational fishing is also allowed with authorization and without anchoring. Lobster fishing is forbidden anywhere in the Reserve. This status entails, in accordance with the classification of marine protected areas of the International Union for the Conservation of Nature, conservation through active management and the sustainable use of its marine resources (Templado & Calvo 2002). The fishing prohibitions are in force since 1991 when a warden house was built; compliance with the fishing regulations is very high although some poaching around the boundaries may occur.

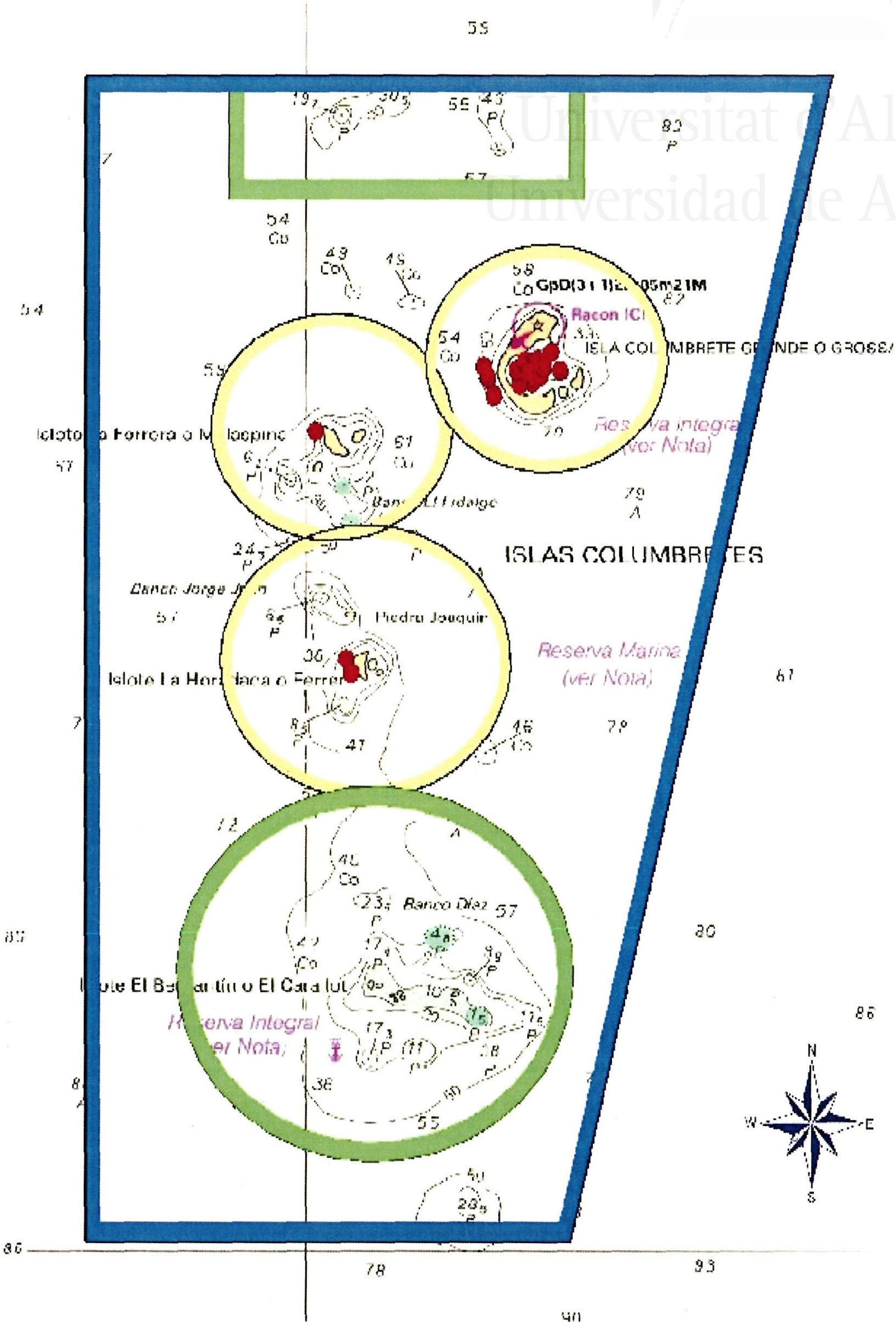


Figure 1.3: Zoning of the Marine Reserve of the Columbretes Islands. Green: no human activities allowed; Yellow: recreational diving allowed; Blue: fishing with restrictions allowed (see text).

In the Columbretes Archipelago adult *P. elephas* inhabit rocky and coralligenous habitats in the circa-littoral stratum from 30-90 m depth, although specimens are occasionally observed in shallower waters generally below the (summer) thermocline (15-25m). Post-larvae and juveniles can settle in very shallow waters (< 10m) but are more abundant at depths >20m.

The lobster *Palinurus elephas*, together with the crab *Maja squinado*, now disappeared from the area, has been one of the traditionally most valued fishing resources in the archipelago and detailed news of their harvest date from the end of the 19th century (Von Salvador, 1895). Fishermen used trammel nets and baited traps to catch lobsters until the development of new materials and hauling techniques in the 1970s and 1980s led to the expansion of trammel-netting for lobsters. Effective fishing effort increased thereafter, fuelled by a growing tourist market around the Mediterranean coast. Since the establishment of the CIMR, fishing effort has concentrated along its outer boundaries and in traditional fishing grounds mainly to the west and north of the archipelago (Figure 1.4).

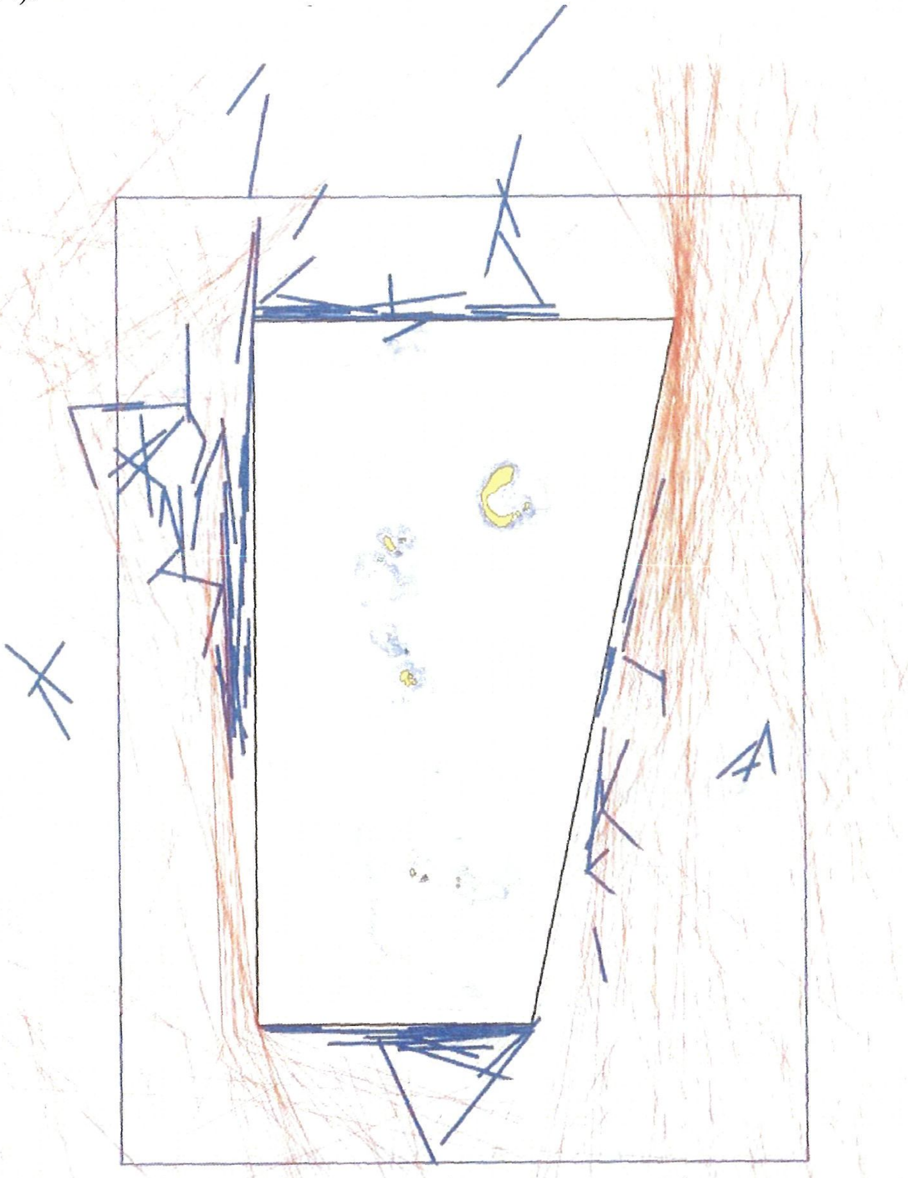


Figure 1.4: Pattern of distribution of fishing activities around the Marine Reserve of Columbretes Islands. Blue lines: artisanal fishing (gillnets, trammel nets and long-line); red lines: paths of bottom trawls. Square shows delimitation of possible expansion of the MPA. Source: Data collected by wardens of the CIMR in 2003.

1.3. Effects of protection on spiny lobster populations in marine reserves

Of all the European seas, the Mediterranean harbours the largest number of marine reserves; approximately 50 were in operation by 1999 (Boudouresque 2000). Of these, the CIMR is the only one that protects traditional fishing grounds of the species where *Palinurus elephas* is a key component of the benthic ecosystem.

At the time of the establishment of the CIMR no particular attention was given to determining characteristics such as size or level of protection needed for effective protection of any of the resident marine species of major commercial or ecological interest. Only eight years after the creation of the Reserve a study was initiated to investigate the dynamics and responses to the cessation of fishing of the spiny lobster *Palinurus elephas*. Until then, no studies had been conducted within the Mediterranean Sea to assess the effectiveness of marine protected areas (MPAs) on spiny lobsters and only one study had addressed the dynamics of a Mediterranean population (Marin 1987, for *P. elephas* off Corsica).

The responses of spiny lobster populations to protection in MPAs have been assessed in a number of protected areas around the world. The best-studied species are *Panulirus argus* off Florida (e.g., Davis 1977, Davis & Dodrill 1980, Hunt *et al.* 1991) and *Jasus edwardsii* off New Zealand (e.g., Cole *et al.* 1990, MacDiarmid & Breen 1993, Babcock *et al.* 1999, Kelly *et al.* 2000, 2002). From the point of view of a fished population, a number of responses are expected when fishing ceases in a reserve (see reviews in Dugan & Davis 1993, Sánchez-Lizaso *et al.* 2000, Mosquera *et al.* 2000, Halpern & Warner 2002, Russ 2002). The immediate consequence is that mortality declines and population size increases. As organisms in the MPA are allowed to grow, the mean individual size in the population also increases. Since fecundity increases with size, a consequence of the combined effect of larger population and individual size is an increase of the reproductive potential of the population. The greater reproductive potential of a protected spiny lobster population may originate not only from the higher number and larger size of females, but also from the increased mating opportunities and effective fecundity provided by more and larger males available in the unfished population (MacDiarmid & Buttler 1999).

The effects so far described are circumscribed to the MPA. However, increases in density of organisms within no-take marine reserves can also result in the enhancement of yields in neighbouring fisheries through export of eggs and larvae and the emigration of harvestable individuals (see reviews in Dugan & Davis 1993, Roberts & Polunin 1993, Guenette *et al.* 1998, Gell & Roberts 2002, Russ 2002). However, while many studies document the recovery of previously exploited populations inside MPAs, recent reviews highlight the meagre evidence available for protection effects outside MPAs (Russ 2002). Benefits to exploited populations have been difficult to demonstrate, partly because most marine reserves are small and were not designed for fisheries purposes, but also due to the lack of fishery data before reserve creation (Dugan & Davis 1993). Lack of spatial replication is also a problem (Palumbi 2001). In addition, few studies have investigated spillover over long enough periods to see the effect develop fully (Russ *et al.* 2004).

Some spiny lobsters studies have demonstrated increased abundance and mean size within MPAs compared to exploited areas (e.g., Cole *et al.* 1990, Hunt *et al.* 1991, MacDiarmid & Breen 1993, Babcock *et al.* 1999, Kelly *et al.* 2000), while others did not find differences in lobster abundance and mean size between exploited and protected areas. In one case, the relatively large foraging range of *P. argus* in relation to the small size of the core area of an MPA off Florida prevented the recovery of the population in the protected area (Hunt *et al.* 1991). Similarly, the extensive migrations of juveniles of *Jasus verreauxi* made ineffective their protection in a small MPA off New Zealand (MacDiarmid & Breen 1993). In the same study, male *J. edwardsii* are reported to migrate out of the MPA and be caught in the adjacent fishery. From these and other studies has become clear that the size of the protected area relative to the mobility of a species and the type and extent of the habitats encompassed within the MPA play key roles in the recovery of lobster populations.

The reproductive biology of protected spiny lobster populations has been studied in *J. edwardsii* (MacDiarmid 1989a, b) and *P. argus* (Davis 1975, Bertelsen & Mathews 2001) and the increase in reproductive potential has been documented in both species (Annala 1991, Kelly *et al.* 2000, Bertelsen & Cox 2001), although the recovery pattern differed in the MPAs studied (Kelly *et al.* 2000). Dramatic reductions of spawning potential in exploited areas have been associated with severely reduced abundance of large females (Lyons *et al.* 1981, Kelly *et al.* 2000), yet the recovery of numbers of very large male *P. argus* in the Dry Tortugas National Park has been put forward as the reason for the improved mating success of large females (in terms of proportion berried) (Bertelsen & Cox 2001).

Regarding effects outside MPAs, studies of *J. edwardsii* have compared fishery yields near and far from reserve boundaries some time after reserve creation (e.g., Kelly *et al.* 2002), or gradients from the edge towards the centre of the reserve (Davidson *et al.* 2002). Both studies suggest, but do not demonstrate, supply of lobster from the reserves to the adjacent fisheries. Some studies have demonstrated that fish or invertebrates tagged and released inside protected areas are caught outside them (Davis & Dodrill 1980, 1989, Gitschlag 1986, Hunt *et al.* 1991, MacDiarmid & Breen 1993, Attwood & Bennett 1994, Sauer 1995, Yamasaki & Kuwahara 1990, Bohnsack 1998, Goñi *et al.* 1999). However, this kind of studies usually does not demonstrate that emigration is higher than immigration. The few lobster studies that address bi-directional movements report contrasting results (e.g. Davis & Dodrill 1989, Rowe 2001, Kelly & MacDiarmid 2003) depending on the species, life stages, habitats and size of the MPAs considered. Goñi *et al.* (1999) discuss the difficulties inherent to tag-recapture experiments conducted to asses net movement across reserve boundaries when recapture possibilities (fishing effort) is difficult to assess and generally lower inside than outside.

Finally, no studies of lobster species have investigated export of eggs and larvae from MPAs to fished areas, no doubt because of the daunting logistic problems involved in tracing the fate of the pelagic larvae during long periods (Russ 2002).

The effects of protecting *P. elephas* populations have been addressed for the first time in the three studies contained in Chapters 3, 4 and 5 herein conducted in the CIMR since 1997. Of the expected responses of spiny lobster populations to protection described in the previous paragraphs, this work combines the study of aspects of the biology, fisheries and dynamics of *P. elephas* in the protected

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and fished populations to address the effects of protection on the relative abundance, reproductive and spillover potential of the CIMR lobster population. Chapters 2, 3, 4 and 5 of this thesis are self contained, each having specific introduction, methods, results, and discussion sections, when relevant.

Pictures: IEO & IFREMER

CHAPTER 2: BIOLOGY, ECOLOGY AND FISHERIES OF *P. ELEPHAS* (FABRICIUS, 1787)

Extract from manuscript
R. Goñi and Latrouite, D. (in press). Biology, ecology and fisheries of Palinurus spp. of European waters, *P. elephas* (Fabricius, 1787) and *P. mauritanicus* (Gruvel, 1911). *Cahiers de Biologie Marine*.

Abstract

Palinurus elephas is the most important commercial spiny lobster species of the family Palinuridae that occur in the Northeast Atlantic and Mediterranean and has traditionally been the preferred target of lobster fisheries throughout its range. Its high unit value and relative scarcity have been important obstacles to research and knowledge of its biology, ecology and fisheries is limited. Nevertheless, over time a considerable number of studies have been conducted, though most of these are contained in university theses or in publications of limited circulation. This work is an up-to-date review of available knowledge on the biology, ecology and fisheries of *P. elephas*.

2.1 Introduction

Palinurus elephas is the most commercially important spiny lobster species in the Northeast Atlantic and Mediterranean and has traditionally been target of fisheries off Ireland, the UK, France, Portugal, Spain, Italy, Greece, Tunisia, Morocco and adjacent Mediterranean waters. The species has not been extensively studied probably because of the high costs of the animals that reduce sampling and experimental possibilities. Their high unit value also makes the fisheries economically feasible despite low yields and is the prime cause for the overfished status of their populations. Nevertheless, a number of studies have been conducted, mainly before the 1970s, covering various aspects of the biology and fisheries of Atlantic (Cunningham 1892, Bouvier 1914, Fage 1927, Heldt 1929, Orton & Ford 1933, de Vasconcellos 1960, Karlovac 1965, Gibson & O'Riordan 1965, Hepper 1967, 1970, 1977, Corral 1968, Giménes 1969, Moraitopoulou-Kassimati 1973, Ansell & Robb 1977, Hunter *et al.* 1996) and Mediterranean (Santucci 1925, 1926, 1928, Gamulin 1955, Campillo & Amadei 1978, Campillo *et al.* 1979, Campillo 1982, Marin 1985, 1987) populations. Many of these studies were covered in a succinct review of the species published by Hunter in 1999. However, Hunter's review does not cover work done on Mediterranean populations after 1987, or on Atlantic populations after 1996. Yet, in recent years a good deal of new knowledge has become available on this species, particularly on larval ecology and recruitment (Díaz *et al.* 2001, Kitakka & Abrunhosa 1997, Kittaka *et al.* 2001), adult ecology and habitat (Relini & Torchia 1998, Secci *et al.* 1999, Cuccu 1999, Cuccu *et al.* 1999, Quetglas *et al.* 2001), diet (Goñi *et al.* 2001a), reproduction (Latrouite & Noël 1997, Goñi *et al.* 2003a), growth (Cuccu 1999, Follesa *et al.* 2003), genetics (Cannas *et al.* 2003), fisheries (Petrosino *et al.* 1985, Zarrouk 2000, Soldo *et al.* 2001, Gristina *et al.* 2002, Goñi *et al.* 2003b, c, Gristina & Gagliano 2004) and responses of populations to protection (Goñi *et al.* 2001b, Goñi *et al.* 2003a). Some of these studies are in unpublished reports or in publications of limited circulation.

2.2. Description, distribution, ecology and habitat

Class: Crustacea
  Infra class: Malacostraca
    Order: Decapoda
      Sub order: Reptantia
        Family: Palinuridae
          Division: Stridentes
            Genus: *Palinurus*

Species: *P. elephas* (Fabricius, 1787)

Basque: otarrain - **Catalan**: llagosta - **Danish**: languster, langust – **Dutch**: langoesten, hoornkreeft - **English**: spiny lobster, rock lobster, sea crayfish, thorny lobster, crawfish, crayfish - **Finish**: languisti – **French**: langouste rouge – **Galician**: Langosta - **German**: Languste, Panzerkrebs, Heuschreckenkrebs - **Greek**: astakos – **Icelandic**: huma – **Italian:**

aragosta, aragusta, arigosta, aligusta, aliusta – **Norwegian**: languster - **Portuguese**: lagosta-castanha - **Spanish**: langosta - **Swedish**: languster

Description

Spiny lobsters can easily be distinguished from clawed lobsters by the absence of claws, and from slipper lobsters by their long whip-shaped antennae. *P. elephas* can be distinguished from the sympatric species *Palinurus mauritanicus* by the coloration, redbrick, mauve in the first, and pink in the second. The concavity of the anterior margin between the supra-orbital spines is also larger in *P. elephas,* and it has an antero-lateral spine at the extremity of the first walking leg, and a pair of symmetric pale spots on each of the five first abdominal segments and longitudinal pale strips on the walking legs. The third known species of the genus Palinurus, *P. charlestoni* is endemic to Cape Verde Islands (Latrouite & Alfama 1996).

Geographic Distribution

The European spiny lobster *Palinurus elephas* is distributed in the Eastern Atlantic from Norway to Morocco and throughout the Mediterranean, except in the extreme eastern and southeastern regions (Holthuis 1991). Although not cited by Holthuis, it is also present in the Canary Islands (Herrera, pers. comm.) and in the Azores Islands (D'Udekem D'Acoz, pers. comm.) (Figure 2.1).

Ecology and Habitat

Palinurus elephas lives between the shore and 200 m depth on rocky and coralligenous substrates where micro-caves and natural protective holes are numerous (Ceccaldi & Latrouite 2000). In the Western Mediterranean post larvae settle during the summer in holes and in crevices at 5-15 m depth (Díaz *et al.* 2001), although they have also been observed up to 35 m depth in late summer (Goñi *et al.*, unpublished data). Early juveniles leave shelters to forage at night (Díaz *et al.* 2001). Little is known about the preferred habitat of juveniles but observations off Ireland by Mercer (1973) indicate that they occur in groups and tend to inhabit crevices. In contrast with this observation, Marin (1987) reported large quantities of late juveniles (modal size 60 mm CL) off Corsica in experimental trawls over *Posidonia* beds at 15-25 m depth. Their presence in *Posidonia* meadows along the Iberian Peninsula has not been noted despite intensive census work with a variety of objectives over the years.

Adult *P. elephas's* are solitary, in pairs or small groups preferentially at the base of rock or boulders over gravel beds. Like the juveniles, they are primarily active at night, and their movements are generally limited and seem motivated for foraging and reproduction.

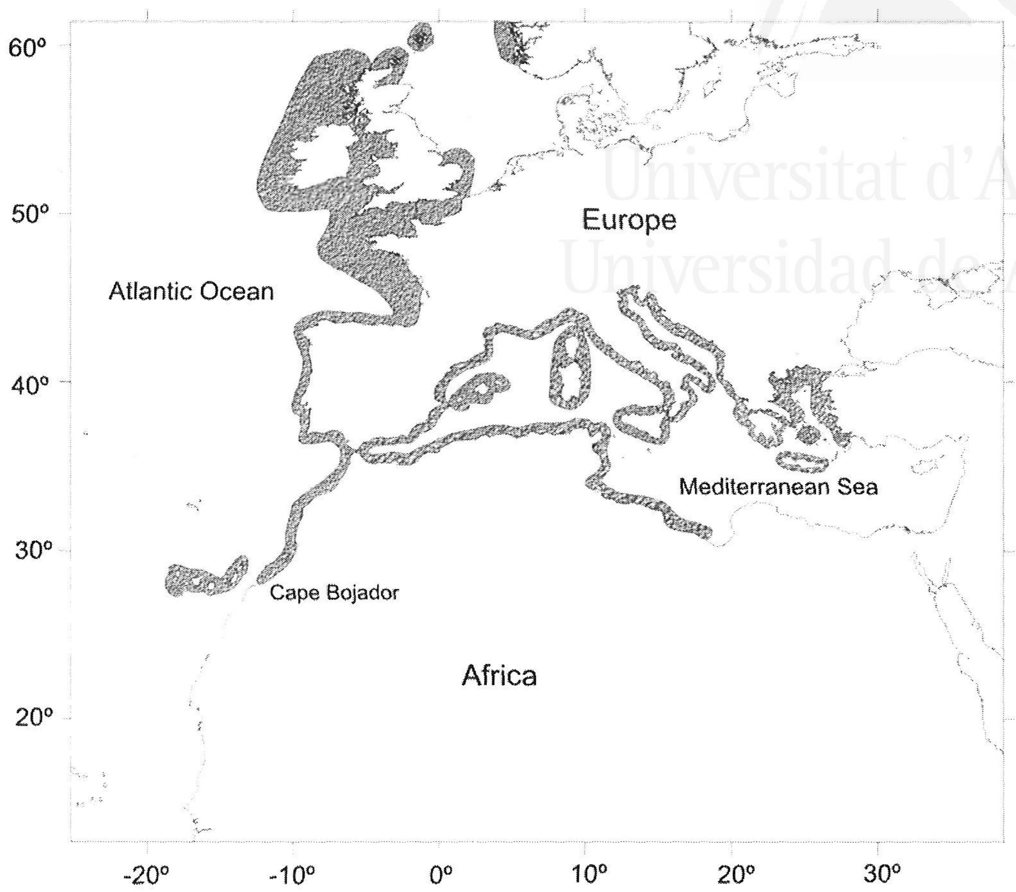


Figure 2.1: Geographic distribution of Palinurus elephias. After Holthuis (1991) except for presence in the Canary that has been recently indicated by local sources (Herrera, pers. comm.). Its presence in the Azores (D'Udekem D'Acoz, pers. comm.) and Madeira Islands has also been indicated (not shaded).

In the Atlantic *P. elephas* undertake a pre-reproductive spring onshore migration and a reverse post-reproductive offshore migration in late autumn (Mercer 1973, Ansell & Robb 1977). A similar behaviour has been postulated for *P. elephas* off the Columbretes Islands (western Mediterranean) (Goñi *et al.* 2001b). Tag-recapture studies conducted both in the Atlantic and the Mediterranean indicate that adult movement is restricted, with most animals moving less than 5 km and exceptionally up to 20 km after 1 to 8 years at large (Hepper 1967, 1970, Marin 1987, Goñi *et al.* 2001b, Cuccu 1999). However, two reports of movements of 50 and 70 km have been made from the Mediterranean (Relini & Torchia 1998, Secci *et al.* 1999).

P. elephas preys on a variety of benthic organisms. Mercer (1973) and Goñi *et al.* (2001a) quantitatively describe their natural diet off Ireland and the Western Mediterranean respectively. *P. elephas* is omnivorous and preys on hard–shelled bottom dwelling organisms, principally molluscs, echinoderms and crustaceans. It is a generalist, opportunistic feeder that changes its food preferences as a function of the abundance of benthic organisms. While molluscs and sea urchins are the most important prey in the diet of the species, other prey such as decapod crustaceans, ophiuroids or coralline algae are consumed in certain areas and not in others (Goñi *et al.* 2001a).

2.3. Growth

Ecdysis in *P. elephas* is similar to that of other Palinurids (see Mercer 1973 for a detailed description). The lobster remains under cover without feeding for one week before moulting which then takes 10-15 minutes to complete. After moulting, it takes about 7-19 days (Karlovac 1965) or 4-7 days (Cuccu 1999) for the new shell to become hardened. The intermoult stage, when increase in weight ceases, is attained 3-5 weeks after moulting (Mercer 1973). In the Mediterranean mature females are berried from mid summer to late winter (Goñi *et al.* 2003a) and moult 1-2 times per year, mainly in April-May (Marin 1987), and possibly also in winter after hatching (Cuccu 1999, Goñi *et al.*, unpublished data). In the Atlantic mature females are berried from mid-autumn to late spring and appear to moult only once per year in June-August prior to mating (Mercer 1973, Latrouite & Noël 1997). According to Mercer (1973), mature males off Ireland follow the same pattern but with a more extended moulting season. Off the Columbretes Islands (Western Mediterranean), males were seen moulting massively in February and data from captive Columbretes males show another moulting peak in the fall (Goñi *et al.*, unpublished data). Observations by Marin (1987) in Corsica showed that the number of moults per year is related to size and decreases after sexual maturity faster in females than in males (Cuccu 1999, Follesa *et al.* 2003). Juveniles moult 2-3 (Marin 1987) and up to 5 times (Corral 1968, Cuccu *et al.* 1999) per year, decreasing to one moult or less per year in adults (Marin 1987).

Growth in the wild

Growth studies of *P. elephas* in the wild have been conducted by means of mark-recapture experiments. Growth increments reported in different studies are difficult to interpret because of the varying size of the lobsters involved, and the different times at large and growth conditions experienced. Common to all growth studies based on mark-recapture is that growth rates will tend to be underestimated, as lobsters moulting more often will be more likely to loose their tags (Hepper 1970). In addition, zero or even negative growth increments are not rare in this type of studies.

Growth per moult of males 55-100 mm carapace length (CL) and of females 55-130 mm off Corsica was arithmetic for both sexes, and larger for males than for females (Marin 1987):

Males: $CL_1 = 0.99\ CL_0 + 6.97$ (mm) (n= 21)
Females: $CL_1 = 0.99\ CL_0 + 5.68$ (mm) (n= 27)

The parameters of the von Bertalanffy growth equation estimated by Marin (1987) resulted in an estimated life span of about 15 years and are:

Males: $CL_\infty = 166$ CL (mm), $K = 0.151$, $t_o = -0.348$
Females: $CL_\infty = 136$ CL (mm), $K = 0.189$, $t_o = -0.342$

Large-sized *P. elephas* tagged-recaptured by Hepper (1970, 1977) off Cornwall indicated mean moult increments <2 mm CL even after more than 2 years at large, while field observations by Mercer (1973) off Ireland yielded much larger growth increments (about 12 mm CL for both males and females). Assuming that it takes one year from the first larval stage to reach 35 mm CL and that juveniles moult at least twice a year up to the size at first maturity, Mercer (1973) estimated the size at age of *P. elephas* off Ireland:

Age	Male (CL-W)	Female (CL-W)
2-3 years	87 mm – 0.455 kg	86 mm – 0.510 kg
5-6 years	123 mm – 1.245 kg	122 mm – 1.225 kg
8-9 years	160 mm – 2.680 kg	158 mm – 2.350 kg

According to the above data from Marin (1987) and Mercer (1973), and contrary to Hunter's (1999) conclusion, *P. elephas* would grow faster and attain a larger maximum size in the Atlantic than in the Mediterranean:

- Western Mediterranean: 175 mm CL (n= 417) and 160 mm CL (n= 278) for males and females off Corsica (Campillo & Amadei 1978).
- Atlantic: 200 mm CL (n= 65) and 170 mm CL (n= 70) for males and females off Brittany (Latrouite and Noël 1997), 190 mm CL (n= 298) and 153 mm CL (n= 586) for males and females off Ireland (Mercer 1973).

Nevertheless, these estimates should be considered with caution as maximum sizes observed in different areas and times are not easy to interpret. The maximum size of lobsters in an exploited population depends on the level and pattern of exploitation and the observed values may be influenced by various factors such as sample size, sampling method, habitat, season and depth.

Biometric relationships

Total length (TL) measured from the tip of the rostrum (medial spine between the eyes) (or from the supra-orbital spine in some studies) to the posterior end of the telson has long been used as the reference for the minimum legal size (MLS), and some authors have used it in scientific publications. However, currently CL, measured from the tip of the rostrum to the posterior margin of the cephalothorax, is commonly employed. Hunter (1999) summarizes the TL-CL and CL-weight (W) relationships published before 1996 for different populations. Not covered in that review, newly available relationships for various areas are:

Brittany (Latrouite & Noël 1997):
Males: $TL(mm)= 2.32 * CL(mm) + 44.2$ (n= 65, range 86-203 mm CL)
$W(g)= 0.0013 * CL(mm)^{2.856}$ (n= 65, range 86-203 mm CL)
Females: $TL(mm)= 2.65 * CL(mm) + 27.1$ (n= 69, range 93-148 mm CL)
$W(g)= 0.0026 * CL(mm)^{2.726}$ (n= 70, range 94-148 mm CL)

Tunisia (Quetglas *et al.* 2005)
Males: $TL(mm)= 2.34 * CL(mm) + 38.36$ (n= 91, range 61-167 mm CL)
$W(g)= 0.0029 * CL(mm)^{2.667}$ (n= 70, range 61-167 mm CL)
Females: $TL(mm)= 2.48 * CL(mm) + 32.54$ (n= 89, range 58-132 mm CL)
$W(g)= 0.0069 * CL(mm)^{2.486}$ (n= 65, range 58-132 mm CL)
Columbretes Islands (protected population, Central-Western Mediterranean) (Quetglas *et al.* 2005):
Males: $TL(mm)= 2.51 * CL(mm) + 32.04$ (n= 370, range 45-169 mm CL)

$W(g)= 0.0012*CL(mm)^{2.882}$ (n= 370, range 45-169 mm CL)

Females: $TL(mm)= 2.88* CL(mm) + 12.51$(n= 441, range 41-142 mm CL)
$W(g)= 0.0016*CL(mm)^{2.834}$ (n= 442, range 41-142 mm CL)

2.4. Reproduction

Mercer (1973) describes the mating process of *P. elephas* in detail. Copulation occurs, sternum to sternum, between intermoult individuals a few weeks after the female moult. The male deposits two spermatophores of a milky-white gelatinous texture on the two sides of the female's sternum, below the genital openings. The spermatophores of *P. elephas* do not harden to form a permanent tar-spot as in other Palinurids and disappear after a short time; thus, they are only occasionally observed (Hunter *et al.* 1996, Goñi *et al.* 2003a).

In the Atlantic, mating is reported to occur between June and October, depending on the region (De Vascondellos 1960, Gibson & O'Riordan 1965, Mercer 1973, Hunter *et al.* 1996). In the Western Mediterranean females bearing spermatophores may be seen from July to September (Marin 1985, Goñi *et al.* 2003a). Oviposition takes place shortly after mating (i.e., 2 days, Mercer 1973; 5-10 days, Ansell & Robb 1977) and eggs are shed across the spermatophoric masses while the female scratches them with the 5th walking leg and the eggs are fertilised; egg extrusion may take place in less than two hours (Mercer 1973). Egg-laying peaks in September in the Western Mediterranean (Gamulin 1955, Campillo & Amadei 1978, Marin 1985, Goñi *et al.* 2003a) and in September-October in the Atlantic (Mercer 1973, Hunter *et al.* 1996, Latrouite & Noël 1997). In Greece, females with eggs have been observed from August to November (Moraitopoulou-Kassimati 1973).

Egg incubation lasts 4-5 months in the Western Mediterranean (Campillo & Amadei 1978, Marin 1985, Goñi *et al.* 2003a) and 6-10 months in the Atlantic (Mercer 1973, Latrouite & Noel 1997, Hunter 1999). Hatching occurs in December-February in the Mediterranean (Gamulin 1955, Campillo & Amadei 1978, Goñi *et al.* 2003a) and in March-June in the Atlantic (Mercer 1973, Hunter *et al.* 1996, Latrouite & Noël 1997). Hatching may be completed in 24 hours (Mercer 1973), although in aquaria it may last up to 8 days (Karlovac 1965).

The mean size at maturity also varies regionally. In Brittany, the mean size of functional maturity (ability to mate and lay eggs) of *P. elephas* was estimated at 95 mm CL (Latrouite and Noël 1997; smallest berried: 92 mm CL). In Ireland, Mercer (1973) estimated the size of 50% physiological maturity of females by the presence/absence of ovigerous setae to be 82 mm CL; he estimated males' size of 50% physiological maturity at 84.5 mm CL. In the Western Mediterranean, a recent study of the reproductive biology of a protected *P. elephas* population concluded that the physiological and functional maturity of females was attained simultaneously at a mean size of 76-77 mm CL, while the males' physiological maturity was attained at a larger size (82.5 mm CL) but at the same age (Goñi *et al.* 2003a). However, off Corsica Marin (1987) observed a 1-year lag between females' physiological (ovary maturation) and functional maturity (86 mm CL), and estimated male's physiological maturity at a mean size of 76 mm CL. Discrepancies between the size at maturity values provided by different authors and between regions are difficult to explain because estimates of size-at-maturity differ depending on the maturity criteria used as well as on the sampling period, and the number and size range of the specimens (Chubb 2000). Furthermore, factors such as food availability, population density, or water temperature are known to influence growth rates and thus size at maturity (Goñi *et al.* 2003a).

P. elephas is 3 to 5 times less fecund than other commercial lobsters of the family Palinuridae, such as the genera *Jasus* or *Panulirus* and only one clutch is incubated annually even in warmer waters (Hunter 1999). Fecundity of *P. elephas* from the Atlantic was studied by Mercer (1973) and the relationship of number of eggs laid and body size was described by the linear equation:

$$F = 2552 * CL - 165602 \ (n = 254, \text{range: } 80\text{-}154 \text{ CL mm}).$$

In the Western Mediterranean the fecundity-body size relationship of *P. elephas* has been studied in the exploited population off Corsica (Campillo 1982) and in the protected population of the Marine Reserve of Columbretes Islands: (Goñi *et al.* 2003a):

Corsica: $F= 3003 * CL - 229809, R^2= 0.97, n= 24$
Columbretes Islands: $F= 2428 * CL - 148988, R^2= 0.85, n= 70$

These equations show that absolute fecundity increases with body size up to the maximum size and, hence, that senescence does not occur. However, maximum relative fecundity (n° eggs / body gram) in Western Mediterranean *P. elephas* is reached at intermediate sizes (100-110 mm CL) (Campillo 1982, Goñi *et al.* 2003a). For most of the mature female size range, individual fecundity in the Corsica population was lower than in the protected population. This could be due to the greater availability of large males in unfished populations and to their potential greater contribution to reproduction relative to small males (MacDiarmid and Butler 1999). Interestingly, size-specific fecundity in the protected population coincides with that estimated by Mercer (1973) on the then lightly fished population off Ireland. These studies do not support either the hypothesis of density dependence of spiny lobster fecundity nor that of higher size-specific female fecundity following exploitation (Goñi *et al.* 2003b). Nevertheless, factors such as increased variation in fecundity among larger females and small sample sizes (in the case of Campillo's sample) complicate attempts to compare size-specific fecundity between populations (Somers 1991).

Egg loss during incubation was estimated at 10% by Mercer (1973) in Atlantic *P. elephas* and at 26-28% by Marin (1985) and Goñi *et al.* (2003a) in Mediterranean specimens. The lower water temperature and the means of capture (by hand instead of netting) may explain the much lower rate of egg loss in the Atlantic study (Goñi *et al.* 2003a).

2.5. Larval ecology and larval settlement

As all Palinurids, the larva of *P. elephas* is a leaf-like, transparent planktonic zoea called phyllosoma (Cunningham 1892), which is adapted to a long offshore drifting life, and is a poor horizontal swimmer being more competent at vertical movements. *P. elephas* larvae measure 2- to 3-mm TL at hatching (Mercer 1973, Kittaka & Ikegami 1988) and are larger than those of other species within the Palinuridae (Kittaka & Ikegami 1988). Based on the morphology of the mouthparts and on their low survival with diatom culture water, Kittaka & Abrunhosa (1997) surmised that *P. elephas* phyllosomas are rapacious predators.

By comparison with other spiny lobster species, *P. elephas* has an exceptionally short larval cycle under culture conditions, ranging from 149 days (9 instars) to 65 days (6 instars) depending on food type (Kittaka *et al.* 2001). In natural plankton samples, Bouvier (1914) described 10 phyllosoma stages, the last of which was found moulting into the puerulus stage, and Santucci (1925, cited in Orton & Ford 1933) described phyllosoma stages I-IX, corresponding to those of Bouvier. However, uncertainties remain in the descriptions of progressive phyllosoma stages because of their reliance on wild source material (Kittaka *et al.* 2001).

Phyllosomas appear to exhibit positive phototropism (Bouvier 1914, Fage 1927, see also Hunter 1999) and Cunningham (1892) collected hundreds of early larvae in surface towed nets. In contrast, Russell (1927) indicated that phyllosomas were rarely found above 10 m and described a large catch, of 75 specimens, at 36 m in July in the Plymouth area. Thus, it is not known when they become negatively phototropic, as has been reported for larvae of other Palinurids (Fage 1927). Based on known behaviour of phyllosomas of *Scyllarus arctus* and *Palinurus gilchrist*, this author suggested that the weight gain through development forces late instars to sink, and that *P. elephas* puerulii are poor swimmers for whom staying in midwater becomes an increasingly difficult task as they gain weight. Because puerulii are very rarely observed and the few existing records originate primarily from midwater trawls (or from stomachs of pelagic fishes, Fage 1927, Heldt 1929), Bouvier (1914) and Fage (1927) concluded that puerulii must spend most of their time sheltered in crevices or among weed, although they prepared for swimming (Caroli 1946). Puerulii were recorded off England in July and September (Bouvier 1914, Orton & Ford 1933), from the Tyrrhenian Sea and the Gulf of Naples in April (Santucci 1926, Caroli 1946) and measure 17.5 to 21 mm TL (Orton & Ford 1933, Caroli 1946). The puerulus has a well-developed abdomen and a translucent exoskeleton that acquires a darker colour and moults (10-15 days later) into the postpuerulus, a young lobster about 2 cm long (Santucci 1926, Orton & Ford 1933). Strikingly, no new knowledge of the larval life of *P. elephas* has been acquired since these early studies.

Eggs apparently hatch inshore, where the early larval stages are common (Mercer 1973). Yet, late larval stages may be found offshore at variable distances (up to 100 miles); thus, metamorphosis to the natant puerulus stage may occur at a considerable distance from the shore (Mercer 1973). The puerulii are again found inshore (Bouvier 1914, Fage 1927, Caroli 1946, Mercer 1973). Since phyllosoma are not capable of swimming large distances, it is thought that water movements govern their movements. Mercer (1973) hypothesizes that off Ireland early larvae are carried offshore and caught up in a series of circular slow-moving currents, where larval development continued, and offshoots of the main currents return the late larval or puerulus stages to coastal waters. In the Atlantic Bouvier (1914) found instars I to X in the summer and Mercer (1973) found early instars (I-III) from June and later stages (VII onwards) from July. In the Adriatic different stage phyllosomas have been recorded from December to March (Gamulin 1955) and in the Western Mediterranean from January to March (references in Hunter 1999). Based on these observations and the hatching periods, the duration of the pelagic larval life has been estimated in 5-6 months in the Mediterranean (Marin 1985) and 10-12 months in the Atlantic (Mercer 1973). However, that post-embryonic development in captivity has been as short as 2 months (Kittaka *et al.* 2001) suggests great plasticity of larval development and raises questions about the validity of these estimated periods.

Settlement of puerulii, measuring 7-8 mm CL, in the North-western Mediterranean has been observed in date (*Lithophaga lithophaga*) holes of limestone rocks from June to July, a few weeks after sea surface temperature starts to rise (Díaz *et al.* 2001). However, underwater visual censuses in different Western Mediterranean locations indicate that post-puerulii may also be found in crevices of volcanic rocks, apparently concentrating in shallow depths (10-30 m, Díaz *et al.* 2001, Goñi *et al.*, unpublished data) and relocating to deeper waters as they grow. On this basis, and to explain the observed concentrations of late juveniles in 60-80 m depth off the Columbretes Islands (Western Mediterranean), Goñi *et al.* (2001b) postulated that a migration of juveniles takes place from the shallow settlement habitats to deeper habitats, presumably during winter or spring. From late June to August many hundreds of juveniles (20-50 mm CL) lying in crevices off Ireland were reported by Mercer (1973). Apart from these few accounts, the life of post-larvae and juvenile *P. elephas* through adulthood remains virtually unobserved.

2.6 Natural mortality

As for many other species, predation is probably the major cause of natural mortality of *P. elephas*, particularly during moulting and juvenile stages (Marin 1985). Both the octopus (*Octopus vulgaris*) and the dusky grouper (*Epinephelus marginatus*) are known predators of *P. elephas* in the Western Mediterranean (Quetglas *et al.* 2001). Other known predators in the region are *Labrus* spp., *Scorpaena* spp., and *Serranus* spp. (Marin 1987) but pelagic fishes also predate on puerulii (Fage 1927, Heldt 1929, Legendre 1936 cited in Caroli 1946). A study of *P. elephas* diet did not reveal cannibalism under natural conditions (Goñi *et al.* 2001a) although it has been observed in captivity (Marin 1987). Based on knowledge of the life cycle of the species – slow growth, large size – Marin (1987) estimated the instantaneous coefficient of natural mortality to be in the range of 0.15-0.30. By means of mark-recapture experiments, Hepper (1977) estimated a coefficient of natural mortality of 0.11 for *P. elephas* in the Atlantic.

2.7. Fisheries

Fishing methods

Traditionally *P. elephas* was captured by means of traps/pots and sometimes by diving (Hepper 1977, Hunter 1996, Goñi *et al.* 2003a, Gristina & Gagliano 2004). A major change in the exploitation strategy took place during the 1960s and 1970s with the progressive introduction of trammel-nets that virtually replaced other fishing methods. This change in fishing strategy not only had an impact on exploitation levels, demography and sex composition of the exploited populations (e.g. Hunter *et al.* 1996, Goñi *et al.* 2003b), but also on the image that we may obtain from the population by sampling commercial catches as they are strongly influenced by the selectivity of the gear and gear-related catchability. A comparative study of the catchability of *P. elephas* in traps and trammel-nets (Goñi *et al.* 2003b) demonstrated similar catchability for males and females in trammel-nets and reduced catchability of large males in traps. Comparing the selectivity of those two gears, the same study indicated that small lobsters (<70 mm CL) are poorly retained in traps and that large (>130 mm CL) ones are less likely to enter traps due to behavioural factors, physical limitations or because they are able to feed without entering. Ongoing studies also demonstrate that by comparison with traps, trammel-nets have poor species selectivity generating higher bycatch rates and greater physical impacts on benthic habitats through the incidental catch of structure forming species, such as sponges, bryozoans, corals and coralline algae (Goñi *et al.* 2003c).

Structure of exploited populations

Knowledge of the structure of exploited *P. elephas* populations comes from scattered data of commercial or survey catches carried out in different regions since the early 1950s. These data are scant and discontinuous, therefore temporal and spatial assessments of populations' size or sex structure are difficult. In Corsica, Campillo (1982) first studied the size composition of trammel-net commercial catches through a sampling programme in 1977. The maximum sizes observed were 160 and 175 mm CL in females and males respectively, and the corresponding modal sizes were 96 and 104 mm CL. The size composition of the commercial catches in Corsica was again established through a two-year sampling program in 1983-1984. Results indicate that both modal - around 75 mm CL in both males and females - and maximum sizes - 120 and 140 mm CL in females and males respectively - had decreased substantially (Marin 1987). Although Campillo (1982) acknowledges that in 1977 the fishery already showed signs of overexploitation, effort intensification and the widespread introduction of trammel-nets in the late 1970s and early 1980s had reduced the number of large lobsters in the population. As the traps used in the Western Mediterranean exclude, and thus protect, large *P. elephas* (mostly males), it is plausible that the change of gear, as well as the increased fishing effort, tapered the demographic structure of the fished population. The size structure of a population of *P. elephas* 10 years after the establishment of the marine reserve of Columbretes Islands (Western Mediterranean) presented modes around 100 and 100-130 mm CL for females and males. The maximum sizes were 148 and 173 mm CL in females and males (Goñi *et al.*, unpublished data) that resembled the sizes observed earlier by Campillo (1982).

The earliest published data on the structure of Atlantic populations comes from Portugal and dates back to 1958 (de Vasconcellos 1960); the modal size was 120 mm CL for males and females and the maximum sizes were 190 and 180 mm CL respectively. Hepper (1977) studying the size structure of commercial trammel-net catches from Cornwall in 1965-1975, observed males' mean and maximum sizes of 145-160 mm CL and 182 mm CL, and females' mean and maximum sizes of 122-134 mm CL and 152 mm CL. Ansell and Robb (1977) also found similar maximum size lobsters off Scotland during 1972-1975. Later field observations by Hunter *et al.* (1996) off Cornwall (1993-1994) showed that the size structure of the male Cornish populations had altered dramatically (the mean size had declined to 126 mm CL) since Hepper's (1977) study while the females' mean size had not changed (132-135 mm CL). A comparison of the Cornish with the less exploited Welsh populations and with Hepper's (1977) data from Cornwall led Hunter *et al.* (1996) to conclude that the reduction in the mean male size was due to the change in exploitation pattern brought about by trammel-nets replacing pots during the 1970s. In Brittany, occasional sampling of trammel-net catches during 1983-2003, show that few individuals smaller than 100 mm CL are caught, modal sizes fall between 120 and 150 mm CL for males and females and maximum sizes reach 200 and 170 mm CL in males and females respectively (Latrouite & Noël 1997). These large maximum sizes in Brittany are unexpected given the alleged overexploited status of the populations in the area.

National fisheries

Published data on *P. elephas* fisheries are scant despite their past and present socio-economic importance. Most of the following information has been found in unpublished reports or has been obtained through personal communications (Dr Oliver Tully for Ireland, Dr. Margalida Castro for Portugal, Dr. Hicham Masski for Marocco and Dr Christina Mytilineou for Greece). We are confident that the major historic and present fisheries are covered here; nevertheless, there may be fisheries of lesser but significant local importance that have not been brought to our knowledge and are not included in this overview.

Irish fisheries

Presently a small fleet of 20-25 vessels target *P. elephas* from May to September with trammel-nets, although bycatch in static net fisheries, and to a lesser extent in trawls also occurs. As in other fisheries a major change occurred in the 1970s when pots were replaced by trammel-nets that lead to a depletion of the stocks and a very significant reduction in lobster mean size. During the period 1990-2000, annual official landings have declined from 175 to 33 t. The MLS is currently 110 mm CL (15 mm over the EC MLS) and there are two areas closed to fishing with nets. Attempts are being made by the authorities to revert to fishing with pots.

British fisheries

In the UK, targeted *P. elephas* fisheries are restricted to Cornwall and Western Wales with occasional catches from the Scottish Western Isles (Hunter 1999). In common with fisheries elsewhere, the species was traditionally fished with pots (and occasionally by diving), and although traps are still used in some areas, tangle and trammel netting is now the principal means of capture. Pot CPUE declined steadily during the period 1979 to 1997 and the populations are depleted (Hunter *et al.* 1996).

French fisheries

According to several authors (Dupouy 1920, Postel 1962, Gloux and Manach 1976), while *P. elephas* and *Homarus gammarus* had been appreciated and marketed in France for several centuries, directed fisheries in the Atlantic only started at the end of the 19th century, when a small-specialised fleet developed in Brittany and fished coastal grounds. At the beginning of the 20th century, a fleet of larger boats expanded its activity to England, Ireland, Scotland, Spain, Portugal, Morocco and Tunisia. After 1960, impoverishment of the lobster stocks and closure of some foreign grounds led most vessels to shift from lobster to crab (*Cancer pagurus* and *Maja brachydactyla*) fishing. Currently *P. elephas* is primarily a bycatch, though economically important, of some 150 boats (12 meters in average) netting for monkfish (*Lophius piscatorius)*, rays (*Raja spp.*), turbot (*Psetta maxima)* and brill (*Scophtalmus rhombus)* with trammel nets of 240-320 mm stretched mesh (inner panel). Catches from potters and trawlers are anecdotic. Landings in 2003 were estimated at around 50 tons (Latrouite, unpublished data). Although fishing occurs year round, 80% of the fishing occurs between April and November. The MLS of 95 mm CL (EC regulation) is the only regulatory measure in place.

In the Mediterranean, a small-scale fishery developed around Corsica at the end of the 19th century (Marin 1985). In the 1960's introduction of more efficient fishing methods (echo sounders, net-haulers, nylon trammel-nets) led to a substantial effort increase (Giménes 1969) followed by a sharp decline in catches. Currently the fleet is composed of about 200 boats (average 8 meters) fishing mainly in coastal waters with trammel-nets of 125-160 mm stretched mesh (inner panel). Landings were estimated at 65 t in 2004 (Pere, pers. comm.). The MLS is 80 mm CL, the fishery is closed from September to March and eight sanctuaries covering about 80 km^2 in total are distributed around the island.

Administration and industry reports indicate that national landings (Atlantic plus Mediterranean) were over 1000 tons between 1920 and 1925, peaked in 1947 with 2678 tons, and have decreased continuously since then. Mean annual landings were 867 tons in the 1950s, 360 tons in the 1970s, 160 tons in the 1990s and around 50 tons in recent years. Even if the accuracy of the official data is poor, the trend is robust and reflects a drastic decline of the stocks primarily due to fishing mortality, especially with nets (even if not always targeting spiny lobsters).

Portuguese fisheries

In Portugal *P. elephas* is currently fished on the southwest coast by an artisanal fleet of around 40 vessels owning a "more than one gear" licence. During spring and summer, when catches are higher, this fleet targets spiny lobster with tangling or trammel-nets, which they leave permanently in the water and haul at 1 to 4 day intervals. During the last decade *P. elephas* landings have declined sharply from an average of 400 t in 1990-1992 to an average 6 t in 2000-2002, and the species has virtually disappeared from depths shallower than 30 meters. The decline in the fishery can in part be accounted for by an increase in the proportion of lobsters sold outside the legal market, but the main reason is the depletion of the resource following the change from traps to gillnets and trammel-nets during the late 1960's and 1970s, and a substantial increase in fishing effort over the last 10 years due to the modernization of the fleet. The only pieces of legislation specifically geared for spiny lobster are the MLS (95 mm CL) and the prohibition of landing ovigerous females.

Spanish fisheries

Lobster fishing has a long tradition off the coasts of Spain (Von Salvador 1895, Iglesias *et al.* 1994). Presently, *P. elephas* fisheries are mostly restricted to the Mediterranean while in the Atlantic the species is caught as bycatch in finfish gillnet fisheries. In the Spanish Mediterranean, over six hundred artisanal vessels and some 1100 fishermen engage in lobster fishing every year (Alarcón 2001). As occurred elsewhere, trammel-nets have replaced traps in all areas, except for a relict, vanishing trap fishery in the Balearic Islands. Massuti (1973) collected catch and effort data of the lobster fishery in the Balearic Islands from 1940-1970. Mean annual catches in the period 1940-1945 were around 90 t, declining to 40-50 t in 1950-1955 and to 20 t in 1965-1970 while fishing effort tripled. As trammel-nets replaced traps at the end of that period catches increased.

Official landings in 2000 amounted to some 2 t in the Atlantic and around 98 t in the Mediterranean. However, ongoing studies of some local fisheries in the Mediterranean indicate that official figures underestimate lobster landings because significant but variable portions are sold directly to consumers (mostly restaurants) and go unreported. Use of correction factors developed for particular locations suggest that annual *P. elephas* landings in Spain reach 200 t. It is suspected that fishing mortality rates have increased at all grounds and that most fisheries are overexploited. As no reliable fishery statistics are available, it is not possible to estimate exploitation levels, however the high recapture rates (up to 61%) of lobsters released in grounds near the Columbretes Islands (Western Mediterranean) suggest high rates of fishing mortality in that area (Goñi *et al.* 2000).

In the Mediterranean fishing effort is regulated by an annual 6-month closure during the egg-bearing period (September to February), the prohibition of fishing on weekends, and caps on the amount of gear fished per boat (4500 m trammel-nets or 350 traps). The mesh size of the trammel-net outer and inner panels (minimum of 200 and 65 mm respectively) is also regulated. Finally, it is forbidden to land lobster smaller than 24 cm TL (approximately 80 mm CL) or berried females.

Italian fisheries

No information on *P. elephas* fisheries is available in the literature at a national level. In Sardinia, where *P. elephas* fishing is important, the fishery started at the end of the 19th century, mainly with traps (Secci *et al.* 1995), and catches showed continuous growth. During the 1970's increased fishing effort led to a depletion of the stocks and at present yields are lower than those recorded in the 1920s and 1970s. Nowadays about 250 artisanal boats (7 meters) exploit this resource with trammels nets (only two fishermen are still using traps). In Southern Italy (Golfo di Taranto and Sicily) *P. elephas* was fished exclusively with traps until the 1950s when they were replaced by trammel-nets (Petronsino et al 1985, Gristina & Gagliano 2004). The MLS is 300 mm TL (or 107 mm CL), the fishery is closed from January to April and berried females are to be returned to the water (Gristina *et al.* 2002).

Croatian fisheries

In the eastern Adriatic, the most important *P. elephas* fishing grounds are the southern sides of distant islands (Soldo *et al.* 2001). High product value, small catches and multiple fishing gear characterizes the commercial fishery in the area. Historically, *P. elephas* was caught using lobster pots and gillnets. In recent years, due to deficient legislation, the mesh size of lobster gillnets have been reduced from 240 mm to 120 mm and trammel-nets of 80 mm mesh (inner panel) have been introduced (Soldo *et al.* 2001). Reported annual landings were highest in 1953 with 83 t, while they ranged between 23 and 43 t in the period 1985-1998. Although official landings have not declined in the last decade, all evidence (fishermen, inspections, market figures) indicates that the resource is heavily exploited and that total catches, mean lobster size and CPUE have declined significantly (Soldo, pers. comm.). The MLS is 240 mm TL (82 mm CL), the fishery is closed from October to April and berried lobsters must be returned to the sea (Soldo, pers. comm).

Greek fisheries

A census of the Greek artisanal fisheries carried in 2001 led to an estimate of 18 000 small coastal fishing boats but the number of those involved in lobster fishing is not known. Trammel-nets and gill nets are the main gears used to fish lobster but bycatch by trawlers appears also significant. *P. elephas* and *Homarus gammarus* are fished together and official statistics merge landings of the two species; the estimated proportions of the species are 80% and 20% respectively. Mean annual landings for the 1990s have been estimated at 200 t while official figures are only 23 t, indicating that large amounts of lobsters are directly sold to consumers or restaurants. The fishery is regulated by a MLS of 85 mm CL, prohibition of landing berried females, and a four-month (September-December) closed season.

Tunisian fisheries

The Tunisian lobster fleet grew rapidly during the 1990s, reaching over 80 vessels, although currently has only 56 vessels (mean size 14 meters) operating primarily in the fishing the grounds of La Galite and Esquerquis (Quetglas *et al.*, in press). As in other fisheries, trammel-nets (75 mm stretched mesh size inner panel) have progressively replaced traps. Tunisia has a reliable series of statistics because the species is exported for foreign consumption. Annual landings during the period 1990-2002 peaked at 74 t in 1993, declining gradually to 33 t in 2002 (Quetglas *et al.*, in press). Stocks are considered overexploited and protective measures such increasing MLS, extending the closed season and reintroducing traps are being proposed (Zarrouk 2000). The fishery is regulated by a 200 mm TL MLS (67 mm CL), an annual closure from mid September to February and the prohibition of landing berried females (Zarrouk 2000).

Moroccan fisheries

P. elephas is fished all along the Moroccan coastline, but abundance is higher in the Atlantic than in the Mediterranean. In addition to *P. elephas* and *P. mauritanicus*, *Panulirus regius* inhabits Moroccan waters. The three species are fished with nets or traps by a fleet of large (15-23 m long) wood artisanal vessels based in fishing harbours and by a fleet of small boats (less than 6 m) based near specific fishing locations. The first data on lobster landings date from the 1960s, concern the Mediterranean and the Atlantic (from Tanger to Agadir), and amount to 12 and 17 t respectively for 1966 and 1967 (Collignon 1966, 1967). National statistics for the recent period are 166 t in 2002 and 112 t in 2003 but they include the three spiny lobster species and the proportion of *P. elephas* is not known. A MLS of 170 mm TL is the only piece of regulation of the *P. elephas* fishery.

2.8. Status of the populations

The *Palinurus* genus is composed of five species of temperate, deep-water spiny lobsters (Phillips *et al.* 1980), two of which, *P. elephas* and *P. mauritanicus*, are present in European waters. Of the two, *P. elephas*, inhabits shallower habitats and was formerly common near the coast, but is now rare at less than 40 m and fisheries that in the past were productive have now virtually disappeared; viable fisheries remain only in the most remote traditional fishing grounds of the Mediterranean. Understanding the possible causes, including climate change, of these trends will require reliable information on past and current geographic limits of the species. Uncertainty about this is illustrated by lack of reference by Holthuis (1991) of its presence in the Canary Islands, where it was traditionally fished (Herrera, pers. comm.) or in the Azores Islands (D'Udekem D'Acoz, pers. comm.) and presumably also in waters around the Madeira Archipelago.

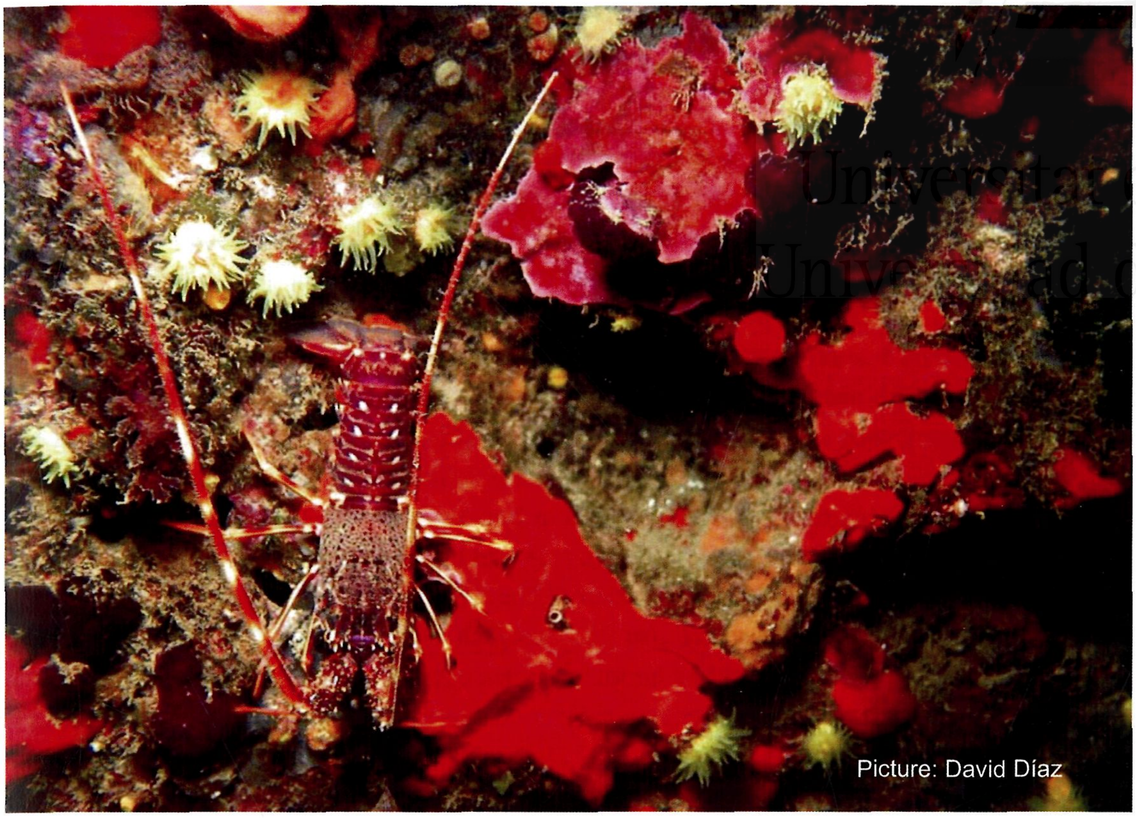
The high unit value together with the biological and ecological characteristics of *P. elephas* in the Eastern Atlantic and Mediterranean makes it highly vulnerable to overexploitation. *P. elephas* has a low growth rate, a long life span and low fecundity by comparison to most other commercial spiny lobsters. Additionally, the amplitude of adult movements is small. Although nothing is known about the stock-recruitment relationship, the pelagic larval life is long and dispersal by ocean currents may be extensive. As recruitment may occur far from the parental grounds, decoupling between spawning stock biomass and recruitment is likely.

Although reports of overfishing of *P. elephas* appear as early as the 1930s (e.g., Ninni 1934), the widespread decline of *P. elephas* fisheries may be traced back to the 1960s-1980s depending on the area. During those years, fishing effort increased dramatically as pots (and diving) were replaced by trammel-nets and hauling gear and other technological advances were introduced. However, lack of reliable historical catch and effort data prevents testing the hypothesis that these changes led to overfishing. In all European and African countries where *P. elephas* and *P. mauritanicus* are fished, FAO landing statistics between 1984 and 1996 are registered as "*Palinurus* spp » (distinction only in France). These cumulative annual landings range between a maximum of 8710 t and a minimum of 4242 t, and show a decreasing trend from 1988 to 1996. Unfortunately, no confidence can be placed on these figures, which may be overestimated, underestimated, irregularly reported (most countries), or which include other species. Based on the best available information, rough estimates of current landings of *P. elephas* range between 500-800 t/year in the Mediterranean and between 150-300 t/year in the Atlantic. These values are in striking contrast to landings of several thousand tones in the first half of the 20th century (e.g. landings only in France reached 3000 t in the 1940s).

All circumstantial evidence points the blame at the great efficiency of nets in catching lobsters, excessive fishing effort and to the poor selectivity of trammel-nets relative to pots. Recent studies indicate that trammel-nets catch a greater proportion of large lobsters than pots, and that their impact on lobster habitats and benthic communities is far greater. In the Atlantic, the problem is exacerbated by the fact that lobsters are also a substantial bycatch in nets dedicated to fishes (monkfish, rays, turbot, brills, etc.). *P. elephas* are fished by a large number of artisanal vessels typically distributed in many ports along the coastline. Therefore, at-sea effort control of fisheries is difficult and it is common for the limits on net length per boat to be amply exceeded. Additionally, while pots had to be hauled every day to restock the bait, trammel-nets are left in the water two or more days (to bait the net with fishes entangled during the first day). Due to bad weather conditions, nets are often soaked for longer periods resulting in loss of catch and return of undersized specimens to the water in poor survival condition, if returned at all.

The MLS of *P. elephas* in most Mediterranean fisheries barely exceeds the size of physiological maturity. A recent study of the reproductive potential of a protected population of *P. elephas* shows that such MLS protects only about 1% of the population potential egg production (Goñi *et al.* 2003a). Lacking estimates of fishing mortalities, and thus a full assessment of the impact of various MLS on the reproductive potential of *P. elephas* populations, the study points to the need to increase the MLS to allow lobsters to reproduce a minimum of once or twice before becoming eligible for fishing. However, larger MLS in some fisheries (e.g. Croatia) alone does not appear to have protected the populations from overfishing. A similar observation comes from Brittany where an increase of MLS above the mean size at maturity did not prove to be sufficient to restore the stock. Thus, a larger MLS may be seen as a necessary technical measure, but is far from sufficient.

Our knowledge is inadequate to discriminate between increased fishing mortality due to greater fishing effort and the changes in size and sex related catchability associated with trammel-netting as the factors responsible of the depleted status of *P. elephas* fisheries. As a high value commodity, *P. elephas* continues to be pursued despite low yields and rapidly growing prices maintain viable fisheries. Due to this, fishermen are requesting managers to impose more restrictions to help rebuild stocks (Hunter 1996) and additional measures, such as areas open only to pots and programmes to promote the reintroduction of pot fishing should and are being considered in some areas (e.g. Balearic Islands, Corsica, Ireland, Brittany). In this context, permanent closures of fractions of the fishing grounds or of spawning grounds may provide the solution. Relatively small marine protected (MPA) areas enhance *P. elephas* adult stock biomass (e.g., Goñi et al 2001b) and it is known that MPAs are most effective in species of intermediate movements (e.g., Russ 2002), such as *P. elephas*. However, for MPAs to be effective their implementation must be based on genetic studies (e.g. Cannas *et al.* 2003) and on a good understanding of the connectivity among metapopulations (e.g., Tuck & Possingham 2000), both of which are lacking.


Picture: David Díaz

CHAPTER 3: DYNAMICS OF THE *P. ELEPHAS* POPULATION IN THE COLUMBRETES MARINE RESERVE

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Abstract

A protected population of spiny lobster, *Palinurus elephas*, was studied eight years after the establishment of the Columbretes Islands Marine Reserve (western Mediterranean). Experimental trap fishing in the reserve and at two unprotected sites revealed that cessation of fishing in the reserve is probably responsible for high catch rates observed there and that the annual 6-month closure of the fishery is effective in rebuilding populations in exploited areas. In the reserve, variations in abundance, sex ratio, and size of lobsters were conspicuous. Catch rates were always higher in deep (50–80 m) than in shallow areas (20–50 m). Bathymetric differences in abundance were smallest in early summer, possibly because of seasonal onshore movements associated with reproduction. Females were always more abundant than males and less variable in number and size. Ancillary data suggest that reproductive and moulting behaviour, particularly of males, influences population estimates of *P. elephas* from trap surveys. Presence of subadults in deeper waters of the reserve suggests that 2- to 3-year-old juveniles undergo ontogenetic migration from the shallow settlement habitats (<30 m) to deeper habitats (>50 m). The results highlight the effectiveness of fishing restrictions in rebuilding *P. elephas* populations and suggest that the lobster population in the reserve is not closed.

3.1. Introduction

To date, no studies have been conducted within the Mediterranean Sea to assess the effectiveness of marine protected areas (MPAs) on *P. elephas,* and only one study has addressed the dynamics of Mediterranean populations (Marin 1987, for *P. elephas* off Corsica). The responses of spiny lobster populations in MPAs have been assessed in a number of protected areas around the world. The best-studied species are *P. argus* off Florida (e.g., Davis 1977, Davis & Dodrill 1980, Hunt *et al.* 1991) and *Jasus edwardsii* off New Zealand (e.g., Cole *et al.* 1990, MacDiarmid & Breen 1993, Babcock *et al.* 1999). Studies in some cases have demonstrated increased abundance and mean size of spiny lobsters within MPAs compared to exploited areas (e.g., Cole *et al.* 1990, Hunt *et al.* 1991, MacDiarmid & Breen 1993, Babcock *et al.* 1999), and no differences in lobster abundance and mean size between exploited and protected areas in other cases (e.g., Hunt *et al.* 1991, MacDiarmid & Breen 1993).

The aim of this study was to examine the effectiveness of the Columbretes Islands Marine Reserve as it pertains to *P. elephas* and to study the dynamics of the protected population. We surveyed lobster-fishing areas in the reserve and in comparable areas open to fishing in different periods to assess temporal dynamics of the population and to study spatial differences in abundance, which could be attributable to the cessation of fishing in the reserve. We predicted that, after more than eight years of protection, lobsters would be more abundant within the reserve than in comparable areas where fishing is allowed.

3.2. Materials and Methods

Trap surveys and abundance indices

We estimated lobster abundance and size structure through experimental fishing with traps. Traps were used in the reserve because they have minimal impact on benthic communities and produce low by-catch (Miller 1990), but a number of factors are known to affect trap catches. Of those identified by Miller (1990), only length of deployment, gear saturation, lunar cycles, and bait type could be controlled in the present survey design. Thus, to use catch rates as indices of abundance, we standardized length of deployment to one night. The outcome of a small number of 2- and 3-night trap sets produced below-average yields, suggesting more escape than entry (Miller 1990, Cockcroft *et al.* 1995). These same data showed that maximum catches were reached at deployments approaching 24 h, indicating that gear saturation did not occur earlier. Standardizing deployment length was also necessary to control the size structure of the catch (Miller 1990). Because, for some palinurids, catch per trap can depend on the phase of the lunar cycle (high at new moon and low at full moon, Miller 1990), the surveys were always conducted during the same lunar phases (first to last quarter). Finally, the same bait, spotted dogfish (*Scylliorhinus cannicula*), was employed in all surveys. Professional fishermen commonly use this bait because of its low price and durability.

Traps employed in the study were made of plastic material with steel ring frames and open laterally when placed on the seabed. The sampling unit was a long-line with 40 traps. These long-lines are identical to those used by the few remaining trap lobster fishers. Replicate trap long-lines were placed randomly over rocky and coralligenous substrates where lobsters were known to reside.

The number and sex of all lobsters caught per trap were recorded and the carapace lengths (CL ± 1 mm) were measured mid-dorsally from the posterior edge of the carapace to the tip of the rostral spine. Abundance indices were calculated as the mean number of lobsters caught per trap per 24 h. This index has the advantage of being comparable to the catch rates of the commercial trap fishery.

Sampling design and statistical analysis

Spatial comparison of abundance indices

For the spatial comparison, two areas outside the marine reserve - Placer de la Barra Alta (PLA) and Subarra (SUB) - were used as controls of the effects of protection in the Columbretes Islands Marine Reserve (COL) on P. elephas populations. These reference areas are traditional artisanal lobster-fishing grounds operating from the nearest mainland ports. The COL and the PLA present steep vertical reliefs from 0 to 80 m and from 11 to 80 m, respectively. In contrast, the SUB is a comparatively flat and homogeneous plateau extending over depths of 60–80 m. The PLA and the SUB are located 8.6 km south-west and 15.3 km north-west of the Columbretes Islands, respectively. On this basis, they were considered independent and without significant spatial autocorrelation with each other or with the reserve.

Sampling was carried out in each area (COL, PLA, and SUB) between 50 and 80 m depth during three different surveys: June (1997), August–September (1998), and February (1999). These surveys were timed to coincide with the middle, end, and beginning of fishing seasons, respectively. Constraints on ship availability dictated that the surveys take place in consecutive years, rather than within the same calendar year. These three periods were deemed relevant for evaluation of the relative influence of natural variability and fishery impacts on changes in lobster abundance.

The relationship between sample size and level of precision was assessed with data from the June 1997 survey (see below). In view of the magnitude of the difference in catch rates between the reserve and control areas obtained from preliminary data, nine replicate sets per area (40 traps/set) were deemed sufficient for the spatial comparison of abundance indices, so a sample size of nine was used in 1998 and 1999. Abundance data were analysed by orthogonal analysis of variance (ANOVA) with area (COL, PLA, SUB) and time (June 1997, August–September 1998, February 1999) as fixed factors. As catch rates were nonnormally distributed and the variances were not homogeneous (Cochran's C test), the data were log-transformed (Underwood 1981). Comparisons of means of significant effects after ANOVA were done by Student-Newman-Keuls (SNK) q tests (Zar 1984).

Temporal dynamics of the protected population

Five surveys were carried out in the COL during June (1997), August–September (1998), February (1999), September (1999), and June (2000). The timing of the surveys was chosen to accommodate the objectives of the spatial comparison (first three surveys) and to assess temporal variation in lobster abundance within the marine reserve. Unfortunately, budgetary problems did not allow replication of the February survey. Preliminary data indicated a gradient in lobster abundance (positive) and size (negative) with depth, so the reserve was divided into two depth strata: shallow (20–50 m) and deep (50–80 m).

With the data of the June 1997 survey, we assessed the level of precision of the abundance estimates as a function of the number of replicate trap long-line sets. Estimates of abundance indices attained a relatively stable level of precision (standard error of the mean) when 10 replicates were used. A sample size of 15 replicate trap long-line sets per depth stratum, as completed in the first survey, was therefore retained for the rest of the study, but additional sets were carried out whenever possible to improve the collection of lobster size and sex data.

Changes in lobster abundance and size with time (5 surveys), depth (two strata), and sex within the protected area were analysed with three-way orthogonal ANOVAs. In both analyses depth, sex, and time were fixed factors. To obtain equal sample sizes for the analysis of abundance data, we drew random subsets of 15 replicates per depth stratum from the surveys where more were available. As catch rates were nonnormally distributed and the variances were not homogeneous (Cochran's C test), abundance data were Ln (x+1) transformed. Lobster size data were not transformed, as transformations did not reduce nonnormality or heteroscedasticity, but plots of the residuals of the ANOVA against predicted values indicated only mild departures from the assumptions. Comparisons of means of significant effects after ANOVA were carried out by SNK q tests (Zar 1984).

3.3. Results

Spatial comparison of abundance indices

Mean catch rates of *P. elephas* varied significantly according to area and time (2-way ANOVA; area: df = 2, 72, $F = 188.52$, $P < 0.0001$; time: df = 2, 72, $F = 4.95$, $P = 0.01$), but a significant Area-×-Time interaction effect ($P = 0.001$) precluded contrasts across the main effects. Catch rates of *P. elephas* were conspicuously higher in the COL than in either of the unprotected sites (PLA and SUB) irrespective of time (Figure 3.1). Abundance indices in the open fishing areas were 0.6–20% of those in the reserve depending on the period (Figure 3.1). Temporal changes in relative abundance followed different patterns in the reserve and in the unprotected sites. For example, catch rates in the reserve were higher in June (prior to mating), although not significantly so, whereas in the open fishing areas abundance was significantly higher in February (end of the 6-month closed season) than in other periods (Figure 3.1; SNK tests). At PLA, which was the location least accessible to mainland ports, catch rates in February, following a 6-month closed season, increased significantly with respect to both June and August (Figure 3.1; SNK tests). At SUB, abundance followed the same trend as at PLA, but temporal differences were not significant (Figure 3.1; SNK tests).

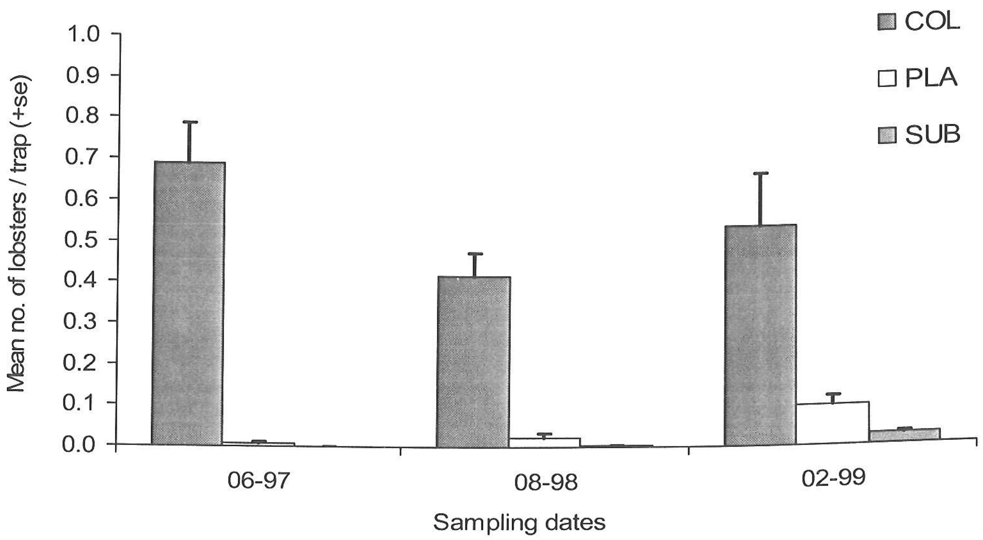


Figure 3.1: Mean catch rates (±SE) of P. elephas from deep waters (50–80 m) in the Columbretes Islands Marine Reserve (COL) and from two areas open to fishing (Placer Barra Alta, PLA; Subarra, SUB) during surveys in June 1997 (06-97, n = 27 trap sets), August–September 1998 (08-98, n = 27 trap sets), and February 1999 (02-99, n = 27 trap sets).

Temporal dynamics of the protected population

Abundance and bathymetric distribution

Lobster catch rates varied conspicuously with time, depth, and sex, but significant Time-×-Depth and Time-×-Sex interaction effects (Table 3.1) prevented comparisons across the main effects. Lobster catch rates in the reserve underwent twofold changes between maximum values in early summer 1997 (mean 0.59 ± 0.07 SE) and minimum values in early fall 1999 (mean 0.27 ± 0.04 SE). Relative to June 1997, the mean catch rate was 54% in August 1998, 66% in February 1999, 44% in September 1999, and 61% in June 2000. Catch rates were always higher in the deep stratum (overall mean 0.49 ± 0.04 SE) than in the shallow one (overall mean 0.24 ± 0.03 SE) (Figure 3.2). The minimum differences in abundance indices between depth strata were observed in early summer, and the maximum in late summer.

Table 3.1: Effects of time, depth and sex on the abundance of Palinurus elephas in the Columbretes Islands Marine Reserve, Western Mediterranean. Data were Ln (x+1) transformed. Transformation reduced but did not eliminate heterogeneous variances; Cochran's C = 0.11599; P = 0.048. NS = non-significant at P > 0.05.

Source of variation	SS	df	MS	F	Probability
Depth	44.68	1	44.69	81.32	< 0.001
Sex	30.94	1	30.94	56.32	< 0.001
Time	34.92	4	8.73	15.89	< 0.001
Depth × Sex	0.15	1	0.15	0.27	NS
Depth × Time	8.07	4	2.02	3.67	0.006
Sex × Time	23.12	4	5.78	10.52	< 0.001
Depth × Sex × Time	0.50	4	0.13	0.23	NS
Residual	153.84	280	0.55		
Total	296.23				

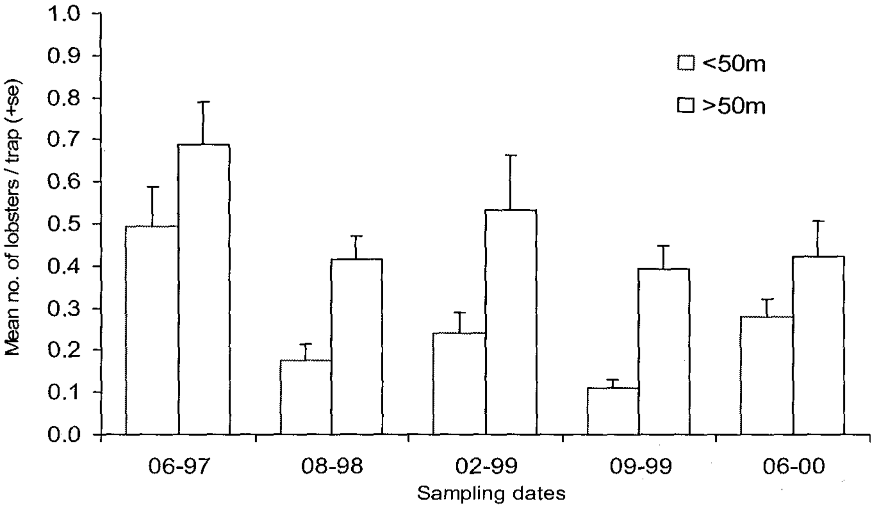


Figure 3.2: Mean catch rates (±SE) of P. elephas by depth strata in the Columbretes Islands Marine Reserve during surveys in June 1997 (06-97, n = 30 trap sets), August–September 1998 (08-98, n = 48 trap sets), February 1999 (02-99, n = 34 trap sets), September 1999 (09-99, n = 42 trap sets), and June 2000 (06-00, n = 52 trap sets). <50m = 20–50 m; >50m = 50–80 m.

The catch rates of female lobsters were consistently higher (overall mean 0.27 ± 0.02 SE) than those of males (overall mean 0.14 ± 0.02 SE), but male catch rates underwent more dramatic changes over the study period (fourfold) than did those of females (twofold) (Figure 3.3). Females were more abundant in the February 1999 survey than in any other period, whereas males were more abundant in June 1997 (Figure 3.3; SNK tests).

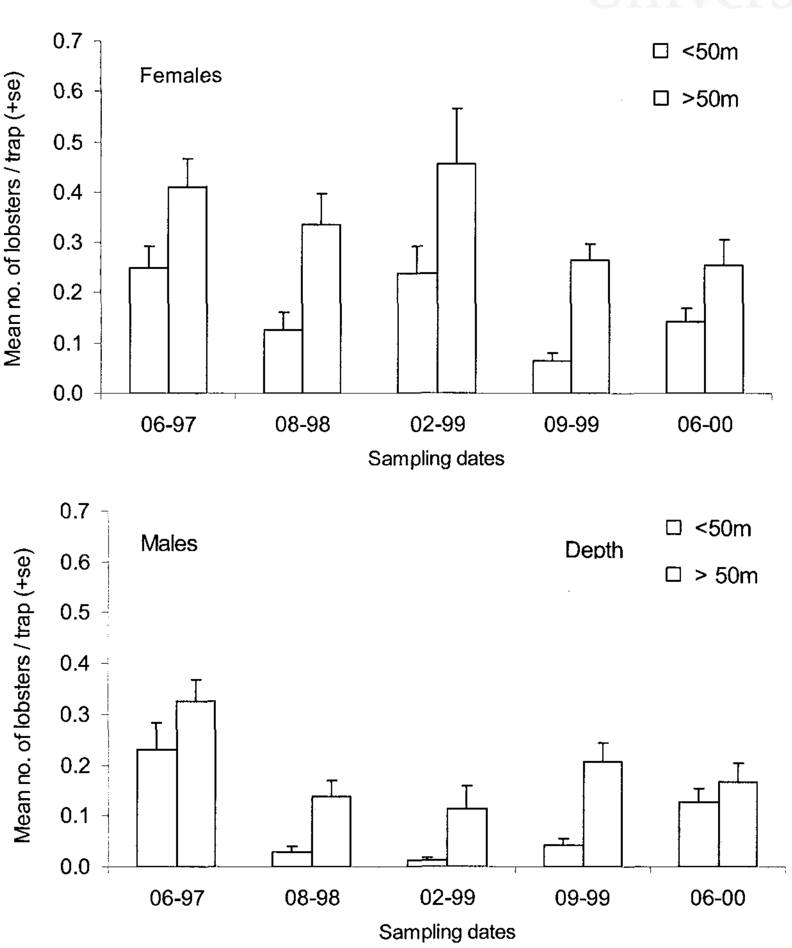


Figure 3.3: Mean catch rates (±SE) of female and male P. elephas by depth strata in the Columbretes Islands Marine Reserve during surveys in June 1997 (06-97, n = 30 trap sets), August–September 1998 (08-98, n = 48 trap sets), February 1999 (02-99, n = 34 trap sets), September 1999 (09-99, n = 42 trap sets), and June 2000 (06-00, n = 52 trap sets). <50 m = 20–50 m; >50m = 50–80 m.

Sex ratio

The overall sex ratio in the reserve (five surveys combined) was biased toward females (66%, χ^2 = 176, $P < 0.05$, $n = 3503$; Figure 3.4). Female dominance in trap catches was highest in winter 1999, when they comprised 94% of the specimens caught in shallow water and 83% of the specimens from the deep stratum. In the other sampling periods, except August 1998, the sex ratio approached 50% (Figure 3.4).

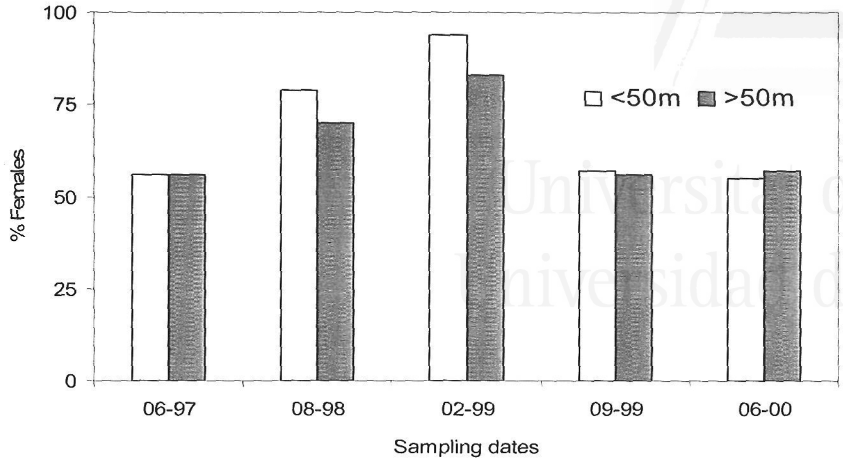


Figure 3.4: Sex ratio of P. elephas by depth strata in the Columbretes Islands Marine Reserve during the June 1997 (06-97, n = 752 lobsters), August–September 1998 (08-98, n = 640 lobsters), February 1999 (02-99, n = 794 lobsters), September 1999 (09-99, n = 561 lobsters), and June 2000 (06-00, n = 754 lobsters) surveys. <50m = 20–50 m; >50m = 50–80 m.

Size structure

Lobster catches were composed mainly of adults between 80 and 110 mm CL (Figure 3.5). Females' modal sizes ranged between 100 and 110 mm CL in shallow water and between 86 and 100 mm CL in deep water (Figure 3.5). Female lobsters larger than 120 mm CL were always found in the shallow stratum. Adult males caught in shallow waters were also larger (modes between 100 and 110 mm CL) than those from deeper areas (modes between 86 and 106 mm CL) (Figure 3.5). Males larger than 130 mm CL made up minor but distinct modes in the deep stratum. They were also present in shallow waters in early summer but were notably absent in both shallow- and deep-water samples in February 1999 (Figure 3.5). Immature specimens (<76 mm CL, Marin 1985) were almost exclusively in the deep stratum.

Table 3.2: Effects of time, depth, and sex on the size of Palinurus elephas from the Columbretes Islands Marine Reserve. NS = non-significant at P > 0.05.

Source of variation	SS	df	MS	F	Probability
Depth	108 962	1	108962	545.2	< 0.001
Sex	34 539	1	34539	173.1	< 0.001
Time	21 988	4	5497	27.5	< 0.001
Depth × Sex	612	1	612	3.1	NS
Depth × Time	3 685	4	921	4.6	< 0.001
Sex × Time	23 943	4	5986	29.9	< 0.001
Depth × Sex × Time	553	4	138	0.7	NS
Residual	696 307	3484	200		
Total	890 644				

The mean size of *P. elephas* varied with sex as well as with depth and time, but significant Time-×-Depth and Time-×-Sex interaction effects (Table 3.2, Figure 3.6) precluded contrasts across the main effects. On average, males were larger than females, and both females and males caught in shallow water were significantly larger than those from deep water (Figure 3.6). The size of females (overall mean, shallow, 105.5 ± 0.6 SE mm CL; overall mean, deep, 93.3 ± 0.3 SE mm CL) remained remarkably constant through time in shallow water (SNK tests). In deep water, females were significantly larger in late summer than in other periods (Figure 3.6; SNK tests). Male size (overall mean, shallow, 109.8 ± 1.1 SE mm CL; overall mean, deep, 98.1 ± 0.7 SE mm CL) varied significantly with time in both shallow and deep waters of the reserve (SNK tests). The most dramatic differences in size were observed in the deep stratum during February 1999, when males were significantly smaller than in any other period (SNK tests).

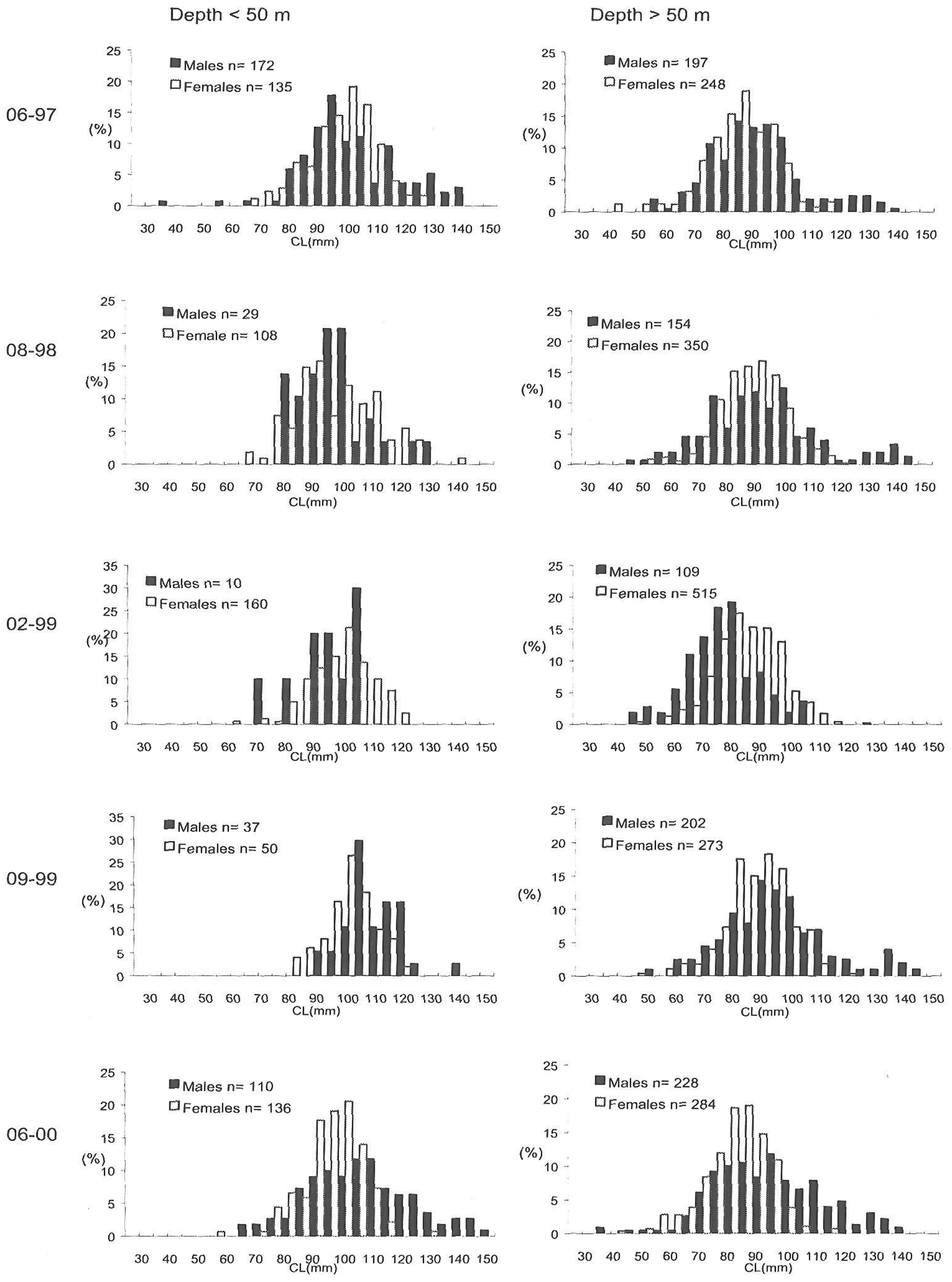


Figure 3.5: Size distributions of male and female P. elephas from two depth strata at the Columbretes Islands Marine Reserve during surveys in June 1997 (06-97), August–September 1998 (08-98), February 1999 (02-99), September 1999 (09-99), and June 2000 (06-00). <50 m = 20–50 m; >50 m = 50–80 m. n = number; CL = carapace length.

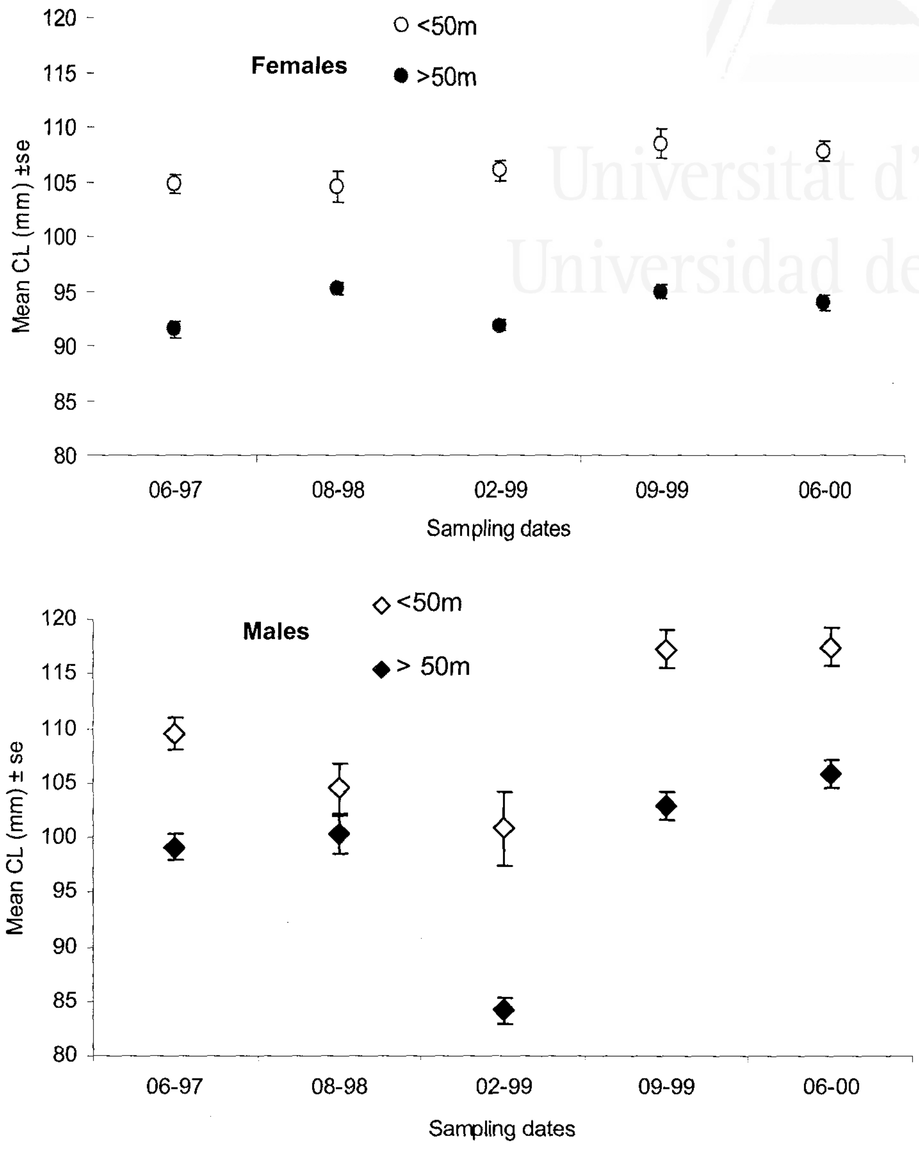


Figure 3.6: Mean size (±SE) of female and male P. elephas from two depth strata of the Columbretes Islands Marine Reserve during surveys in June 1997 (06-97), August–September 1998 (08-98), February 1999 (02-99), September 1999 (09-99), and June 2000 (06-00). <50 m = 20–50 m; >50 m = 50–80 m. CL = carapace length. Sample sizes as in Figure 3.4.

3.4. Discussion

Populations of deep-water spiny lobsters are often assessed by fishing because direct underwater observation is precluded over much of their bathymetric range. The data presented here are the first estimates ever obtained of the size, distribution, and relative abundance of *P. elephas* in the Columbretes Islands Marine Reserve. Lobster catches may be influenced by a variety of factors other than abundance, such as behaviourally or environmentally driven changes in catchability and gear saturation (Morgan 1974, Miller 1990, MacDiarmid 1991). The results of our study are therefore discussed in light of these factors, making use of preliminary data from a related study dealing with the relative size and sex selectivity of traps and trammel nets.

The significantly higher catch rates in the protected area than in the two fished control areas suggests strongly that the cessation of fishing has led to an increase in the lobster population in the marine reserve. This effect is expected given the high levels of exploitation observed in *P. elephas* fisheries (Pereiro and Fernandez 1974, Marin 1987, Ceccaldi and Latrouite 1994) as in most spiny lobster fisheries (Childress 1997). A positive response to the cessation of fishing has been reported for other species of spiny lobsters, such as *Panulirus argus* in the Dry Tortugas National Park of Florida (Hunt *et al.* 1991) and *Jasus edwardsii* in the Cape Rodney to Okakary Point (CROP) marine reserve off New Zealand (Cole *et al.* 1990, MacDiarmid & Breen 1993). Conversely, the Poor Knights Islands Marine Reserve was deemed inadequate for the effective protection of *Jasus verreauxi* because of the extensive migrations undertaken by juveniles (MacDiarmid & Breen 1993). Hunt *et al.* (1991) made a similar observation regarding the extent of the foraging range of *P. argus* relative to the small size of the core area of the Looe Key National Sanctuary (LKNS). The size of the protected area relative to the mobility of a species, and the type and extent of the habitats encompassed within the MPA, play important roles in the recovery of lobster populations (Cole *et al.* 1990, Hunt *et al.* 1991, Jones *et al.* 1993, MacDiarmid & Breen 1993, Childress 1997, Mayfield *et al.* in press). For species that move long distances at some time in their life cycle, only protection of very large areas will produce an appreciable change in population size structure (Childress 1997). Tag-recapture data from the Columbretes Islands indicate that *P. elephas* has limited mobility (mean distance < 5 km, Goñi *et al.*, unpublished data, see also Hepper 1977, Marin 1987, Hunter 1999). The Columbretes reserve is small (14 km^2) compared to the Dry Tortugas National Park (190 km^2) but large compared to the core area of the LKNMS (0.5 km^2) or the CROP reserve (5.5 km^2). Although the LKNMS core area has proven small for *P. argus*, the CROP reserve and the Columbretes Islands Marine Reserve seem of adequate size to rebuild populations of *J. edwardsii* and *P. elephas*, respectively.

Although the high catch rates of *P. elephas* within the protected area suggest a protection effect, the lack of other comparable protected sites and of data collected before protective measures were in place, prevents a reliable assessment of the effects of protection on *P. elephas* off Columbretes (Underwood 1992). This is a common problem aggravated by the frequent establishment of reserves in singular areas or to protect unique ecosystems (see, *e.g.*, Cole *et al.* 1990, Carr and Reed 1993, Jones *et al.* 1993, MacDiarmid & Breen 1993). Unfortunately, this problem cannot be solved, and the dilemma underscores the importance of conducting baseline studies before reserves are established. Of the two unprotected sites studied, the PLA most resembles Columbretes in substrate and topography. This resemblance and the location of PLA farther from the main fishing ports than SUB probably explain the higher catch rates obtained in the PLA in all surveys. The lower accessibility of this area also results in a more marked recovery of the lobster population than in the SUB during the 6-month annual closure. The effectiveness of the annual closure in the fished areas suggests that the permanent cessation of fishing is the likely cause of the high lobster abundance in the reserve.

The observed temporal variability in the size of the protected *P. elephas* population over the study period suggests that segments of the population reside outside the reserve at certain times. In general, studies of the temporal response of spiny-lobster populations to MPAs have yielded varying results according to the size of the MPA and the habitats encompassed relative to the needs of the species (*e.g.*, Hunt *et al.* 1991, Blonder *et al.* 1992, MacDiarmid & Breen 1993, Childress 1997). Spillover of lobsters from the MPA could make segments of the population vulnerable to fishing (Davis and Dodrill 1980, 1989, Hunt *et al.* 1991, MacDiarmid & Breen 1993, Sanchez-Lizaso *et al.* 2000). The fishery that has developed at the boundaries of the Columbretes Islands Marine Reserve confirms that a certain amount of spillover takes place. The potential impact of this fishery on the dynamics of the protected *P. elephas* population cannot be ascertained with the present data. In all the studies reviewed as well as in the present study, the effectiveness of the protection afforded by the MPAs appears to be limited by the impacts of fishing on lobsters that undergo daily foraging movements or seasonal migrations outside the MPA.

The reserve encompasses depths of up to 80 m, so the shallow stratum includes the lower quartile of the lobster's bathymetric distribution, and the deep stratum encompasses the second and part of the third quartiles. As a consequence, biological or environmentally driven changes in population abundance and structure are expected to be more marked in the shallow than in the deep waters of the reserve. Our results are consistent with this expectation, as temporal changes in catch rates were more marked in the shallow than in the deep stratum. Nevertheless, the broadly similar temporal trends in catch rates in the two strata suggest that, whatever the cause of the observed changes, it exerts an effect on the bulk of the population.

The temporal pattern of female abundance in shallow water, which was high in early summer and winter and low in early fall, is consistent with annual onshore-offshore movements of *P. elephas* in the Atlantic (Mercer 1973, Ansell & Robb 1977), common in populations of temperate spiny lobsters (Herrnkind 1980). After mating and oviposition (July–October in the western Mediterranean, Marin 1985), the bulk of the female population would move down to deeper waters (extending beyond the reserve boundaries) during egg development and would return to inshore areas prior to egg hatching (December–February in the western Mediterranean, Marin 1985). Despite these variations in female abundance, female size structure did not vary greatly with time, suggesting that, if onshore-offshore movements caused changes in female numbers, they would affect a more or less constant segment of their population, probably adults of 80–110 mm CL. Large females would remain in shallow waters year-round, whereas subadults would inhabit deeper waters.

The trend of male abundance in shallow waters of the reserve, with maximum values in June and lowest in February, could be explained by a similar migration pattern, except that the onshore migration would take place later (April–May) than for females. This point is clearly contentious, as Mercer (1973) notes that off Ireland large males appear to overwinter in the shallow areas, whereas

Ansell & Robb (1977) indicate that off Scotland males move inshore earlier than females. In contrast to that of females, the size structure of males in trap catches changed substantially over time. In particular, mean male size in shallow water during August–September 1998 and February 1999 was low relative to that in other periods. This difference paralleled that of the male catch rates during the same periods. If onshore-offshore movements do occur in males, the changes in size frequencies with depth and sample date suggest that large lobsters participate in these migrations comparatively more often than smaller ones, probably because of reproductive activity. An observation that supports this notion is that large males were found in shallow water in June prior to mating later in summer.

The balanced sex ratio prior to mating recorded in the present study appears to be a common feature of *P. elephas* populations (Mercer 1973, Campillo 1982, Hunter *et al.* 1996), but the observed female predominance in *P. elephas* over much of the year, also noted by Campillo (1982) off Corsica and Hunter *et al.* (1996) off Wales, cannot be explained with the available data. Kanciruk (1980) indicated that differences between male and female movements appear to cause these unbalanced sex ratios in a number of other spiny lobster species. Mercer (1973) observed short-term aggregations of entirely male or female *P. elephas*, some of which consisted of newly berried females. The availability of shelters for egg extrusion appeared to cause these groupings, but no explanation was found for similar congregations at other times of the year (Mercer 1973).

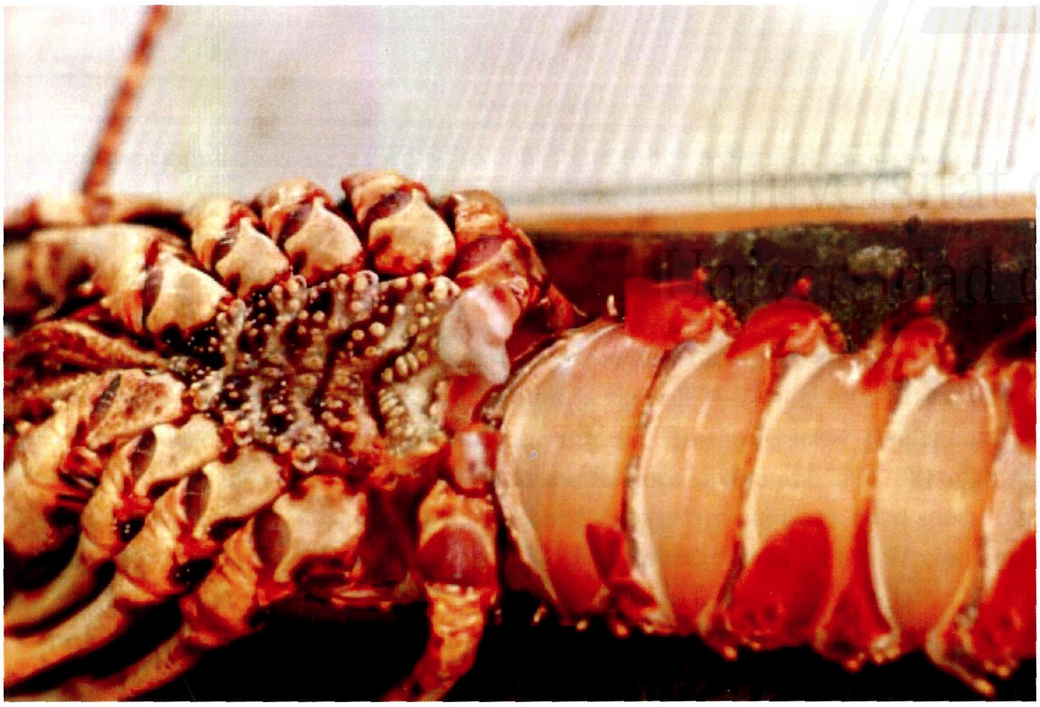
Although some studies have shown trap catch rates to be a reliable indicator of lobster abundance (Morgan 1974, Polovina 1989, Miller 1990), trap performance may be influenced by many factors other than local abundance. The effect of variables such as duration of deployment, trap saturation, bait type, and moon phase were controlled in the present study (see Methods), yet catchability in traps may also depend on physiological and environmental factors, such as moulting, reproduction, and temperature (McLeese and Wilder 1958, Davis 1977, Jernakoff and Phillips 1988, Phillips 1990, Fogarty and Addison 1997). Although it has not been possible to identify these factors in the current study, a related study on the relative selectivity of traps and trammel nets has yielded preliminary data useful in interpreting the results of our trap surveys (Goñi *et al.* in prep.). These data reveal a discrepancy in the sex ratios of trap and trammel-net catches that indicates lower catchability in traps of male lobsters than of females. Reduced catchability appears to intensify with male size and may be more marked at certain times of the year (*e.g.* late summer relative to early summer) (Goñi *et al.* in prep.). Because the largest lobsters in the population are males, it is not possible to ascertain whether the reduced catchability is sex or size related. Therefore, an alternative to our suggestion of onshore-offshore migrations of *P. elephas* in the Columbretes Islands Marine Reserve are temporal changes in catchability. Changes in catchability, affecting males and females differentially, would result in apparent lower abundances of lobsters, and especially of males, at certain times.

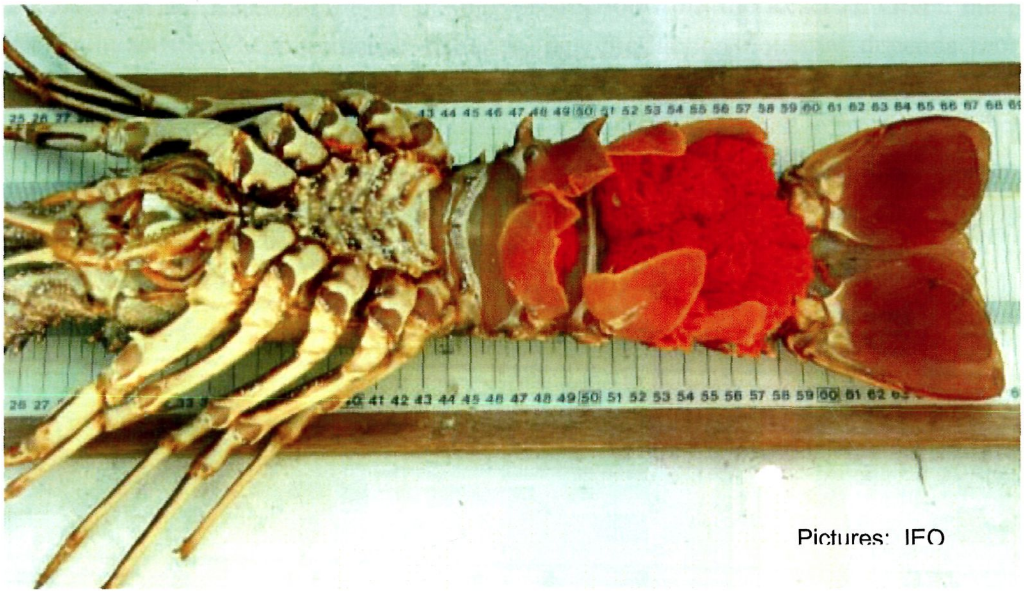
The differential catchability of males and females could be mediated by sex- or size-specific behavioural patterns (Herrnkind 1980, Miller 1990, Phillips 1990, Hunter *et al.* 1996), by variations in feeding or locomotor activity related to moult stage (Heydorn 1969, Newman & Pollock 1972, Morgan 1974, Lipcius & Herrnkind 1982, MacDiarmid *et al.* 1991), or by reproductive behaviour (Miller 1990, MacDiarmid *et al.* 1991, Hunt *et al.* 1991, Blonder *et al.* 1992, Cockcroft *et al.* 1995). From the design of the traps employed in our study, it is apparent that very large lobsters may be less likely to enter, but also to escape, than medium and small specimens, an observation also made by Hepper (1977). Certainly, the maximum size observed in trammel nets (165 mm CL) exceeds that in traps (155 mm CL). Although a number of studies report increased trap catchability of decapods with size (see Miller 1990 for a review), Heydorn (1969) and Newman & Pollock (1972) noted that large male *J. lalandii* were less likely to enter traps. Mercer (1973) observed that large male *P. elephas* off Ireland are sedentary and prefer solitary den occupation. Presence of conspecifics in a trap could therefore deter entrance of large males, at least during no reproductive periods. Finally, increased activity prior to mating, or when water is warmer (Hepper 1977), has been noted in *P. elephas* off Corsica (Campillo 1982, Marin 1985) as in other spiny lobsters (*e.g. P. argus*, Davis 1977, *J. edwardsii*, MacDiarmid *et al.* 1991). This differential activity rate could result in higher catch rates of both sexes during early summer than in other survey periods. Although Hepper (1977) attributed patterns of abundance of *P. elephas* from trap catch rates to seasonal changes in catchability associated with water temperature, this attribution does not seem feasible in Columbretes, where temperatures peak in late summer.

The scarcity of males in samples of February 1999 is noteworthy and may indicate a substantial sex segregation of the *P. elephas* population at this time (see, *e.g.*, Mercer 1973, Pollock 1982), but the presence of recent postmoult males in the February 1999 samples also suggests reduced activity, and thus catchability, in relation to ecdysis (*e.g. J. lalandii*, Newman & Pollock 1971, 1972). A decrease of about 70% in catchability has been estimated for late postmoult *P. argus* (Lipcius & Herrnkind 1982) and *Panulirus cygnus* (Morgan 1974); changes in catchability linked to ecdysis could therefore explain the observed low male catch rates in February 1999, which were 23–42% lower than the maximum observed in the June surveys. Nevertheless, male peak moulting in the western Mediterranean appears to occur later in the year (April–May) (Campillo 1982, Marin 1987), so the low catch rates of male *P. elephas* observed in February 1999 are probably due to a combination of reduced vulnerability and reduced availability.

The concentration of juveniles in the deeper waters of the reserve is noteworthy because settlement appears to occur in shallow waters. Post settlers (mean size 16.5 mm CL, Goñi *et al.* unpublished data) were observed in underwater censuses in late summer between 15 and 20 m depth, and 30–40 mm CL juveniles (2 years old; Marin, 1987) were observed at about 30-m depth the following summer (Goñi *et al.* unpublished data). Because the smallest juveniles caught in traps measured 40–45 mm CL (2–3 years old; Marin 1987), a relatively rapid migration of juveniles takes place from the shallow settlement habitats to deeper habitats, presumably during winter or spring. Although no direct evidence of this migration exists for *P. elephas,* similar ontogenetic migrations have been described in other palinurid lobsters (Herrnkind 1980, Morgan *et al.* 1982, Lyons 1986).

The present study highlights the effectiveness of seasonal and permanent fishing restrictions in rebuilding *P. elephas* populations, but despite the limited scale of movements of adult *P. elephas*, the temporal variability in abundance observed in the Columbretes Islands Marine Reserve suggests that lobsters undertake seasonal migrations to greater depths. Changes in lobster behaviour linked to reproduction and moulting, particularly of males, probably also influence population estimates of *P. elephas* from trap surveys. In contrast to those of better-studied shallow-water palinurids, the roles of seasonal movements and of changes in catchability cannot be readily partitioned in *P. elephas* in the Mediterranean because its deep distribution hampers direct observation by divers. If adult *P. elephas* undertake limited migrations in depth, the effectiveness of the Columbretes Islands Marine Reserve in rebuilding the local lobster population could be improved by enlargement of the reserve to encompass a greater proportion of deep habitats. Tag-recapture data suggest that at present the Columbretes Islands Marine Reserve is contributing to increasing fishery yields through dispersal of adults to nearby areas perhaps on a seasonal basis (Goñi *et al.* unpublished data). Tag-recapture information could better identify how migration patterns by size and sex influence population dynamics of *P. elephas* at the Columbretes Islands Marine Reserve and help evaluate the impacts of fishing mortality on population abundance. A further important challenge is to investigate the movement patterns of juveniles, which may reveal whether the protected population is self-recruiting and how the nearby exploited grounds are replenished annually.





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CHAPTER 4: REPRODUCTIVE BIOLOGY AND SPAWNING POTENTIAL OF *P. ELEPHAS* IN THE COLUMBRETES MARINE RESERVE

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Abstract

Protected lobster populations are expected to contribute to the replenishment of fished populations through increased egg production. We studied the reproductive biology and egg production potential of a population of the spiny lobster *Palinurus elephas* protected from fishing since 1990 in the Columbretes Islands Marine Reserve (western Mediterranean). An index of spawning potential was derived to compare egg production potential in the Reserve and in western Mediterranean exploited populations. Females' physiological (ability to reproduce) and functional maturity (ability to mate and bear eggs) occurred at a size of 76-77 mm CL. Males physiological maturity occurred at a slightly larger size - 83-83 mm CL. In the Reserve *P. elephas*' individual fecundity increases linearly with body size up to the females' maximum size, although maximum reproductive yield (eggs per body gram) was reached at intermediate sizes. Size-specific fecundity in the protected population was similar to that of lightly fished populations off Ireland and greater than that of western Mediterranean exploited populations. The female size class of 105-110 mm CL contributed most to egg production in the protected population and is well above the minimum landing size (MLS) for western Mediterranean fisheries. Newly mature females (below MLS) generate a very small fraction (1%) of the egg production from the Reserve. Given the pattern of exploitation in western Mediterranean fisheries, egg production potential depends more on the quantity than on the mean size and fecundity of the available females. The role of the greater availability of large males for mating in unfished populations is discussed in terms of the females' individual fecundity and mating success.

4.1. Introduction

Despite the importance of the *P. elephas* fisheries in the Mediterranean, there have been few published studies of its reproductive biology and estimates of the size at onset of maturity or size specific fecundity are available only for *P. elephas* populations of Corsica (Campillo & Amadei 1978, Campillo *et al.* 1979, Campillo 1982, Marin 1985, Marin 1987). Understanding how exploitation affects lobster breeding stocks and egg production is essential for stock management, especially where the relationship between stock and recruitment is not known (Chubb 2000). In the case of *P. elephas* fisheries off Spain, minimum landing sizes were set on the basis of empirical observations of berried females and no studies have been conducted to assess fecundity or egg production.

In the framework of the investigations of the responses of *P. elephas* to the cessation of fishing in the Columbretes Islands Marine Reserve size at maturity, fecundity and reproductive potential were considered a priority. In this Chapter I describe the reproductive biology of the *P. elephas* population in the Columbretes Islands marine reserve and compare its reproductive potential with that of exploited populations in the Western Mediterranean. This is the first study of the reproductive biology of a protected *P. elephas* population and one of the few studies done on aspects of the reproductive biology of non-exploited spiny lobster populations (Davis 1975, MacDiarmid 1989 a, b, Annala 1991, Kelly *et al.* 2000, Bertelsen & Cox 2001, Bertelsen & Matthews 2001).

4.2. Materials and Methods

Data and sample collection

Data were collected in four trammel-net experimental fishing surveys conducted in the Reserve during August-September 1998 ("August"), February-March 1999 ("February"), September-October 1999 ("September") and June 2000 ("June"). The design and methodology used in the surveys has been described in detail by Goñi *et al.*(2003b). Carapace length (CL, mm), measured from the tip of the rostral spine to the posterior edge of the carapace, and weight (W, g) were recorded from all lobsters caught. The presence of external eggs and spermatophores in females and of sperm in males' genital openings were also noted. In each survey, a size-stratified sample (minimum of 5 specimens per sex) of each 5 mm CL size group was set aside for dissection. Ovary maturity stage (according to the 7-stage scale by Marin 1987) and ovary weight were determined in dissected females. Egg masses were removed from all berried females for fecundity estimation. Gonad weight was also determined for dissected males.

Gonad maturation and breeding period

The breeding period was determined by the temporal development of the ovaries in females (Juinio 1987, Chubb 2000) and by the evolution of the gonad index in males and females (Juinio 1987; Plaut 1993). The seven maturity stages of Marin (1987) were grouped as follows: 1: "immature" 2-4: "developing", 5-6: "ripe", and 7: "berried" (or spent). The gonad index (GI) was calculated by the gonad wet weight as a percentage of the total body wet weight (Aiken & Waddy 1980). To reduce the influence of different numbers of immature individuals in the various surveys on the estimates of mean GIs, immature lobster (below a expected minimum individual size at maturity of 70 mm CL) were excluded from the calculations. The presence of external spermatophores in females and of sperm in males was also used as indicator of breeding activity.

Size at maturity

Females

We estimated the size of physiological maturity (or size at which ovaries undergo maturation) and the size of functional maturity (or size at which females participate in the reproductive process and lay eggs). The sizes at which 50% of the females were mature or carried eggs (L50%) were used to define the mean size of physiological and functional maturity respectively (Marin 1987, MacDiarmid 1989 b, Minagawa 1997). The proportion mature or berried (M) in each 5-mm CL class were determined and fitted by a non-linear modelling procedure to the logistic model:

$M = 1/[1 + \exp(a + b * CL)]$, where a and b are parameters of the logistic function and $L50\% = -a/b$ (Sparre & Venema 1992).

Females were considered physiologically mature if they had ovaries in stages 4 or greater during the reproductive season (Marin 1987). Since females may commence mating and egg laying at different times depending on their size (Chubb 2000), functional maturity was estimated at the end of the spawning period (September).

The size at which females undergo ovary maturation for the first time was also assessed by the relationship between gonad weight (GW) and body size (CL) during the spawning period (Aiken & Waddy 1980, Marin 1987). The relationship is of the form: $GW = a * CL^{b}$, where a and b are constants, and was converted to a straight line by a logarithmic transformation.

Males

In male spiny lobsters it is not possible to determine physiological maturity from external characters or from the macroscopic appearance of the testes (Aiken & Waddy 1980, Chubb 2000). Thus, we estimated the size at which male gonads undergo maturation for the first time by the relationship between gonad weight and body size during the spawning period as described above for females. We also used the presence of sperm in the genital openings as evidence of physiological maturity.

Egg stage and size

Egg stage was determined according to the three-stage scale by Beyers & Goosen (1987) (1: embryonic eyes not visible; 2: eyes visible under 10-x magnification; 3: eyes visible to naked eye). Measurements were made of 20 randomly chosen fresh eggs per clutch (random axis at x50) using a dissecting microscope with calibrated eyepiece micrometer. The relationship between egg size and lobster size was assessed by regression analysis. Differences between mean egg size at the beginning and end of the incubation period were assessed by t-test ($\alpha = 0.05$)

Size–fecundity relationship

For this study, fecundity is defined as the number of eggs attached to the female pleopods shortly after extrusion. To minimize egg loss, potential absolute fecundity was estimated from clutches of stage 1 eggs. Egg masses were removed from pleopods by dissection and frozen for storage. Prior to preparation for egg counting, excess liquid was filtered off and the egg masses placed on absorbent towels. Three random sub samples comprising a minimum of 0.5% (by weight) of the females' total egg mass were weighed and separated for processing and counting. Sub samples were soaked in Gilson solution for 24 hours and oven-dried at 60° C for 2-3 hours. Eggs were counted manually using a 10x-desk magnifier. The replicate sub samples were used to estimate the sampling error of fecundity determinations and the average of the three counts was used to calculate relative (eggs per body gram) and absolute fecundity (Juinio 1987; De Martini *et al.* 1993). The parameters of the function relating fecundity to body size were estimated by predictive linear regression analysis. Egg loss during incubation was assessed by comparing fecundity-size equations from samples of berried females at the beginning and end of the incubation period.

ANCOVA was used to compare mean fecundity in the two periods using lobster size as a covariate (Annala & Bycroft 1987). The difference between the predicted fecundity values for a given size interval was used to calculate egg loss in that size range.

Reproductive potential

Two measures of reproductive potential were considered in this study. First, the estimates of mean fecundity at size, the functional maturity-size curve and the size structure of the female population during the June survey were used to calculate the relative reproductive potential (RRPi) by size class of the *P. elephas* population in the Reserve:

RRPi = Mi x Fi x Ci

where Mi is the proportion of mature females in size-class (i), Fi is the mean individual fecundity of size-class (i) and Ci is proportion of size class (i) in the sample (Kanciruk & Herrnkind 1976, Hobday & Ryan 1997, Tully *et al.* 2001). Size frequency data from the June survey were selected because previous studies (Goñi *et al.* 2003b) identified June as the period when the two sexes are more mixed and their catchability/availability is highest. This index identifies the female size classes that have the potential to produce most eggs.

Secondly, a modification of the index of spawning potential of Morgan *et al.* (1982) was used to assess how this reproductive potential may be realised in unfished and fished *P. elephas* populations. The modified index of spawning potential (ISP) was estimated utilising catch per unit effort (CPUE) of mature females as an index of abundance and the mean individual fecundity of the population:

ISP = F * CPUE,

where F is the mean fecundity of the average mature female in the population and CPUE is the mean catch of mature females in a standard trammel net set (i.e., 500 m-long soaked 2 nights). This ISP may also be related to the area fished by this standard unit of effort, which may be assumed constant in all fisheries/areas. While RRP depends on the size structure of the female population, ISP also depends on the abundance of mature females. Thus, ISP provides a more appropriate measure of reproductive potential than RRP when comparing fished and unfished populations. All fecundity values used were corrected for egg loss.

4.3. Results

Gonad maturation and breeding period

A total of 260 females (size range: 46.5-135.5 mm CL) from the June, August, September, and February surveys were used to estimate ovary maturity stage. In the samples, egg-bearing females were observed from August through February, although occasional observations of spawning activity as early as June were made in later visits to the Reserve. Ovarian development occurred from late February to June. In June 85% of the females had developing or ripe ovaries and none were ovigerous. By August almost 50% of the females in the sample had laid eggs, while 32% were still ripe or developing, and by September 84% of the females were berried. In February, only 1% was still incubating eggs. The ovarian index supported this pattern reaching its maximum in June-August and declining sharply after oviposition in September (Figure 4.1). Ovaries of large females developed early in the reproductive season (February) while those of newly mature females developed later (August-September) (Figure 4.2). Spent ovaries appeared in August and increased in September.

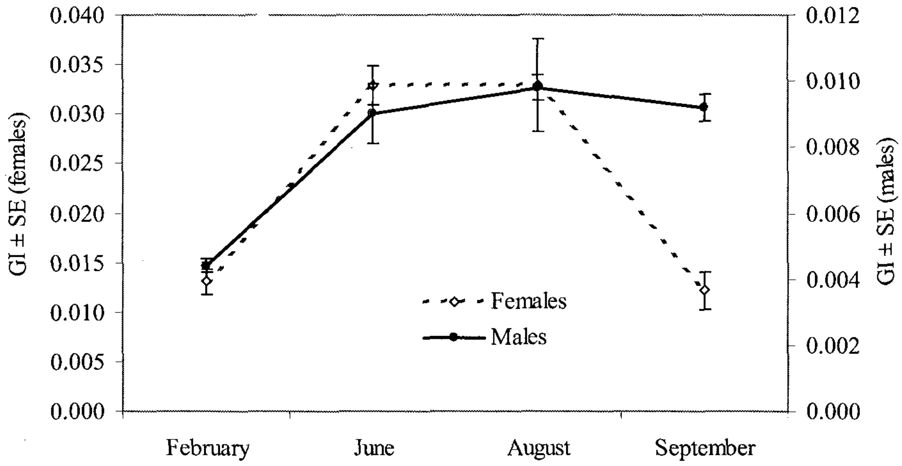

Figure 4.1: Gonad Index (gonad weight/body weight) of female and male P. elephas from the Columbretes Islands Marine Reserve. Only lobsters > 70 mm CL have been used in the calculation of the indices.

The evolution of the males' gonadal index shows that testis developed also during late winter and spring (Figure 4.1). The index reached a maximum in August but remained nearly stable throughout the reproductive season between June and September.

Spermatophores were observed on the sternum of only 15 females (size range: 85-119 mm CL) from 3669 examined during the four surveys. Their appearance was that of ellipsoidal white gelatinous matrices 15-24 mm long and 7-16 mm wide. Spermatophores were also seen attached to the males' genital openings in 6 (size range: 76-138 mm CL) out of 2457 specimens examined.

Size at onset of maturity

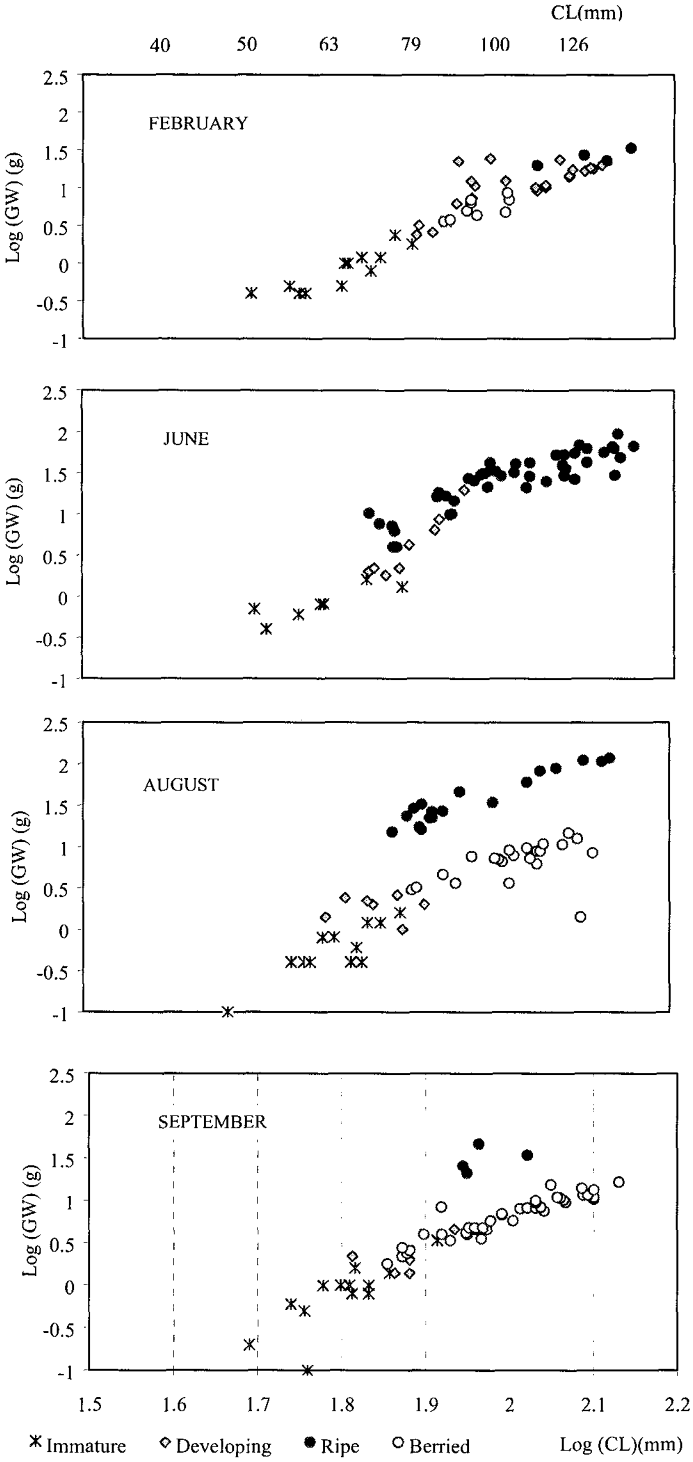

Figure 4.2: Plots of log (gonad weight) (GW) against log (body size) (CL) of female P. elephas from the Columbretes Islands Marine Reserve.

Females

The smallest egg-bearing female encountered measured 71.5 mm CL, although in the June survey ripe females as small as 69 mm CL were observed, suggesting imminent spawning. A total of 192 females (size range: 46-140 mm CL) from the June, August, and September surveys were used to estimate size at physiological maturity. Fitting the logistic model to the proportion mature yielded a L50 value of 76.5 mm CL (± 7.8 SD) (Figure 4.3). Size at functional maturity was estimated from a sample size of 683 females (same size range) caught during the September survey, of which 575 were ovigerous. The proportion of berried females rose rapidly from 70 to 85 mm CL. The estimated L50 size at functional maturity was 77.2 mm CL (± 5.3 SD) (Figure 4.3). At the MLS of 80 mm CL 70% of the females were mature. The size at maturity was also estimated from the plots of log (GW) against log (CL) shown in Figure 4.2. The August plot shows two clearly differentiated groups of points, the lower one corresponding to immature, developing and spent females and the upper one representing pre-spawning or ripe females. The transition between the two groups is distinct and occurs at 74-77 mm CL.

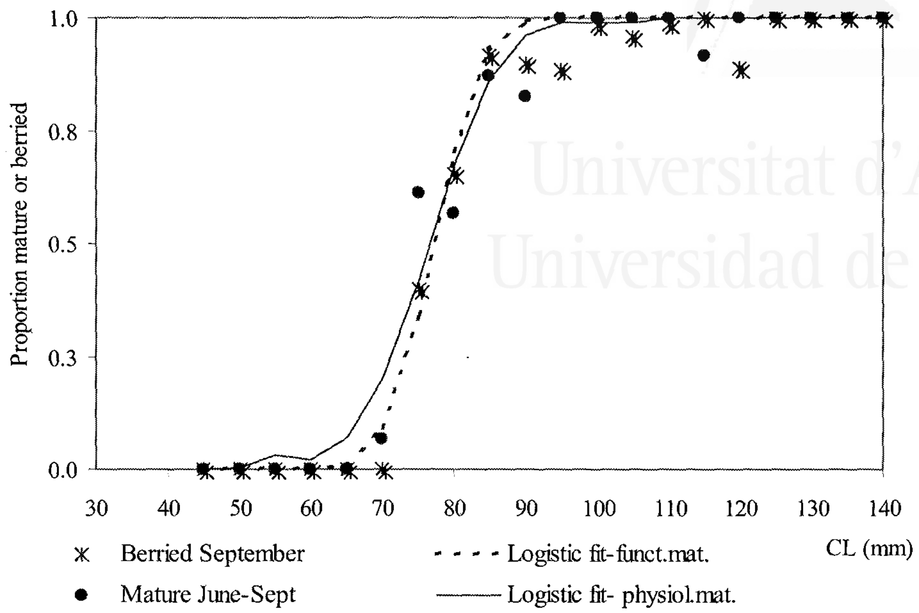

Figure 4.3: Proportion by size class of female P. elephas berried and mature during September and June-September respectively in the Columbretes Islands Marine Reserve. Equations of fitted lines in text.

Males

A sample of 125 males (size range: 49-168 mm CL) from the August and September surveys was available for the analysis of the relationship of log(GW) to log(CL). Gonad weight increased at a higher rate in small immature males than in large mature ones (Figure 4.4). Two groups were defined by points that revealed different slopes representing two physiological states separated by puberty. To avoid using data around the expected intersection, linear models were fitted to the log(GW) and log(CL) pairs of data for males <70 mm CL and for males >90 mm CL and the intersection between the two lines at 82.5 mm CL was taken to be the mid-size at first maturity.

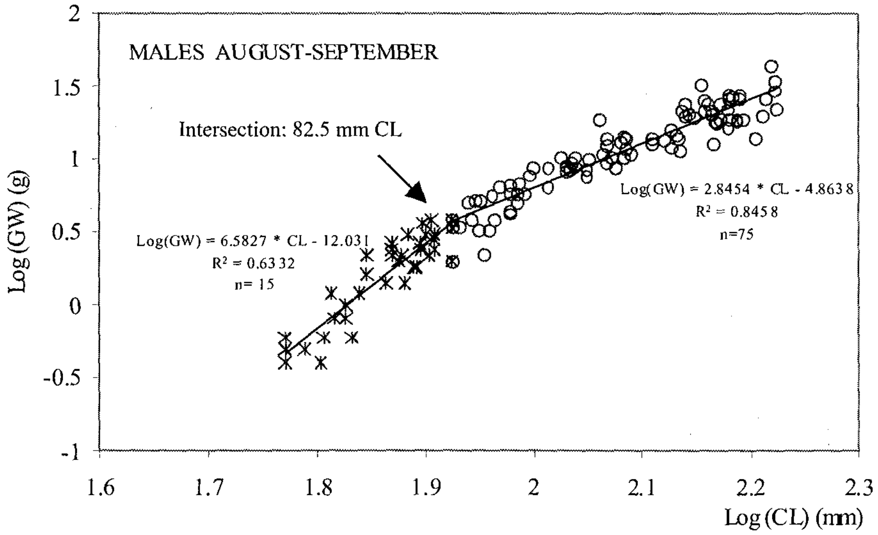

Figure 4.4: Plots of log(gonad weight) (GW) against log(body size) (CL) of male P. elephas from the Columbretes Islands Marine Reserve. Fitted lines for males < 75 mm CL and for males > 90 mm CL and their intersection are shown.

Egg stage and egg size

Berried females caught in the August and September surveys had only stage 1 eggs while females caught in the February survey had exclusively stage 3 eggs. The diameter of stage 3 eggs (mean: 1.33 mm, SD: 0.08 mm, range: 1.23-1.40 mm) was significantly larger than that of stage 1 eggs (mean: 1.02 mm, SD: 0.05, range: 0.90-1.10 mm) ($t_{0.05(2)1,78} = 12.73$, $p<0.0001$). Egg size tended to increase linearly with body size although high individual variability was reflected in a very low R^2 value ($F_{0.05(2)1,68} = 5.08$, $p = 0.02$, $R^2 = 0.07$).

Size-fecundity relationship

The sample of berried females with stage 1 eggs covered the whole size spectrum of matur females in the population (range: 71.5-135.5 mm CL). Egg mass weight varied from 17.7 to 139. grams and a power function linked egg mass weight to body size (Weight egg mass = $2*10^{-5}$ $CL^{3.228}$, $R^2 = 0.86$, n = 70).

The least and most fecund females carried 23483 and 201549 eggs respectively, although there was considerable variation in the number of eggs produced by females of similar size (e.g. 42% difference between two small - 74.5 mm CL - females). The overall coefficient of variation of the triplicate fecundity estimates was 2.3%, similar to the 2% found by De Martini *et al.* (1993). A weak ($R^2 = 0.17$) but significant positive linear relationship was found between the variation in fecundity and body size ($F_{0.05(2)1,69} = 7.66$, $p = 0.0004$).

The number of eggs per clutch varied with body size according to the following linear relationship (Figure 4.5):

$F = 2428 * CL - 148988$, $R^2 = 0.85$, n = 70

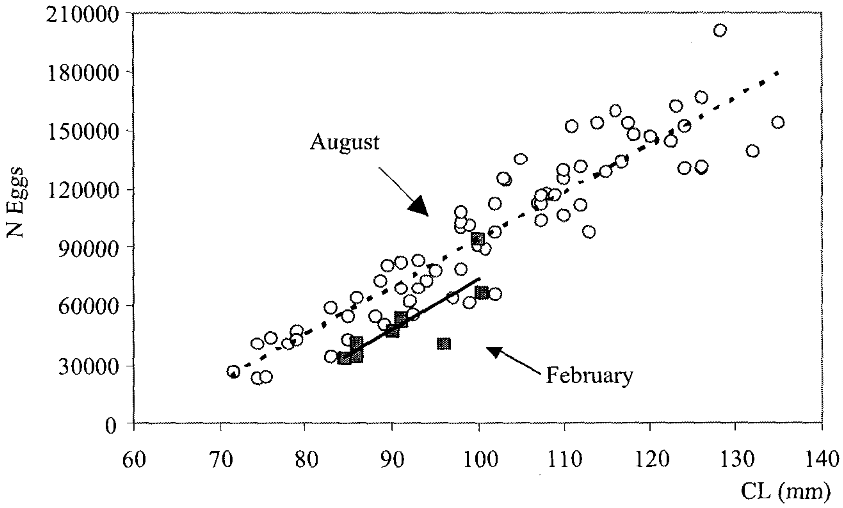

Figure 4.5: Fecundity-size data and fitted lines of female P. elephas from the Columbretes Islands Marine Reserve at the beginning (circles) and at the end (squares) of the incubation period. Equations of fitted lines in text.

The number of eggs per body gram ranged from 67 to 150 and a significant relationship with body size was found indicating that maximum relative fecundity occurred in females of 100-110 mm CL (Figure 4.6):

N° of eggs/ gram = $-0.027.2 * CL^2 + 5.722 * CL - 181.6$, $F_{2(0.05),2,6\,2} = 6.77$, $p = 0.002$, $R^2 = 0.18$

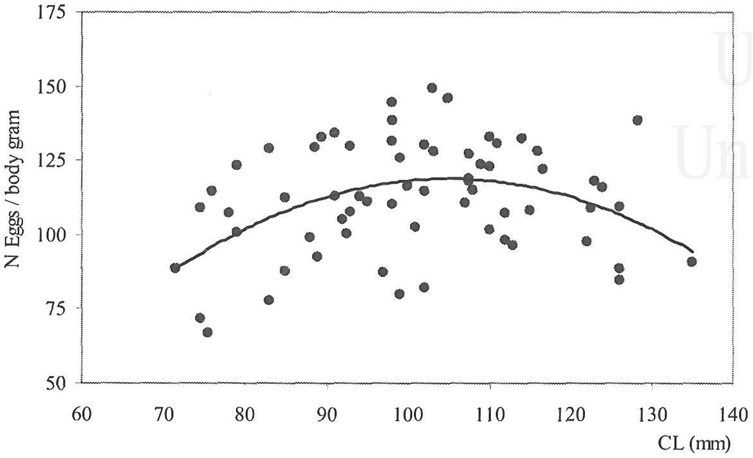

Figure 4.6: Number of eggs per body gram against body size (CL) and fitted line of female P. elephas from the Columbretes Islands Marine Reserve. Equation of fitted line in text

The size range of berried females collected at the end of the incubation cycle (February survey) was restricted to the 85-105 mm CL interval. Thus, egg loss was determined by comparing fecundity-size relationships within that size range at the beginning (F= 2516.6 * CL – 160203, R^2=0.49) and end (F= 2570.3 * CL – 184103, R^2=0.64) of the incubation period. The slopes of the fitted size-fecundity lines were indistinguishable between periods (CL x Period interaction: $F_{2(0.05),1,30}$= 0.0016, p=0.967) while the intercepts differed between periods ($F_{2(0.05),1,30}$= 25.4360, P<0.0001), with mean fecundity at the beginning being significantly greater than at the end of the incubation period (Figure 4.5). The distance between the two fitted lines in the mid-point (92.5 mm CL) indicated a mean egg loss of 26% of the fecundity of newly berried females of that size.

Reproductive potential

Protected population

The modal size class of egg production in the protected population was 105-110 mm CL, which yielded 19% of the population egg production and was similar to the mode of the female size distribution (Figure 4.7). Lobster smaller than the 80mm CL MLS comprised 12% of the population and produced 1% of the eggs. Twenty-five percent of the egg production was contributed by females smaller than 97.5 mm CL which represented 47% of the population.

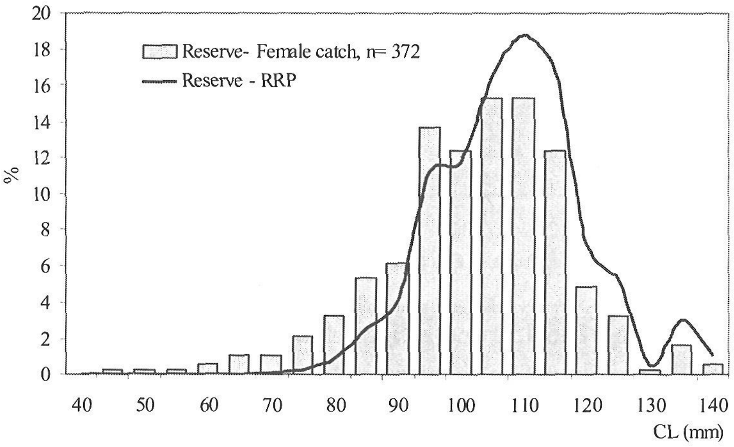

Figure 4.7: Frequency size distribution (June survey) and relative reproductive potential (RRP) of female P. elephas from the Columbretes Islands Marine Reserve. Minimum landing size= 80 mm CL.

Comparison with exploited populations

Data on the reproductive biology of fished Mediterranean *P. elephas* populations available for comparison are summarised in Tables 3.1, 3.2, and Figure 4.8. Campillo (1982) also gave size structure and CPUE data from experimental catches off Corsica in 1977. All CPUE and size structure data from experimental and commercial fishing operations presented here were obtained in trammel net sets of similar characteristics and were thus comparable.

The ISP of the fished populations of Mallorca and Corsica ranged from 69607 to 248596 eggs per unit effort (or unit area fished); that is, 5-18% the ISP of the population in the Reserve (Table 4.2). The higher value corresponds to lightly fished areas off Corsica (Campillo 1982).

Table 4.1: Size at maturity (CL, mm) estimates of P. elephas from western Mediterranean populations. Where relevant estimates are given from two methods: logistic fit to percent mature or berried by size class and intercept analysis from log(gonad weight)-log(carapace length). n= sample size. See text.

Location / Method	Physiological maturity Mean size ± SD		Functional maturity Mean size ± SD	Reference
	Females	Males	Females	
RM Columbretes				
- Percent mature/berried	76.5±7.8 (n= 192)		77.2±5.3 (n= 683)	This study
- Log (Gw)- Log(CL)	74-76 (n= 67)	82.7 (n= 94)		
Mallorca				
- Percent mature/berried	76.9±3.5 (n= 74)			Goñi *et al.* unpublished
- Log (Gw)- Log(CL)	75-77 (n= 74)			
Corsica				
- Percent mature/berried	80 (n= 98)		86 (n= 1169)	Marin 1987
- Log (Gw)- Log(CL)	76 (n= 57)	78 (n= 53)		

Table 4.2. Index of spawning potential (ISP) (see text) of P. elephas from western Mediterranean locations. MR: Marine reserve. Sources of data and details of calculations in footnotes below.

	COLUMBRETES MR	MALLORCA	CORSICA fully exploited	CORSICA lightly exploited
Mean size of mature females (mm CL) (a)	102.5	99.4	98.9	98.9
Mean fecundity (b)	99882	81880	67188	67188
CPUE (c)	18.8	2.7	1.4 (d)	5.0 (d)
ISP (e)	1389559 (100%)	163597 (12%)	69607 (5%)	248596 (18%)

(a) From the size structure of mature females in the Reserve and fished populations. The functional maturity function (see text) of the Reserve population used also to estimate proportion mature in the Mallorca population. For the Corsica population, the functional maturity curve of Marin (1987) was used. The size structure of the female catch in Corsica was not separated by areas with different exploitations levels (Campillo 1982).

(b) Fecundity-size (CL, mm) relationships used as in Figure 4.8; for the two Corsica estimates the fecundity-size relationship of Campillo (1982) was used.

(c) CPUE: Mean number of mature females caught in a standard trammel net set (500 m 2 nights soak time).

(d) CPUE estimates from experimental trammel net sets in heavily and lightly fished areas reported by Campillo (1982): low values (0.1824 kg/50 m) and high values (0.655 kg/50 m); length-weight relationship of Campillo (1982) used to transform catch in weight to numbers; 1:1 sex ratio of the catch assumed; proportion mature from Campillo (1982).

(e) Values corrected for egg loss (26%).

4.4. Discussion

Reproductive Biology

Palinurus elephas in the Columbretes Islands Marine Reserve breed once a year between June-October. As in other spiny lobster species (Chubb 2000), large females mature, mate and lay eggs early in the breeding season while small females develop and spawn towards the end. The analysis of the evolution of male gonads indicates that males copulate and re-charge the gonads repeatedly through the breeding season. Egg incubation extends until February-March, lasting about 5 months. A similar reproductive pattern has been described in *P. elephas* off Corsica (Western Mediterranean) (Campillo & Amadei 1978, Campillo 1982, Marin 1987).

Gonad maturation, mating and egg laying in female *P. elephas* off the Columbretes Islands Marine Reserve occurs for the first time at a mean size of 76-77 mm CL (or 4 years of age; Marin 1987). The size at physiological maturity in the Reserve closely resembles that found for females from Mallorca (74-77 mm CL; Goñi *et al.* unpublished data) and Corsica (76-80 mm CL; Marin 1987). This suggests that in *P. elephas* the size at physiological maturity is a constant trait in separate Western Mediterranean locations where lobsters differ widely in density. Attainment of functional maturity may not be as constant. Marin (1987) estimated a lag of about 1-year between the attainment of physiological maturity (at 76-80 mm CL or 4 years) and the attainment of functional maturity (at 86 mm CL or 5 years) by female *P. elephas* off Corsica.

Several factors may be put forward to explain the larger size at functional maturity of *P. elephas* off Corsica. In spiny lobsters size at maturity appears to be age specific (Beyers & Goosen 1987) and where growth is fast, sexual maturity would be reached at a greater size. Campillo (1982) estimated the relative abundance of *P. elephas* off Corsica during 1977 from CPUE indices obtained in experimental fishing surveys with trammel nets. Mean CPUE was 3-11 lobsters per standard set (500 m net soaked 2 nights) depending on the location, compared to 41 lobsters per standard set in the Reserve during the June survey (Goñi *et al.*, unpublished data). Lower population density off Corsica could translate into lower competition for food (Kanciruk 1980, Beyers & Goosen 1987) or shelter (Polovina 1989) allowing faster growth rates, which would give rise to a larger size at maturity (Chittleborough 1976, Pollock 1993, but see Chubb 2000). Larger size at maturity could also be environmentally driven (e.g. lower water temperatures off Corsica, MEDATLAS 1997) (Kanciruk 1980, Annala 1991, Waddy & Aiken 1991). But against these explanations is the view that any environmental or density-dependent factor should have equally affected both the size of physiological maturity and functional maturity. However, it is well known that estimates of size-at-maturity differ depending on the maturity criteria used as well as the sampling period, number and size range of the specimens (Chubb 2000). Marin's samples of berried females were collected during September-October over a seven-year period and although this should have ensured that most mature females would be berried, only 42% of females in his sample carried eggs (compared to 84% in the Reserve during the September survey). This suggests that the samples for Marin's estimate of functional maturity may not have been obtained at the time of peak production possibly because of a slight delay of the breeding cycle in the colder waters of the more northern population of Corsica (Annala 1991, Waddy & Aiken 1991, Chubb 2000).

As in other lobster species (Aiken & Waddy 1980, Gomez *et al.* 1994, but see MacDiarmid 1989 b), males in the Reserve reach physiological maturity at a larger size (82.7 mm CL) but same age (4 years, Marin 1987) as females. This is to be expected due to their faster growth rates (Marin 1987). In the population off Corsica the estimated size of male physiological maturity (78 mm CL) was similar to that of females' (Marin 1987). This discrepancy in size at maturity of males from the Columbretes and Corsica populations may be due to the greater availability of large males in lightly fished and unfished populations relative to exploited populations (Hunter *et al.* 1996, Goñi *et al.* in press; see below). Nevertheless, it should be noted that the method used here and in Marin's study to estimate male physiological maturity involves a certain degree of subjectivity in the choice of break points for fitting linear equations; thus, both estimates should be considered with caution.

The relationship between body size and number of eggs in *P. elephas* from the Columbretes Islands Marine Reserve was linear, as found in both Atlantic (Mercer 1973) and Mediterranean (Campillo 1982) exploited populations and in populations of other spiny lobsters (Aiken & Waddy 1980) (but see Chubb 2000). The influence of reproductive senescence (or reduced fecundity with age) to egg production of unfished populations is a legitimate concern given the potentially high relative contribution of large females to total population fecundity (Chubb 2000). In this study we demonstrate that in the Reserve *P. elephas*'s individual fecundity increases linearly with body size up to the females' maximum size, although maximum reproductive yield (eggs per body gram) was reached at intermediate sizes (as observed by Bertelsen & Matthews 2001 in *Panulirus argus*). Moreover, we demonstrate that egg diameter increases with female size. In *Jasus edwardsii* larger eggs hatch larger larvae that survive for longer under conditions of low food supply (MacDiarmid, unpublished data). Similar relationships may also apply to *P. elephas*.

Individual variability in fecundity was large with differences of up to 40% among females of similar body size. A high degree of individual variability in fecundity appears to be common in lobsters (Aiken & Waddy 1980, Annala & Bycroft 1987). The slopes of the size-fecundity lines of the Reserve and the Corsica populations were different (ANCOVA: CL x Area interaction: $F_{2(0.05),1,93}= 0.069$, p=0.01) and for most of the mature female size range, individual fecundity in the Corsica population was lower than in the Reserve (Figure 4.8). This could result from the greater availability of large males in unfished populations together with their potential greater contribution to reproduction relative to small males (Berry 1970, MacDiarmid & Butler 1999). Interestingly, size-specific fecundity in the protected population coincides with that estimated by Mercer (1973) for a lightly fished *P. elephas* population off Ireland (Figure 4.8). Conversely, these results do not support either the hypothesis of density dependence of spiny lobster fecundity (Chittleborough 1976) nor that of higher size-specific female fecundity following exploitation (DeMartini *et al.* 1993). However, factors such as increased variation in fecundity among larger females and small sample sizes (n= 24 for the whole size range in Campillo's sample) complicate attempts to compare size-specific fecundity among populations (Waddy & Aiken 1991, Somers 1991).

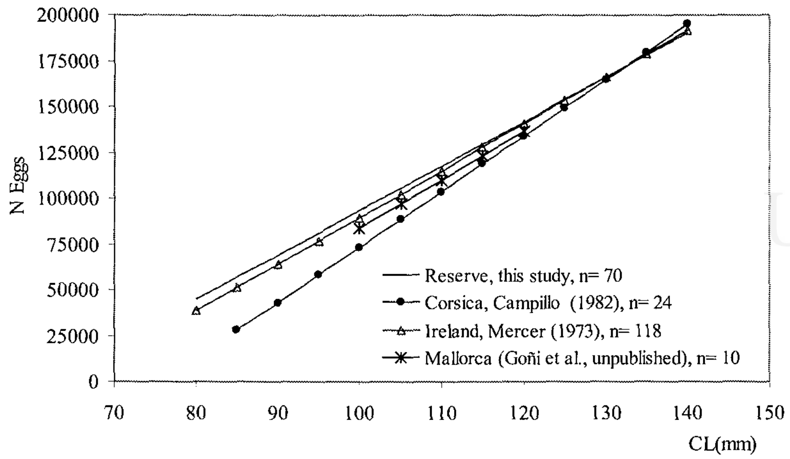

Figure 4.8: Comparison of size-fecundity relationships of P. elephas from this study with those available from other studies.

Assessing egg loss provides an indication of the survival from fertilised eggs through hatching. Egg loss appears to be directly proportional to the duration of the incubation period (Annala & Bycroft 1987). In this study, we estimated egg loss at 26% for females in the 85-100 mm CL size range. Using rates of egg loss from other decapods and accounting for the length of the incubation period Marin (1985) provided a similar (28%) estimate for *P. elephas* off Corsica. These values appear high but clutch attrition of up to 40% has been observed in *Homarus americanus* (incubation lasts 9-11 months) (Kuris 1991). In contrast to our results, Mercer (1973) estimated a mean egg loss of 10% over an 8-month incubation period for Atlantic *P. elephas* females, suggesting that egg loss could be positively correlated with water temperature, possibly through temperature effects on chorion (from which egg stalks are made) synthesis (Waddy & Aiken 1991) or with the degree of stress induced by the means of capture (Waddy & Aiken 1991, Kuris 1991), by hand in Mercer's study and trammel-netting in this and Marin's study.

Reproductive potential and comparison with fished populations

Understanding the impact of fishing upon egg production of a spiny lobster population is crucial to maintaining viable fisheries (Chubb 2000) and it is influenced by the relative size of female lobsters within the population (Lyons *et al.* 1981). However, assessing the relative contribution of different size classes to reproductive potential must be done on populations that are not heavily fished so as to avoid skewing bias in favour of small females (due to commercial cropping of larger individuals) (Kanciruk 1980). In the unfished population of the Columbretes Reserve, the size class of breeding females that contributed most to egg production was 105-110 mm CL (or 7-8 years, Marin 1987). This was also the size of maximum reproductive yield (eggs/body gram) and is well above of the minimum landing size (80 mm CL) and age (4 years, Marin 1987) set for Western Mediterranean fisheries. Newly mature females (75-80 mm CL), protected under the 80 mm CL legal size, only provide an estimated 1% of the total egg production and are 20 times less productive than females in the 105-110 mm CL size group. The important contribution of large females to population reproductive potential and the relatively poor contribution of legally protected females have been observed in other spiny lobster populations (*P. argus* and *Panulirus homarus*, Kanciruk 1980). It has been proposed that MLS limits should be established at a size which affords every individual the opportunity to reproduce at least once before reaching the exploitable size (Jamieson 1993). Simplistically, in the case of four-year-old *P. elephas*, which grow at about 8.5 mm CL per year (Marin 1987), an MLS set at 88.5 mm CL would allow them to reproduce once before reaching the harvestable size. An MLS of 97 mm CL would allow females to reproduce twice before exploitation and would protect 25% of the potential egg production.

Comparison of the indices of spawning potential of unfished and fished populations allows assessment of how *P. elephas* egg production may be influenced by fishing. Taking the population in the Reserve as a reference and assuming similar productivity in all areas, the spawning potential in the Reserve may have increased 6 to 20 times since fishing was banned ten years ago. This is a much greater rate of increase than the 6.6% per year estimated by Kelly *et al.* (2000) for *J. edwardsii* in New Zealand marine reserves. However, Kelly *et al.* observed marked differences in the recovery patterns of the three reserves studied. Our results measure up well to Annala's (1991) egg-per-recruit estimates in fished relative to unfished populations of *J. edwardsii* (1.2% to 36.8% depending on the area; mean= 20.1%).

Lyons *et al.* (1981) for *P. argus* and Kelly *et al.* (2000) for *J. edwardsii* observed dramatic reductions of spawning potential in exploited areas associated with severely reduced abundance of large females. In the fished western Mediterranean populations it appears that the spawning potential of *P. elephas* is influenced more by the abundance than by the size or the fecundity of mature females. Females from the Reserve are only slightly larger than those of nearby exploited populations (see Table 4.2) suggesting that the spawning potential of the protected population is still predominantly influenced by female abundance and has therefore not yet reached the status of "unexploited-stable" *sensu* Bertelsen & Matthews (2001). This is not unexpected as the maximum life span of *P. elephas* is in the order of 20 years (Marin 1987, Goñi *et al.* in preparation) and at the time of the study the Columbretes reserve had only been closed to fishing half that time.

One further aspect of the reproductive biology of spiny lobsters relevant to protected populations that has received limited attention is the importance of greater male size for the success of breeding pairs (MacDiarmid & Butler 1999). Recovery of numbers of very large male *P. argus* in the Dry Tortugas National Park since 1974 has been put forward as the reason for the improved mating success of large females (in terms of proportion berried) since the creation of the Park (Bertelsen & Cox 2001). Similarly, the difference in the average size of male and female *P. elephas* was larger in the Reserve (females: 100 mm CL; males: 116 mm CL) than in the fished populations (Mallorca - females: 95.8 mm CL, males: 100.8 mm CL, Goñi *et al.* unpublished; Corsica - females: 95.6 mm CL, males: 103.7 mm CL, Campillo 1982). Yet reduced male size does not appear to have affected mating success of large *P. elephas* off Corsica since in Campillo's sample (1982), as in our sample, most mature females, and in particular the largest females, carried eggs during the peak spawning period.

These results advance our understanding of the effects of fishing on the reproductive potential of spiny lobster populations and show that, in the absence of knowledge of population parameters of mortality and growth, the concept of relative reproductive potential provides a first guide for establishing legal size regulations in the widely depleted *Palinurus elephas* populations. The high reproductive potential of the unfished population measured in this study indicates that the larvae originating from the Reserve could contribute to sustaining fished populations. However, *P. elephas* larvae spend 4-5 months in offshore waters creating the potential for both long distance dispersal and high recruitment variability due to fluctuations in oceanographic regimes. Thus, while evaluating the reproductive potential of protected *P. elephas* populations has been a first step, understanding the fate of larvae originating from them is imperative for understanding the role of marine protected areas in managing lobster fisheries.

CHAPTER 5: SPILLOVER OF *P. ELEPHAS* FROM THE COLUMBRETES MARINE RESERVE

Submitted as:

R. Goñi, A. Quetglas, and O. Reñones. Spillover of lobster, *Palinurus elephas* (Fabricius, 1787), from a Western Mediterranean marine reserve. *Marine Ecology Progress Series*.

Abstract

Benefits to the local fishery of the Columbretes Islands Marine Reserve through spillover of lobsters (*Palinurus elephas*) were examined by combining CPUE information from monitoring surveys inside the reserve, from the commercial fishery adjacent to the reserve, and with recapture data of lobsters released inside the reserve. Data onboard fishing boats were collected according to a random sampling scheme to obtain a realistic representation of the spatial distribution of effort. Generalized additive models and generalized linear models were employed to describe the relationships of CPUE, catch per unit area, tags per unit effort and ratio of tagged to no-tagged lobsters in the catch as a function of distance to the reserve boundary. CPUE and tags per unit effort showed a significant non-linear decline with distance from the centre of the reserve, with a depression at the boundary followed by a plateau. This depression was associated with high levels of fishing effort in the boundary causing local depletion. The plateau suggests that spillover is sufficient to maintain stable catch rates up to 1000 m from the boundary. Commercial CPUE and effort data were combined to estimate catch per unit area that declined linearly with distance, indicating the existence of a negative gradient of density up to 4.5 km from the boundary. The ratio of tagged to non-tagged lobsters was independent of distance up to 1500 m beyond which no tags were recovered. Tagging data, although not conclusive, suggest that the density gradient is caused by spillover of lobsters from the reserve.

5.1. Introduction

Frequency-dependent models of animal distribution predict that animals should prefer to move towards areas where density is low relative to available resources if this is beneficial to their fitness (Rakitin & Kramer 1996). Hence, increases in density of exploited species within no-take marine reserves could result in the enhancement of yields in neighbouring fisheries either through emigration, seasonal or random movements (e.g. Dugan & Davis 1993, Roberts & Polunin 1993, Guénette *et al.* 1998). But while many studies corroborate that density of exploited populations is higher in reserves than in adjacent fished areas (e.g. reviews in Roberts & Polunin 1991, Dugan & Davis 1993, Rowley 1994, Sánchez-Lizaso *et al.* 2000, Côté *et al.* 2001, Jennings 2001, Halpern & Warner 2002), recent work highlights the meagre evidence available for protection effects outside marine protected areas (MPA) (Botsford *et al.* 2003, Russ 2002, Russ *et al.* 2004). Effects on fisheries have been difficult to demonstrate empirically, partly because most marine reserves are small and were not designed for fisheries purposes, but also due to the lack of fishery data before reserve creation and the absence of spatial replication (Palumbi 2001, Willis *et al.* 2003a). In addition, few studies have investigated spillover over long enough periods to see the effect develop fully (Russ *et al.* 2004). The dearth of conclusive empirical work and the pressing need to assess the value of reserves as fisheries management tools has resulted in the proliferation of modelling studies (see Gerber *et al.* 2003 and references therein).

To address effects of reserves on fisheries some studies have monitored density or catch per unit effort (CPUE) from the onset of protection in grounds adjacent to reserves; they have demonstrated increases after reserve creation (e.g. McClanahan & Mangi 2000, Murawski *et al.* 2004, Roberts *et al.* 2001, Galal *et al.* 2002, Russ *et al.* 2003) or decreases after protection ended (e.g. Alcalá & Russ 1990). Other studies have measured gradients of density or CPUE across or near reserve boundaries years after reserve creation (e.g.Yamasaki & Kuwahara 1989, McClanahan & Kaunda-Arara 1996, Russ & Alcalá 1996, Rakitin & Kramer 1996, Chapman & Kramer 1999, Johnson *et al.* 1999, Millar & Willis 1999, Tupper & Rudd 2002, Kaunda-Arara & Rose 2004, Ashworth & Ormond 2005). These studies have generally shown higher values closer to reserve centres for target species of low to moderate mobility. Similar results have been obtained in the few lobster studies available (Kelly *et al.* 2002, Davidson *et al.* 2002). The most convincing evidence of benefits to nearby fisheries from this type of studies is the build-up of reef fish biomass adjacent to a marine reserve of Philippines continuously for over two decades (Russ *et al.* 2004). Finally, mark-recapture studies have investigated movement of protected species across no-take area boundaries. Some report emigration from reserves to the adjacent fished areas (e.g. Attwood & Bennet 1994, Zeller & Russ 1998, Johnson *et al.* 1999, Martell *et al.* 2000, Cole *et al.* 2000) but most studies do not consider immigration and thus net transfer. The few that address bi-directional movements report contrasting results (e.g. Davis & Dodrill 1989, Rowe 2001, Zeller *et al.* 2003, Kelly & MacDiarmid 2003, Tremain *et al.* 2004) depending on the species, life stages, habitats and size of the MPAs considered.

Studies conducted in the CIMR 7-9 years after its creation showed that abundance of *P. elephas* within the reserve was 6-20 times greater than in comparable fished areas depending on the season (Goñi *et al.* 2001). The spawning potential per unit area in the reserve was also 5-20 times greater than in Western Mediterranean exploited areas depending on their level of exploitation (Goñi *et al.*

2003a). Although information on lobster abundance before reserve implementation is not available to demonstrate that lobster density has increased inside the reserve, local fishermen corroborate that catch rates obtained in experimental fishing surveys conducted inside the CIMR since 1997 are much higher than catch rates they obtained in the area prior to reserve creation. Since then, commercial lobster fishing in the region occurs around the reserve and in scattered grounds 10-30 km from it. In this study we ask whether spillover of post-settlement lobsters from the CIMR is contributing to maintaining or enhancing the adjacent fishery (<5 km from the boundary). We also propose an approach for evaluating net export based on tag-recapture data. We adopt the simple definition of spillover as 'net export of postsettlers' (Russ 2002), which assumes nothing about the causative processes and that could be driven by density-dependent effects or arise because of random movements or seasonal migrations from high to low density areas (Sánchez-Lizaso *et al.* 2000, Jennings 2001, Russ 2002).

For the study, we used catch and effort data of the commercial fishery adjacent to the CIMR, CPUE data from annual experimental fishing surveys conducted inside the CIMR and data of recaptures of lobsters tagged and released inside the CIMR. To address the issue of spillover we asked two questions: (1) is there a declining gradient of lobster density away from the reserve? and (2) if yes, is it due to movement of lobsters from the reserve to the fished areas?

We examined the spatial distribution of commercial CPUE, effort and catch per unit area (CPUA) around the reserve and, assuming homogeneity of habitats, we predicted that if there was a negative gradient of lobster density with distance from the reserve: (1) CPUE should be highest at the boundary and decline with distance from it according to some function that will be affected by, *inter alia*, the spatial distribution of fishing effort, (2) fishing effort should concentrate on the boundary of the reserve, and (3) as a result of the above, CPUA should be highest near the boundary.

Data of net animal movement across MPA boundaries are rare and difficult to obtain (Russ 2002). This study was no exception and to investigate movement from the reserve to the fished areas we used data from recaptures of lobsters tagged and released only inside the reserve. We reasoned that if both tagged and untagged lobsters were moving out of the reserve and supplying the adjacent fishery, we could make the following predictions: (1) the number of tag returns per unit effort (TPUE) in the fishery should decline with distance from the reserve and the pattern of decline should be similar to that of the CPUE, and (2) the proportion of tagged lobsters (PROP) in the commercial catch should be independent of distance from the reserve.

5.2. Materials and Methods

Study site

This study took place between July 1998 and August 2002 on the CIMR and surrounding fishing grounds. The reserve encompasses four small island groups and protects 4400 ha of mostly volcanic rock and coralligenous habitats that extend down to 80 m depth. Fishing grounds adjacent to the CIMR consist of isolated patches of rock and maërl over vast expanses of sand and mud at depths of 60-100 m. The CIMR was a traditional lobster fishing ground before it was closed to fishing. It appears that since then the number of boats participating in the lobster fishery has declined, while fishing effort per boat has increased steadily. Presently, two to six boats fish consistently during the lobster season in the grounds near (<5 km) and around (10-40 km) the CIMR (Figure 5.1). The CIMR legislation prohibits most types of fishing and all lobster fishing. Although occasional poaching by recreational anglers may occur, the fishing prohibition is well enforced.

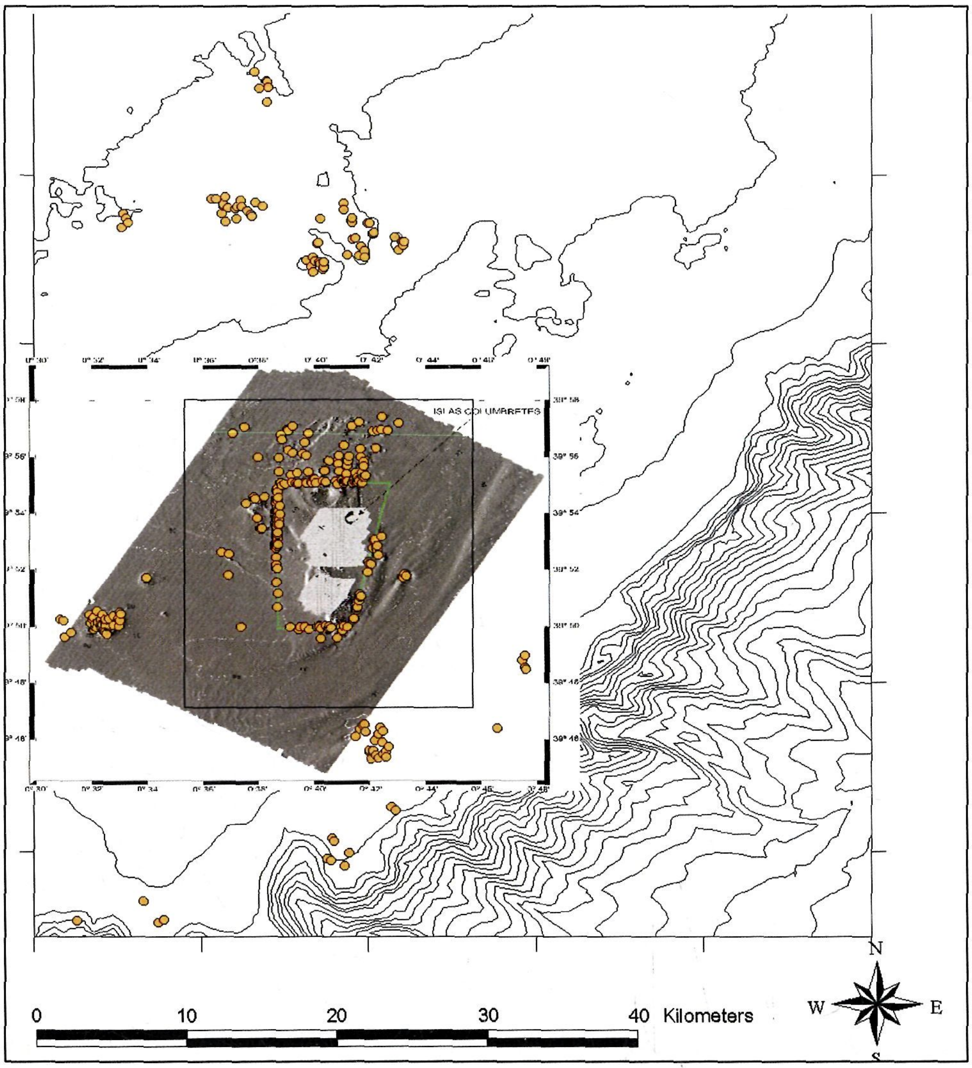

Figure 5.1: Location of commercial fishing sets sampled in the fishery adjacent to the CIMR (yellow dots inside thin black line square) and in separate fishing grounds (yellow dots outside square).

Data collection

Commercial fishery

Catch and effort of the commercial fishery was recorded monthly from 1999 to 2002 during the six-month (March-August) annual lobster fishing season, and during July 1998. Whenever possible sampling took place during one week per month on board one of the three boats that consistently fished lobster in the region. To ensure that the data of spatial distribution of fishing effort were representative of the true distribution of fishing effort in the fishery, the observer sampled all the fishing sets that were carried out in that week without directing where fishing sets should be allocated.

Table 5.1. Fishing sets sampled by year, month and reserve boundary in the commercial lobster fishery adjacent to the Columbretes Islands Marine Reserve.

Year	Month	Boundary				Total
		North	East	South	West	
1998	7	4		2	7	13
1999	3	4		3	3	10
	4	9		1	3	13
	5	3	1			4
	6	1	1	1	4	7
	7	2	1	1	1	5
2000	3	7	2			9
	4	2		2		4
	5	3	1		1	5
	6				3	3
	7	4			8	12
	8	2			1	3
2001	3	3			3	6
	4	5	1		3	9
	5	6	1		2	9
	6	7		2	2	11
	8	4	5	1	17	27
2002	5	3	5	2	4	14
	6			4	7	11
	7	1	6	5	3	15
	8	15	8		1	24
	Total	85	32	24	73	214

In this fishery lobsters are caught with trammel nets (gear description in Goñi *et al.* 2003b) set over rocky and coralligenous substrates and left for several days, depending on weather conditions, before hauling (mean 4-5 days). The location, depth, duration and lobster catch of every set were noted. A total of 346 valid fishing sets were recorded over the study period. Of these, in this study we used 214 fishing sets that occurred within 5 km of the reserve boundary (Table 5.1; Figure 5.1).

Four kilometres is the maximum mean distance travelled by lobsters released inside the CIMR (Goñi *et al.*, unpublished data). Furthermore, the absence of fishing activity at distances between 5 and 10 km from the reserve indicates a marked discontinuity of lobster habitats in that area (Figure 5.1). CPUE was calculated by the number of lobsters caught (retained plus discarded) per 500 m of trammel net after correcting for soak time.

Experimental fishing

Experimental fishing surveys in the CIMR are conducted annually in June as part of a monitoring programme started in 1998. Data available from this study were for the period 1998-2002, totalling 112 fishing sets. Experimental fishing in the CIMR is done with trammel nets following a stratified (two depth strata), random sampling design over rock and coralligenous habitats. A detailed description of the survey methods is provided in Goñi *et al.* (2003b). Experimental fishing surveys are carried out with one of the commercial boats and the same gear fishermen use in commercial operations outside the reserve. Soak time in surveys was one day and experimental CPUE was estimated by the number of lobsters caught per 500 m of net.

Tag-recapture

Lobsters caught during the annual fishing surveys have been routinely tagged using Hallprint t-bar tags and released in the CIMR. Upon capture, lobsters were tagged dorso-laterally between the first and second abdominal segments and released as close as possible to the site of capture. Of 10683 lobsters tagged between 1997-2002, 811 were recaptured in the fishing sets studied, 726 in the reserve and 85 in the adjacent fishing grounds.

Data analysis

The study area was divided in boxes of 1x1 km. The distance to the reserve was measured by the distance from the midpoint of the box for of the portion of the box outside the Reserve in those that cross the boundary to the nearest boundary. The position of each fishing operation was determined by the midpoint of the net, and the distance to the reserve was the distance from that point to the nearest boundary.

Effort per unit area was calculated by the number of fishing sets occurring in each box (nº sets per squared kilometre), all data within the box combined. The total standardized catch per box was calculated by the product of the box mean CPUE by the number of sets in the box.

For each set, the number of tagged lobsters caught per unit effort (TPUE) was estimated in the same manner as the respective CPUE's. The proportion of tagged lobsters in the catch of each fishing set (PROP) was also calculated.

Generalized additive models (GAM), or generalized linear models (GLM) when effects were linear, were employed to explore and describe the relationships of CPUE, CATCH, TPUE and PROP with distance to the reserve. GLM and GAM are generalizations of multiple linear regressions. GAM's allow relation of changes in these variables without restricting the functional form of the relationship. In the models, depth was introduced as a covariate and, where relevant, reserve boundary was modelled as a four-level factor (North, East, South, West). CPUE, TPUE and PROP from experimental and commercial fishing were combined to study gradients across the reserve boundaries. In these analyses, experimental data from depths <60 m were excluded because the commercial fishery occurs at depths greater than 60m. CATCH data were modelled for the commercial activity only.

To fit GAM's and GLM's we used routines contained in the S-Plus (MathSoft Inc.) programming environment, based on Hastie & Tibshirani (1990) and functions developed by Venables and Ripley (2000). Distance to the reserve was first introduced as a continuous smooth variable modelled non-parametrically using a loess smoother described in Hastie & Tibshirani (1990). The probability distribution of CATCH, CPUE and TPUA were determined by regressing the logarithm of the mean (by 500 m distance intervals) against the logarithm of the variance (Crawley 2003). Explanatory variables were assessed using F-tests (or χ^2 test in the case of PROP) to determine whether they explained a significant portion of the corresponding model deviance (Hastie & Tibshirani 1990). The non-linearity and the appropriate smoothing parameters of the smooth variable were assessed by the F and χ^2 tests and visual inspection of the fits to the observations.

Examination of the benthos bycatch of each fishing operation indicated no measurable differences in bottom habitat, suggesting that all fishing operations took place over similar substrates. Thus, for the analyses we assumed homogeneity of habitat quality in all the areas where fishing had taken place. Year and seasonal (month) effects on the modelled variables could not be explored due to the small sample size of the various year-month combinations.

5.3. Results

CPUE

Experimental CPUE inside the reserve ranged from 4 to 154 lobsters/500m/day, while commercial CPUE adjacent to the reserve ranged from 0 to 10 lobster/500m/day (Figure 5.2). The frequency distribution of CPUE was skewed and the variance proportional to the square of the mean (log(var) = 2.0851 x log(mean) - 0.3007, $R^2 = 0.84$, n=8), therefore the gamma variance and logarithmic-link functions were used to relate the expected CPUE to the predictors. Analysis of deviance of experimental and commercial CPUE as a function of distance to the reserve using GAM's (Table 5.2) indicates a significant non-linear relationship between CPUE and distance from the reserve's centre (probability of F=0). There is also a significant negative linear relationship between CPUE and depth (probability of F = 0.01). The fraction of the total deviance explained by the model is 85% (pseudo-coefficient of determination $R^2 = 0.85$; Swartzman *et al.* 1992). Fitted values for GAM's including 95% confidence bands (Figure 5.3) show a steep downward gradient of CPUE from inside to outside.

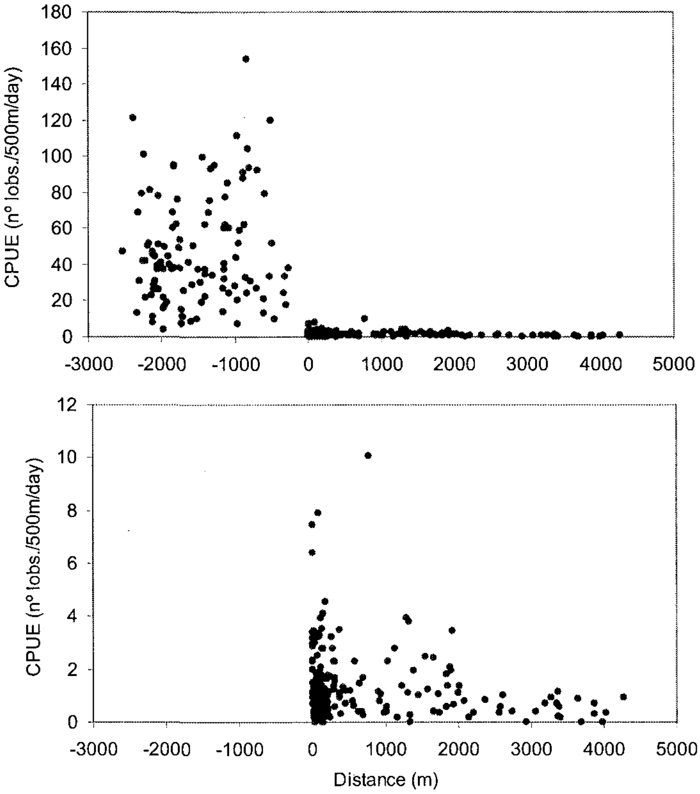

Figure 5.2: Plots of CPUE (number of lobsters caught per 500 m of net and day) against distance from fishing set to CIMR boundary. Second graph shows commercial fishery data on an expanded scale.

Table 5.2: Analysis of deviance table for GAM fitted to experimental and commercial CPUE data. Model was fitted incorporating logarithmic link and gamma variance functions. Distance (-3000 to +5000m) and depth (>60m) are continuous variables. Term indicates the variables in the model. "Res.dev" and "Res.df" are the deviance and degrees of freedom of the model. "Test" gives the variable excluded from the full model, with "df" and "Deviance" being the difference excluding the tested variable. The probability column corresponds to the significance of the deviance portion explained by each model term. Interaction (not significant) is excluded from the model.

Term	Res. dev	Res. df	Test	d.f.	Dev	F	P (F)
Null	942.39	256					
lo(distance)+depth	165.59	247					
lo(distance)			-depth	1	4.16	5.612	0.018
depth			-lo(distance)	6	407.80	83.556	0

Results of GAM's of commercial CPUE outside the reserve as a function of distance from its limit (Table 5.3) indicate a significant non-linear negative relationship (probability of F = 0.01). CPUE also decreased linearly with depth (probability of F = 0.02). The side of the reserve did not affect mean CPUE (probability of F = 0.65) and the interaction distance:side was not significant (excluded from the model). The model explains a small fraction of the deviance in the data (pseudo $R^2 = 0.20$). The fitted values for the GAM show that the non-linearity of CPUE with distance is due to a local CPUE minimum, followed by a plateau within 1500 m from the reserve boundary (Figure 5.4). After the plateau, CPUE declines linearly with distance.

Table 5.3: Analysis of deviance table for GAM fitted to CPUE data from the commercial fishery data. Model was fitted incorporating logarithmic and gamma variance functions. Distance (0-5000m) and depth are continuous variables and side is a fixed, four level factor (North, East, South, West). Interaction distance:side (not significant) is excluded from the model. Other information as in Table 5.2.

Term	Res. dev	Res.df	Test	d.f.	Dev	F	P (F)
Null	131.70	197					
lo(distance)+depth+side	105.47	188					
lo(distance)+depth	106.99	191	-side	3	1.52	0.548	0.650
lo(distance)+side	110.24	189	-depth	1	4.77	5.157	0.024
depth+side	119.27	193	-lo(distance)	5	13.79	2.834	0.015

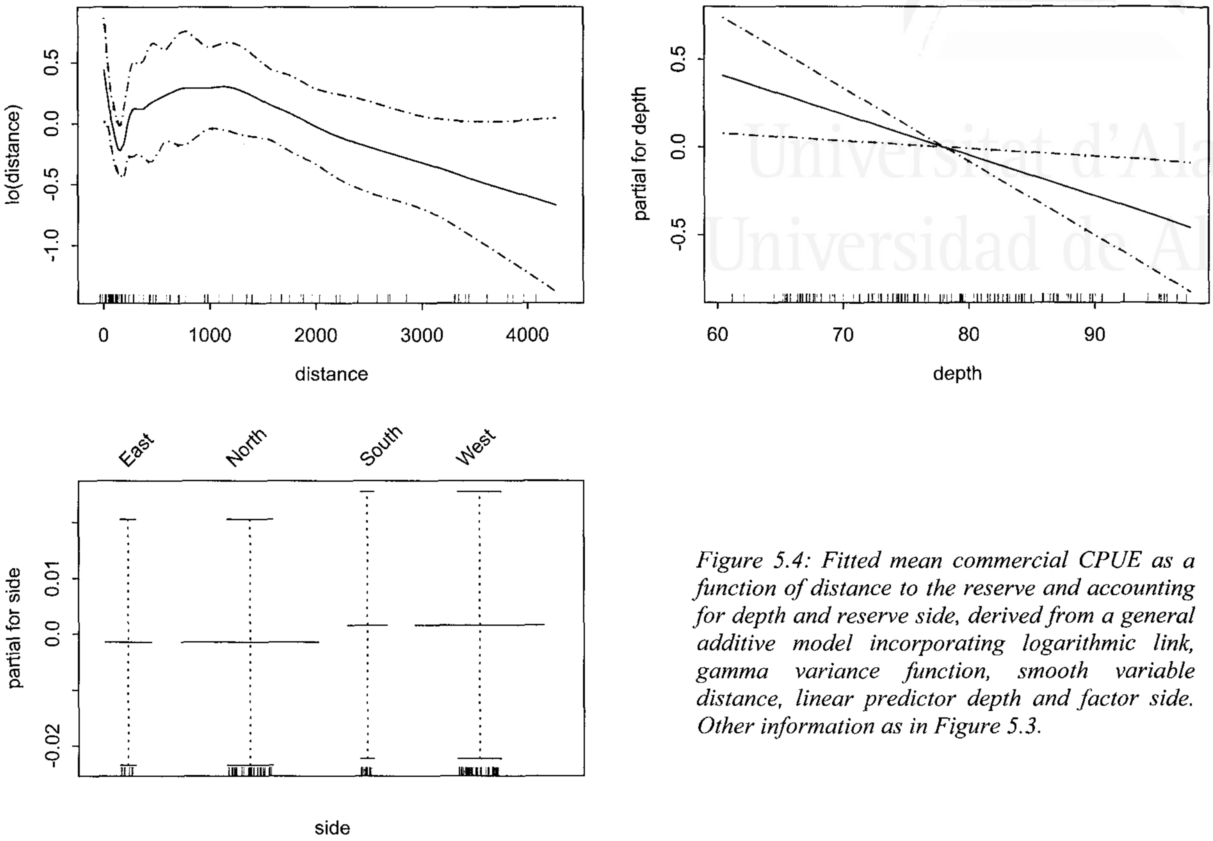

Figure 5.4: Fitted mean commercial CPUE as a function of distance to the reserve and accounting for depth and reserve side, derived from a general additive model incorporating logarithmic link, gamma variance function, smooth variable distance, linear predictor depth and factor side. Other information as in Figure 5.3.

EFFORT

The plot of number of sets per box as a function of distance to the reserve (Figure 5.5) shows that maximum effort per unit area was found in boxes adjacent to the boundary (< 1 km), although there were low effort boxes at all distances. Lobster fishing extended farther from the reserve in the North and West sides where lobster habitats are more extensive. The most intensively fished boxes occurred in the North and West sides (14-16 sets each) and in the East (13 sets).

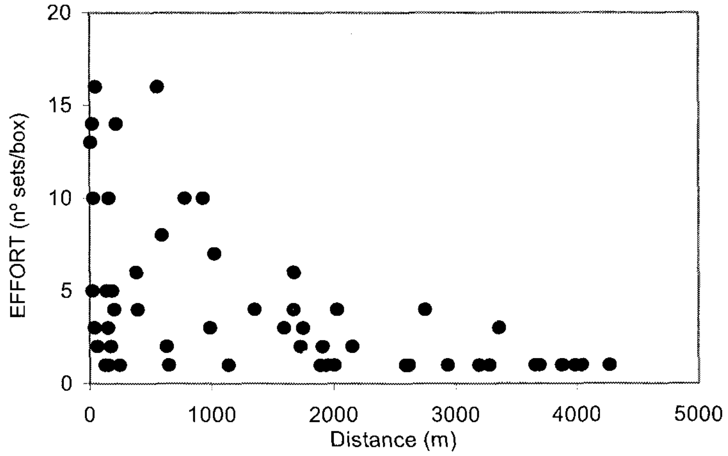

Figure 5.5: Plot of EFFORT (number of commercial fishing sets per box) against distance from box to CIMR boundary.

CATCH

Plots of catch per box (Figure 5.6) show that the most productive boxes were located within 1 km of the reserve boundary, with productivity declining rapidly with distance. The most productive boxes occurred in the East (265 lobster/km^2) and North (180 lobster/km^2) boundaries, although there were also fished boxes adjacent to the reserve that produced small catches.

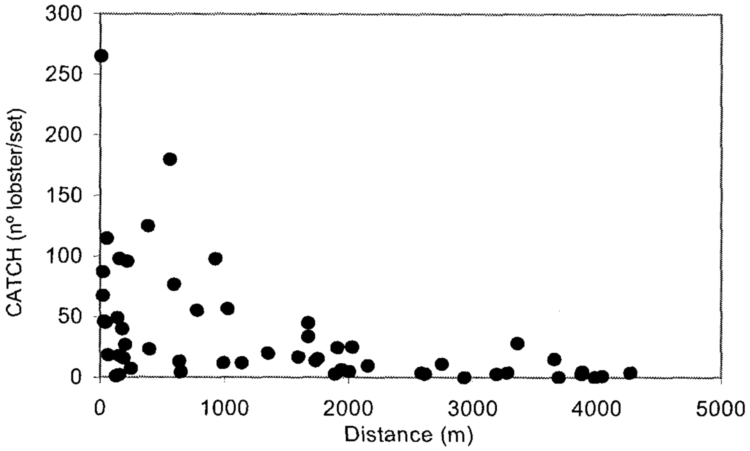

Figure 5.6: Plot of CATCH (commercial catch in number per box) against distance from box to CIMR boundary.

The frequency distribution of catch per box was skewed and the variance proportional to the square of the mean (log(var) = 1.938 x log(mean) - 0.0343; R^2 = 0.97, n=8). Therefore, the gamma variance and logarithmic-link functions were used to relate the expected CATCH to the predictors. Results of the GAM (not shown) indicate a linear effect of distance on catch per box. Accordingly, a GLM was fitted to catch per unit area with distance to the reserve as the predictor, and depth and reserve boundary as covariates. Analysis of deviance (Table 5.4) indicates a significant effect of distance (probability of F<0.01), and non-significant effect of depth (probability of F = 0.50) or boundary (probability of F = 0.98). The model explained about half the deviance in the data (pseudo R^2 = 0.47). The model fits (Figure 5.7) indicate that catch per box declines exponentially (linear in a log scale) as distance from the reserve increases, and that this pattern is similar on the four sides of the reserve. Catch per box was not affected by depth.

Table 5.4: Analysis of deviance table for GLM fitted to catch per box data. Model was fitted incorporating logarithmic link and gamma variance functions. Distance (0-5000m) and depth are continuous variables and side is a fixed, four level factor (North, East, South, West). Interaction distance:side (not significant) is excluded from the model. Other information as in Table 5.2.

Term	Res. dev	Res.df	Test	d.f.	Dev.	F	P (F)
Null	94.93	53					
distance+depth+side	50.93	48					
depth+side	68.90	49	-distance	1	17.97	16.792	0.0001
distance+side	50.93	49	-depth	1	0.0002	0.0002	0.988
distance+depth	53.48	51	-side	3	2.554	0.795	0.502

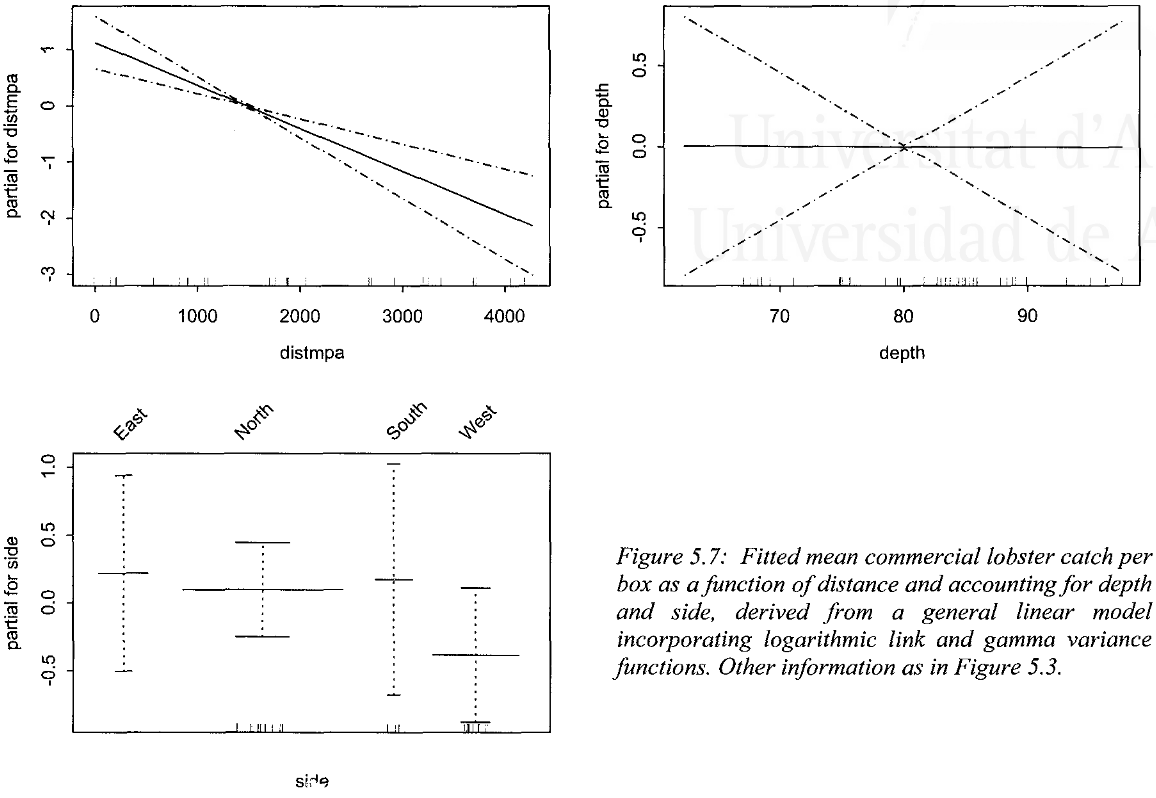

Figure 5.7: Fitted mean commercial lobster catch per box as a function of distance and accounting for depth and side, derived from a general linear model incorporating logarithmic link and gamma variance functions. Other information as in Figure 5.3.

TPUE

TPUE in experimental fishing sets in the reserve ranged from 1 to 31 tags/set/day (TPUE = 0 in 22 sets out of 113) and in the commercial fishery from 0.05 to 0.55 tags/set/day (TPUE = 0 in 164 sets out of 214) (Figure 5.8). No tags were recovered beyond 1500 meters from the reserve boundary. Therefore, we modelled TPUE up to 2000 m from the boundary. To eliminate zeroes TPUE's were transformed (TPUE+0.01).

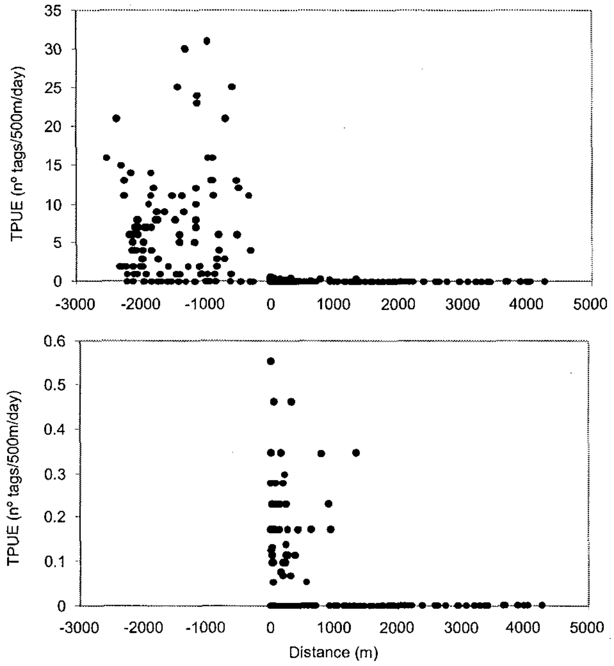

Figure 5.8: Plot of TPUE (number of tags in experimental and commercial fishing sets per 500 m of net and day) against distance from set to the reserve boundary. Second graph shows commercial fishery data on an expanded scale.

The frequency distribution of TPUE was skewed and the variance approximately proportional to the square of the mean (log(var) = 1.610 x log(mean) + 0.1364, $R^2 = 0.8557$ n=8), therefore the gamma variance and logarithmic-link functions were used to relate the expected TPUE to the predictors. Analysis of deviance of TPUE as a function of distance to the reserve and depth using GAM (Table 5.5) indicates a significant non-linear relationship between TPUE and distance from the reserve's centre (probability of F=0). There was no significant relationship between TPUE and depth (probability of F = 0.57). Pseudo R^2 was 0.70. No significant interaction between the variables occurred. Fitted values for GAM's including 95% confidence bands (Figure 5.9) show an abrupt decline in TPUE across the reserve boundary.

Table 5.5: Analysis of deviance table for GAM fitted to experimental and commercial TPUE data. Model was fitted incorporating logarithmic and gamma variance functions. Distance (-3000 to +5000m) and depth (>60m) are continuous variables. Interaction (not significant) is excluded from the model. Other information as in Table 5.2.

Term	Res. dev	Res. df	Test	d.f.	Dev	F	P (F)
ll	1615.37	240					
(distance)+depth	488.71	233					
o(distance)			-depth	1	0.76	0.319	0.572
depth			-lo(distance)	6	358.51	24.497	0

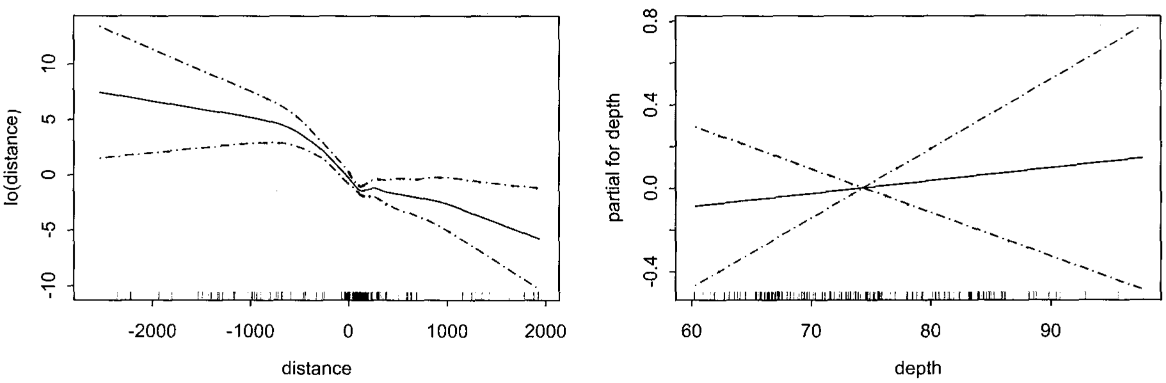

Figure 5.9: Fitted mean TPUE in commercial and experimental sets as a function of distance to the reserve boundary and accounting for depth, derived from a general additive model incorporating logarithmic link, gamma variance function, smooth variable distance and linear predictor depth. Other information as in Figure 5.3.

Analysis of deviance of TPUE outside the reserve boundaries as a function of distance to its limits, depth and reserve side (Table 5.6) indicates a significant non-linear relationship between CPUE and distance (probability of F = 0.01). Neither depth (probability of F = 0.74) nor reserve side (probability of F = 0.12) significantly affected TPUE. Pseudo R^2 was 0.12. The fitted values for the GAM show that the non-linearity of TPUE with distance is due to a local TPUE minimum followed by a hump within 1000 m from the reserve boundary (Figure 5.10). After the hump, TPUE declines linearly with distance.

Table 5.6: Analysis of deviance table for GAM fitted to commercial TPUE data. Model was fitted incorporating logarithmic and gamma variance functions. Distance (0-2000m) and depth (>60m) are continuous variables and side is a fixed, four level factor (North, East, South, West). Interaction distance:side (not significant) is excluded from the model. Other information as in Table 5.2.

Term	Res. dev	Res. df	Test	d.f.	Dev	F	P (F)
Null	366.01	171					
Lo(distance)+depth+side	300.90	162					
Lo(distance)+depth	318.34	165	-side	3	17.44	1.928	0.127
Lo(distance)+side	301.23	163	-depth	1	0.33	0.109	0.741
Depth+side	343.28	167	-lo(distance)	5	42.38	2.194	0.016

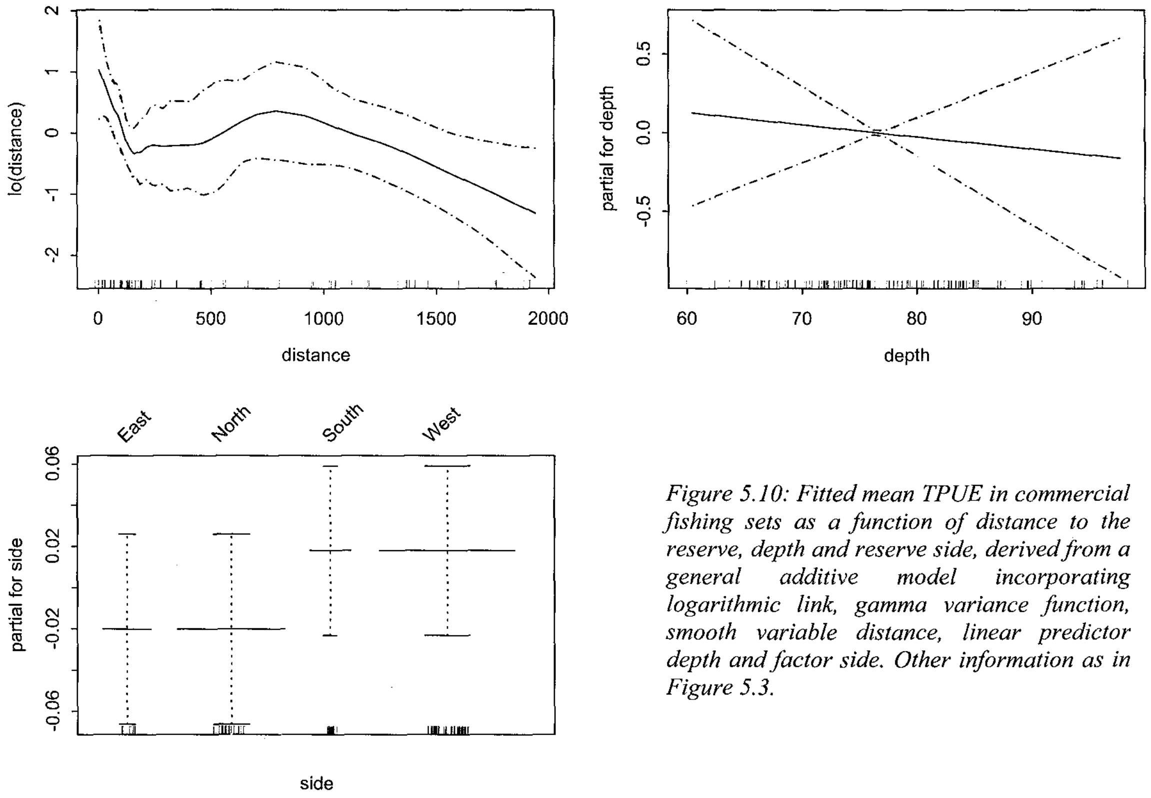

Figure 5.10: Fitted mean TPUE in commercial fishing sets as a function of distance to the reserve, depth and reserve side, derived from a general additive model incorporating logarithmic link, gamma variance function, smooth variable distance, linear predictor depth and factor side. Other information as in Figure 5.3.

Proportion tagged

A plot of the proportion of tagged lobsters in relation to distance from the reserve is shown in Figure 4.11. Because the probability of a tag recovery declines rapidly with the size of the catch and the exploratory analysis was driven by the large number of zeroes, only data from sets with at least one tag recovery were considered in further analysis of PROP. Excluding zeroes, the proportion of tags in the catch per set ranged from 0.02 to 0. 46 (mean = 0.17 ± 0.11 SD) in the reserve and from 0.02 to 0.50 (mean = 0.15 ± 0.16 SD) in the adjacent fished grounds.

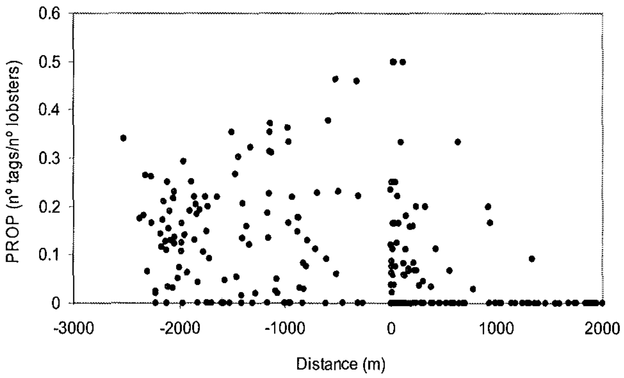

Figure 5.11: Plot of PROP (proportion of tagged lobsters in commercial and experimental catch) against distance from fishing set to reserve boundary.

To model the relationship between the proportion tagged and the predictor, the binomial variance function and the logit-link function were used (Crawley 2003). Analyses of deviance of the proportion tagged as a function of distance to the reserve and accounting for depth using GAM (not shown) and GLM indicate the absence of a significant relationship between PROP and distance to the reserve's boundary (probability F = 0.92) or depth (probability of F = 0.58) (Table 5.7 and Figure 5.12), and the model explained very little of the variance of PROP (pseudo $R^2 = 0.05$).

Table 5.7. Analysis of deviance table for GLM fitted to data on proportion of tagged lobsters in catch of experimental and commercial fishing sets. Model was fitted incorporating logit link and binomial variance functions. Distance (-3000 to + 2000m) and depth (>60m) are continuous variables. Interaction (not significant) is excluded from the model. Other information as in Table 5.2

Term	Res. dev	Res. df	Test	d.f.	Dev	P (χ^2)
Null	9.65	94				
distance+depth	9.24	91				
distance			-depth	1	0.30	0.582
depth			-distance	1	0.009	0.923

Analysis of deviance of PROP outside the reserve yielded the same result (Table 5.8 and Figure 5.13). Pseudo R^2 was 0.12.

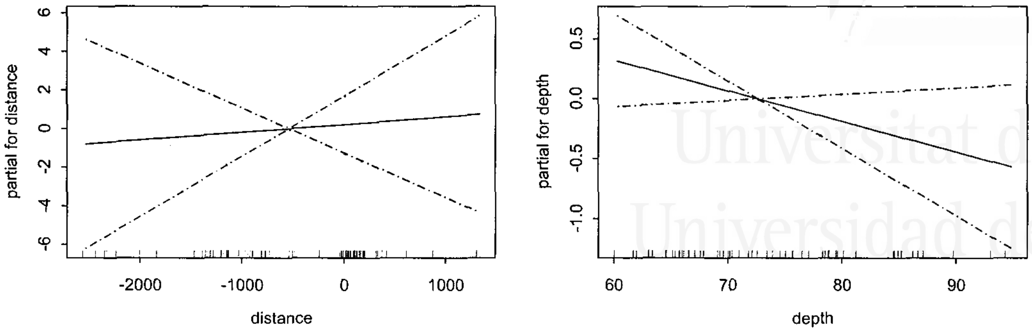

Figure 5.12: Fitted mean tag proportion in the catch of experimental and commercial fishing sets as a function of distance to the reserve boundary and depth, derived from a general linear model incorporating logit link and binomial variance functions. Other information as in Figure 5.3

Table 5.8. Analysis of deviance table for GLM fitted to data on proportion of tagged lobsters in the catch of commercial fishing sets. Sets with no recoveries are excluded. Models were fitted incorporating logit link and binomial variance functions. Distance (0 to +2000m) and depth are continuous variables. Interaction distance: side (not significant) is excluded from the model. Other information as in Table 5.2.

Term	Res. dev	Res. df	Test	d.f.	Dev	P (χ^2)
Null	4.56	44				
distance+depth +side	4.04	39				
distance+depth	4.31	42	-side	3	0.28	0.964
distance+side	4.17	40	-depth	1	0.14	0.710
depth+side	4.07	40	-distance	1	0.03	0.846

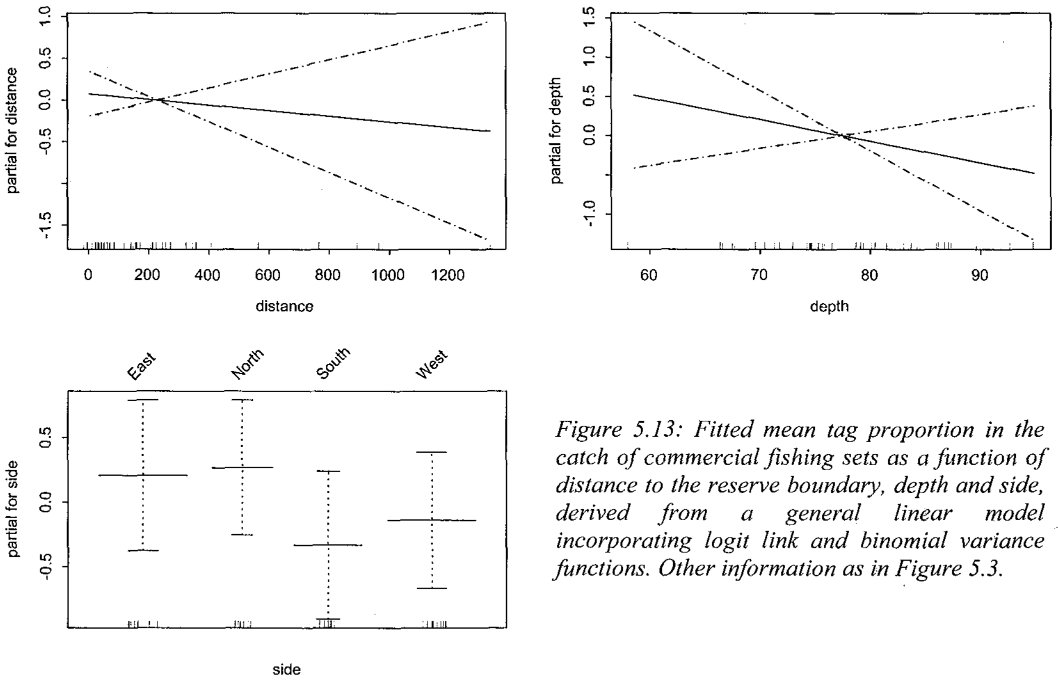

Figure 5.13: Fitted mean tag proportion in the catch of commercial fishing sets as a function of distance to the reserve boundary, depth and side, derived from a general linear model incorporating logit link and binomial variance functions. Other information as in Figure 5.3.

5.4. Discussion

Net emigration of animals across reserve boundaries should create a gradient of density whose spatial pattern will depend on the movement behaviour as well as on the catchability and exploitation rates of the species in the adjacent fishery (Rakitin & Kramer 1996, Russ *et al.* 2003). In this study we use a combination of tag-recapture methods, fishing surveys and commercial fishery data to demonstrate the existence of a negative gradient of lobster density away from the Columbretes Islands Marine Reserve (NW Mediterranean) up to a distance of 4.5 km. Tagging data, although not conclusive, provide evidence that the density gradient is caused by spillover of lobsters from the reserve. Our approach is novel in that it combines standardized survey and commercial CPUE data to study gradients across reserve boundaries, explicitly incorporates commercial fishing effort to derive density gradients outside reserve boundaries and uses tag-recapture information to examine the origin of the lobsters caught in the adjacent fishery. The use of generalized additive models to explore and describe gradients is also novel in this context.

Lobster CPUE in the CIMR declines abruptly at the reserve boundary in accordance with the high catchability (Goñi *et al.* 2003b) and exploitation rates in the adjacent lobster fishery (Goñi *et al.* 2000), as well as with the limited movement of the species (see below). The pattern of decline of the catch rates of tagged lobsters across the reserve boundary is similar to that of the CPUE; this is expected if the tagged population in the reserve is well mixed and behaves as the non-tagged population. Both sets of data show a similar pattern of decline with distance from the centre of the reserve, with a depression at the boundary followed by a plateau and a linear decline as distance increases. The CPUE depression, also noted by McClanahan & Mangi (2000) and Willis *et al.* (2003b), is associated with high levels of fishing effort near the reserve ('edge fishing' or 'fishing the line') causing local depletion (see below). McClanahan & Kaunda-Arara (1996) suggest that intense edge fishing was enough to collect all the fish export from a marine reserve in Kenya. In our case, the plateau following the depression suggests that export from the reserve is sufficient to maintain stable catch rates up to 1000 m from the boundary. As distance increases, the limited mobility of *P. elephas* and the high fishing pressure combine to reduce gradually the number of available lobsters.

Despite lower catch rates near the boundary, fishermen prefer the edge of the reserve to set their nets. One characteristic of the fishing effort exerted on the boundaries, which contributes to the observed local depression in catch rates, is the strategy of fishers to occupy those desirable fishing spots through the season regardless of catch rates. Effort concentration along the boundaries of marine reserves has been noted by many authors studying fisheries near marine protected areas (e.g. references above; Yamasaki & Kuwahara 1989, Johnson *et al.* 1999, Murawski *et al.* 2004, Kelly *et al.* 2002, Ashworth & Ormond 2005). In fishing grounds not associated with reserves, fishermen tend to relocate their nets when catch rates drop.

Maury & Gascuel (2001) examined the local overfishing phenomenon as a function of the detection and fishing efficiency of the vessels involved and their degree of cooperation (or spying). The case of the lobster trammel-net fishery around the CIMR fits best their category 1 where the vessels, although with low detection capacity, are endowed with high fishing capacity inducing high local rates of exploitation. Under such circumstances, they deplete the area quite rapidly and their yields fall markedly when effort increases. In the extreme, if vessels always fished in the same place and exerted very high local fishing mortality, they would catch (at each time step) all the lobster diffusing from the unfished zone (high local rates of exploitation compared with diffusive replacement).

When commercial CPUE and effort data were combined to estimate the standardized lobster catch per unit area as a function of distance from the reserve, we obtained a linear decline. This negative gradient of lobster catch away from the reserve lends support to the idea that the local depletion in CPUE observed near the reserve is caused by the spillover of lobster in that area being harvested at a greater rate than further away. This result emphasizes the importance of knowing the distribution of fishing effort to assess the fishery effects of reserves and shows that such assessments should consider cumulative spatial effects (Walters 2000).

The ratio of tagged to non-tagged lobsters in the catch is independent of distance from the fishing set to the boundary up to a distance of 1500 m, beyond which no tagged lobster were recaptured. This result, although not conclusive given the large number of zeroes in the data, suggests that the source population and that caught in the adjacent fishery are the same. Preliminary results of the tag-recapture study and of previous studies indicate that adult and subadult *P. elephas* undertake limited movements (Hepper 1977, Marin 1987) on average not exceeding 2-3 km and 3-4 km for small and large adults respectively (Goñi *et al.* 2003c). However, in our tag-release programme a small number of tags have been recaptured at greater distances (up to 20 km) from the CIMR. It is, therefore, somewhat surprising that in the fishing sets studied here no tagged lobsters were caught beyond 1500 m. Note that, given the large size of the CIMR, a lobster tagged inside the reserve and recaptured 1500 m away from it may have moved several kilometres depending on the precise location of release. It is also possible that a few lobsters moving out of the CIMR during the fishery closed season (September to February) were able to reach greater distances and be harvested in distant fishing grounds the next season. This would be consistent with hypothesized winter-spring inshore and fall offshore migrations of segments of the protected population (Goñi *et al.* 2001). In this case, our sample of commercial fishing sets may be too small to fully represent the spatial distribution of tag recaptures. Hence, this result should be interpreted with caution.

Kelly *et al.* (2002) considered evidence of spillover of the lobster *Jasus edwardsii* that CPUE around the Leigh marine reserve in New Zealand was similar to that in unprotected areas despite the loss of access to inshore reefs. The high variability of catches adjacent to the reserve and the movement patterns of the species from tag recapture studies supported their conclusion (Kelly 2001, Kelly & MacDiarmid 2003). Although seasonal variability could not be studied here, variability of catch rates of *P. elephas* was also highest near the CIMR (as sample size was), possibly reflecting fluctuations associated with seasonal movements. Kelly & MacDiarmid (2003) observed that despite great site fidelity of *J. edwardsii*, 20% of the lobsters registered movements in and out of the Leigh marine reserve and attributed these movements to homing behaviour. The study of a more mobile decapod, the crab *Chionoecetes opilio,* reports declining gradients of CPUE extending up to 13 km from a no-take area off Japan (Yamasaki & Kuwahara 1989).

So far, in our ongoing tag-recapture study about 50% of the recaptures of lobsters tagged in the reserve have been caught outside the CIMR (Goñi *et al.* unpublished data). Tag-recapture studies in reserves have been criticized because they do not provide information on net emigration rates that are required to truly assess spillover (Russ 2002). But conditions needed to assess net transfer - tagging effort proportional to abundance inside and outside and recapture effort known inside and outside (Reñones & Goñi 2000) - are very difficult to meet (Zeller *et al.* 2003). Tag and release of lobsters fished outside the CIMR was attempted in 1997 with little success (very few lobsters were available for tagging in fished areas). Here we have eluded this problem by exploring the application of tag catch rates and of ratios of tagged to non-tagged lobsters in the catch to trace the origin of the lobsters caught in the fishery.

Species more likely to show strong responses to protection are those that are subject to high levels of fishing mortality and have limited movements in relation to the size of the protected area (Kramer & Chapman 1999, Jennings 2001, Kelly & MacDiarmid 2003). High exploitation rates and limited mobility of adult *P. elephas* suggests that the size of the CIMR (9x4.5 km) is adequate to build-up a reproductive population (Goñi *et al.* 2001, Goñi *et al.* 2003a) while ensuring a steady supply of lobsters to the adjacent fishery. However, much remains to be understood about the migration and movement patterns of *P. elephas* in the region and with the available knowledge, it is not possible to determine the relative contribution of seasonal migrations and of density-dependent movements to spillover. In spite of these uncertainties, we offer a tentative lesson from this study. In terms of the size of the protected area and level of effective protection (no lobster fishing allowed), the CIMR surpasses most marine reserves in the world (most with less than a few km^2, Bohnsack 1998) and offers an extraordinary case study of the effects of protection on populations and communities. However, when considering exclusively the objective of lobster export to the adjoining fishery, the CIMR may be too large for the extent of movement of the species in the area. In fact, it might be that for adult phases of most spiny lobster species, with average movements of a few kilometres (e.g. Davis 1977, Booth 1997, Rowe 2001), several small reserves would promote more direct benefits (adult export) to the fisheries than a large one. Caution should be exercised though, because as MPA size declines, losses of biomass density to dispersal increase alongside perimeter-area ratios (Walters 2000, Dayton *et al.* 2000).

Although the geographic extent of the effects on catches observed here appears small, it is large by comparison to effects estimated in studies of coral reef fishes, which do not exceed a few hundred to 2000 m from the protected area (e.g. Russ & Alcalá 1996, McClanahan & Mangi 2000, Roberts *et al.* 2001, Russ *et al.* 2004, but see Yamasaki & Kuwahara 1989). Interestingly, recent work by Parsons *et al.* (2003) suggests that protection in MPAs could select for individuals with the highest tendency to exhibit residential behaviour. In the CIMR this would mean that the extent of lobster spillover might have been greater, or could decline overtime as the more mobile individuals are caught in the adjacent fishery.

Factors other than spillover could cause the negative gradient of lobster density away from the CIMR. The CIMR could be the focus of lobster populations in the area if puerulus recruit in shallow waters (e.g. Díaz el al. 2001). However, current data on post-puerulus density in the CIMR suggest average to low levels of settlement relative to other areas (Goñi *et al.* 2003c). Alternatively, the CIMR could be a natural hotspot for *P. elephas* and the quality of the lobster environment could decay from its centre. This concern highlights the importance of incorporating relevant environmental variables, such as habitat characteristics, in studies of reserve effects (Chapman & Kramer 1999, García-Charton *et al.* 2004). Unfortunately, no detailed habitat information is available and, in fact, the CIMR could be a natural hot spot for *P. elephas* because fishermen

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continued to fish there when other fishing grounds were at low levels. In hotspots, population increases following protection may be small because the habitat may be highly utilized, in which case abundance increases will result in export to adjacent areas (Jennings 2001).

In sum, because of their limited mobility relative to the size of the CIMR and the overfished status of the populations, *P. elephas* has in all likelihood responded swiftly to protection in the CIMR in terms of population density and reproductive potential (Goñi *et al.* 2001, Goñi *et al.* 2003a). In this case, the negative gradient of lobster catch with distance from the reserve and the concentration of fishing effort on the boundaries can best be explained by a process of adult export. Our tagging data also indicates that the CIMR is supplying the adjacent fishery. This is not to say that the CIMR is providing net benefits to the fishery as here, once again, lack of data before reserve creation prevents a true assessment of the potential fishery benefits of the reserve. It is important to bear in mind that understanding if a particular marine reserve works requires that it be evaluated in the context of the goals inherent to their establishment (Palumbi 2001). Many marine reserves, including the CIMR, have been created to meet unspecified conservation benefits rather than verifiable management objectives (Jennings 2001). Thus, because location, size and habitats protected were chosen with no particular species in mind, the *post hoc* evaluation of their effectiveness should not be used as tests of the benefits of marine reserves, but rather to draw lessons for establishing future reserves. When the case arrives, replicates of both reserves and harvested populations monitored before and after reserve establishment will be needed to unambiguously assess fishery benefits of reserves (Carr & Reed 1993, Russ 2002).

Picture: David Díaz

CHAPTER 6: GENERAL DISCUSSION

P. elephas has a slow growth, a long life-span and low fecundity by comparison to most other commercial spiny lobsters (Chapter 2). Additionally, the amplitude of adult movements is small (Chapter 5). These biological and ecological characteristics indicate that it is highly vulnerable to overfishing. Nothing is known about the stock-recruitment relationship of *P. elephas*, but its pelagic larval stage is long and dispersal by ocean currents may be extensive (Cunningham 1892, Hunter 1999). Thus, as recruitment may occur far from the parental grounds, decoupling between local spawning stock biomass and recruitment is possible.

The fact that targeted *P. elephas* fisheries in the Atlantic have disappeared, along with the overfished status of Mediterranean ones, support this prediction. The poor status of *P. elephas* fisheries may be traced back to the 1960s-1970s, when fishing effort increased dramatically with the replacement of pots (and diving) by trammel nets and the introduction of nylon, hauling gear and other technological advances (Chapter 2). All circumstantial evidence point to the great efficiency of nets in catching lobsters, to excess fishing effort and to the poor selectivity of trammel nets relative to pots, as the culprits. Recent studies indicate that trammel nets catch a greater proportion of large lobsters than pots (Goñi *et al.* 2003b) and that their impact on lobster habitats and benthic communities is far greater (Goñi *et al.* 2003c). *P. elephas* are typically fished by a large number of artisanal vessels distributed in many ports along the coastline and at-sea effort control of fisheries is difficult. Additionally, while pots have to be hauled every day to restock the bait, trammel nets are left in the water two or more days (to bait the net with entangled fishes). Due to bad weather conditions, nets are often soaked for longer periods resulting in loss of catch and return of undersized specimens to the water in poor survival condition (Quetglas *et al.* 2005).

Lack of information prevents discriminating between increased fishing mortality (resulting from greater fishing effort associated with trammel netting) and the ensuing changes in exploitation pattern (selectivity and size and sex related catchability, Goñi *et al.* 2003b) as the factors responsible of the depleted status of *P. elephas* stocks. As a high value commodity, *P. elephas* continues to be pursued despite low yields and rapidly growing prices maintain viable fisheries. Because of that, fishermen are requesting managers to impose more restrictions to help rebuild the stocks (Hunter 1996) and additional measures, such as closed areas, areas open only to pots and programmes to promote the reintroduction of pot fishing are being considered in some areas (e.g. Balearic Islands).

In this context assessing the effectiveness of marine reserves to improve the status of *P. elephas* populations and their potential to enhance fisheries is of the outmost importance. The CIMR provided this unique opportunity as it harbours traditional *P. elephas* fishing grounds where exploitation rates were very high. The first expected consequence of a reduction of fishing mortality in a protected population is that abundance increases (Russ 2002). The expected recovery of lobster abundance in the CIMR was assessed by comparing abundance indices in the CIRM and in two similar grounds open to fishing. This comparison was done in late spring, fall and winter in order to evaluate seasonal variation. The results indicated that seven to ten years after the creation of the Reserve lobster abundance was up to 20 times greater in the CIRM than in the two fished areas compared, depending on the season. This effect was expected given the high levels of exploitation observed in *P. elephas* fisheries (Pereiro & Fernandez 1974, Marin 1987, Goñi & Latrouite 2005) as in most spiny lobster fisheries (Childress 1997). A positive response to the cessation of fishing has been reported for other species of spiny lobsters (Hunt *et al.* 1991, Cole *et* *al.* 1990, MacDiarmid & Breen 1993) but wide-ranging ontogenetic migrations and foraging movements relative to the size of the protected area have been associated with the failure of some MPAs to rebuild lobster populations (Hunt *et al.* 1991, MacDiarmid & Breen 1993). Differential responses by sex have also been observed due to their different movement patterns (MacDiarmid & Breen 1993). The data from the CIMR indicate that *P. elephas* has limited mobility (maximum mean distance < 5 km) and that therefore the size of the CIRM (9 x 4.5 km) is adequate to rebuild populations of *P. elephas* (Chapter 5).

The protected population undergoes marked seasonal variations in abundance and structure (sex and size) (Chapter 2), although, overall, the abundance appears to remain stable while mean individual size continues to increase (Goñi *et al.* 2003d). This suggests that the recovery of the population in terms of numbers may have achieved a limit, possibly related to the carrying capacity of the CIRM. A complementary explanation is that population density in the Reserve has reached a level such that any increase translates into emigration from the Reserve to the adjacent fishery. Nevertheless, the seasonal oscillations observed appear to be linked to inshore-offshore migrations that take certain components of the lobster population in and out of the Reserve (Chapter 2). Caution should be exercised however, as seasonal changes in lobster behaviour linked to reproduction and moulting, particularly of males, also influence population estimates of *P. elephas* (Goñi *et al.* 2003b).

The greater lobster density inside the CIRM translates into a negative gradient of lobster catch per unit area in the adjacent fishery as distance to the Reserve increases. This effect is most pronounced within 1-1.5 km of the boundary but it extends to over 4 km. Data from lobsters tagged and released in the CIRM and caught in the surrounding fishing grounds strongly suggest that the CIRM is acting as source of lobsters to the adjacent fishery (Chapter 5). This process of spillover could be driven by density-dependent effects or arise because of random movements or seasonal migrations from high to low density areas (Sanchez-Lizaso *et al.* 2000, Jennings 2001, Russ 2002). Seasonal migrations may definitely play a role as the seasonal changes in the bathymetric distribution of males and females in shallow waters of the CIMR are consistent with annual onshore-offshore movements observed in Atlantic *P. elephas* (Mercer 1973, Ansell & Robb 1977) and common in populations of other temperate spiny lobsters (Herrnkind 1980).

Commercial catch rates decline abruptly near the reserve boundary in accordance with the concentration of effort there, the high catchability (Goñi *et al.* 2003b) and exploitation rate in the adjacent lobster fishery (Goñi *et al.* 2000), as well as with the limited movement of the species (Goñi *et al.* 2003d). The depression is followed by a plateau that suggests that spillover is sufficient to maintain constant catch rates up to 1.5 km from the reserve boundary (Chapter 5). One characteristic of the fishing effort exerted on the boundaries, which contributes to the observed local depression in catch rates, is the strategy of fishers to occupy those desirable fishing spots through the season regardless of catch rates. Effort concentration along the boundaries of marine reserves has been noted by many authors studying fisheries near marine protected areas (e.g., Yamasaki & Kuwahara 1989, Johnson *et al.* 1999, Murawski *et al.* 2004, Kelly *et al.* 2002, Ashworth & Ormond 2005). In fishing grounds not associated with MPAs, fishermen tend to relocate their nets when catch rates drop. The high fishing efficiency of the commercial vessels, associated with the great efficiency of trammel nets at catching lobster, induce high local rates of exploitation and deplete the area quite rapidly. In the extreme, if vessels always fished in the same place and exert very high local fishing mortality, they could catch (at each time step) all the lobster diffusing from the Reserve (Maury & Gascuel 2001).

In general evidence of spillover of lobsters from MPAs is scarce. Kelly *et al.* (2002) considered evidence of spillover that CPUE of lobster around an MPA in New Zealand was similar to that in unprotected areas despite the loss of access to the best inshore reefs. The high variability of catches adjacent to the MPA and the movement patterns of the species from tag recapture studies (Kelly 2001, Kelly & MacDiarmid 2003) supported their contention. Davidson *et al.* (2002) inferred spillover from the declining gradient of lobster density from the centre to the edge of the MPA. Among crustacean examples, the most convincing evidence is the declining gradients of CPUE of the crab *Chionoecetes opilio* extending up to 13 km from a no-take area off Japan (Yamasaki & Kuwahara 1989).

For the first time in the Spanish Mediterranean, the reproductive period, size at onset of maturity, fecundity and, what is more important in the context of a marine reserve, the reproductive potential of the unfished population were determined. In Columbretes *P. elephas* reproduces from June to October with a peak of spawning activity in September. Egg incubation takes about 5 months and eggs hatch in December-January. Sexual maturity occurs at the same age (4 years, Marin 1987) but slightly different sizes in females (77 mm CL) and males (82 mm CL) (Chapter 4). The fecundity of *P. elephas* in the protected population increases linearly with body size up to the females' maximum size. This is important in the context of protected populations as has been suggested that reproductive senescence of large females could lead to lesser than expected benefits in terms of increased spawning potential of protected lobster populations (Chubb 2000). Nevertheless, maximum reproductive yield (eggs per body gram) is reached at intermediate sizes, as observed by Bertelsen & Matthews (2001) in *Panulirus argus*. It was also noted that egg diameter increased with female size, suggesting that larger females hatch larger eggs that survive for longer under conditions of low food supply, as occurs in *J. edwardsii* (MacDiarmid, unpublished data)

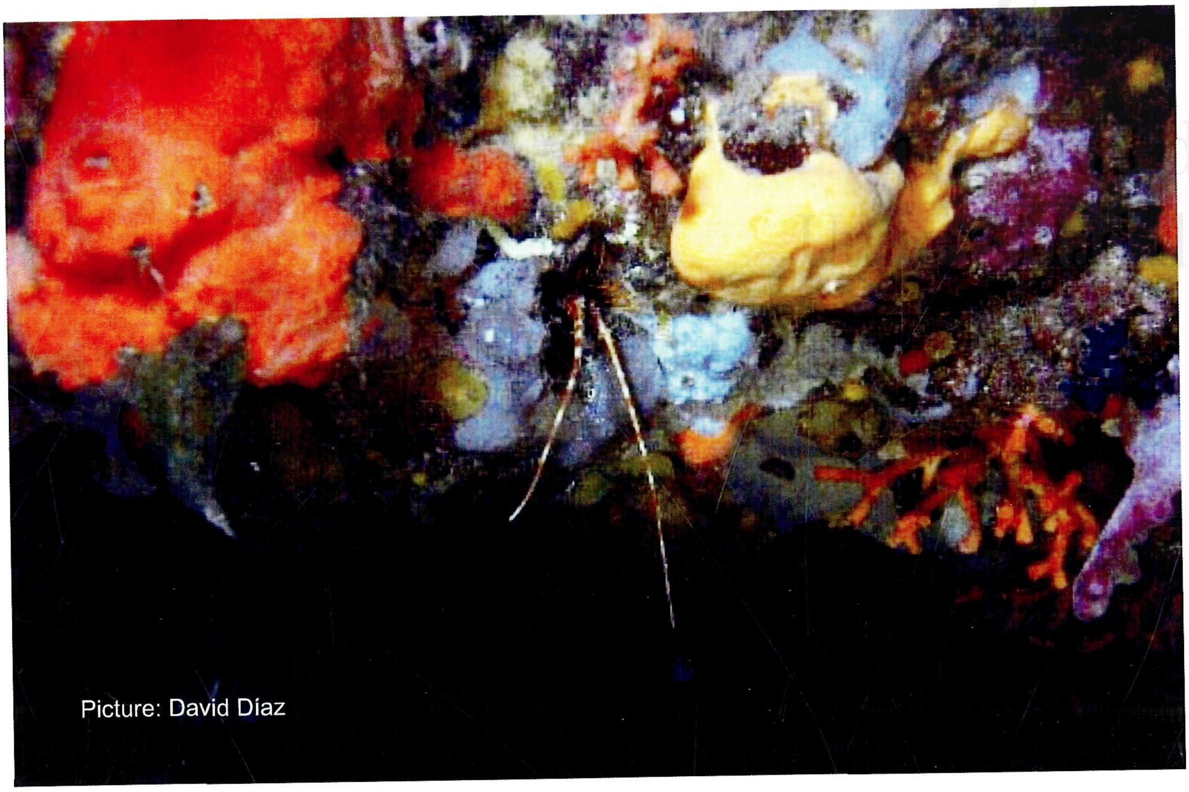
For most of the mature female size range, individual fecundity in the Reserve is greater than in the other Mediterranean populations studied (Corsica) (Chapter 4). This could result from the greater availability of large males in the unfished population together with their potential greater contribution to reproduction relative to small males (MacDiarmid & Buttler 1999). Interestingly, size-specific fecundity in the protected population coincides with that estimated for a lightly fished *P. elephas* population off Ireland (Mercer 1973). The study of the fecundity of the protected population has provided a unique opportunity to assess conventional hypotheses of density dependence of spiny lobster fecundity (Chittleborough 1976) and of higher size-specific female fecundity following exploitation (DeMartini *et al.* 1993). The results of the study of the *P. elephas* population in the CIMR do no support these hypotheses.

A useful result of this work shows that the MLS of *P. elephas* in Mediterranean fisheries (80 mm CL) is just over the size of female physiological maturity and only accounts for 1% of the unfished population potential egg production (Chapter 4). The much greater contribution of large females to population reproductive potential has been observed in other spiny lobster populations (*P. argus* and *Panulirus homarus*, Kanciruk 1980). Jamieson (1993) proposed that the MLS, of *P. elephas* in this case, should be increased to allow specimens to reproduce a minimum of once or twice before becoming susceptible to fishing. However, larger MLS alone does not appear to have protected some *P. elephas* populations from overfishing (e.g., Croatian fisheries, Soldo *et al.* 2001; fisheries off Brittany, Latrouite & Noel 1997). Thus, a larger MLS may be seen as a necessary technical measure but far from sufficient.

Protected populations are characterized not only by their superior abundance and relative egg production but also by the greater number of large individuals (naturalization of the population structure) and, thus, by its high reproductive potential (Russ 2002). Thus, comparison of the indices of spawning potential of unfished and fished populations allows assessment of how *P. elephas* egg production may be influenced by fishing. Results of the study indicate that, taking the population in the Reserve as a reference and assuming similar productivity in all areas, the spawning potential in the Reserve may have increased 6 to 20 times since fishing was banned ten years ago (Chapter 4). This result measures up to Annala's (1991) egg-per-recruit estimates in fished relative to unfished populations of *J. edwardsii* (1.2% to 36.8% depending on the area; mean= 20.1%), and is greater than the estimated mean 6.6% annual increase of Kelly *et al.* (2000) for the same species in three MPAs.

The growth of lobster spawning potential in the CIMR appears to be mainly due to the larger number of mature females available in the Reserve (rather than to their slightly greater mean size) and to the higher fecundity of large females (Chapter 4), possibly associated with the greater number of large males available for copulation (MacDiarmid & Buttler 1999). Finally, although crucial for the full understanding of the effectiveness of the CIRM, the study of the pattern of dispersal (export) of larvae and of the link between the egg production in the Reserve and subsequent recruitment imposes enormous logistic difficulties and has not been tackled yet.

In sum, *P. elephas* density, mean size and spawning potential in the CIRM are greater than in exploited areas and suggest a protection effect. Furthermore the spatial pattern of catches and effort in the adjacent fishery indicate that lobsters are emigrating from the Reserve and supplying the adjacent fishery. However, the lack of other comparable protected sites and of data collected before protective measures were in place prevents a reliable assessment of the responses of *P. elephas* in the CIMR (Underwood 1992). This is a common problem aggravated by the frequent establishment of reserves in singular areas or to protect unique ecosystems (see, *e.g.*, Cole *et al.* 1990, Carr and Reed 1993, Jones *et al.* 1993, MacDiarmid & Breen 1993). Unfortunately, this problem cannot be solved, and the dilemma underscores the importance of conducting baseline studies before reserves are established.



Picture: David Díaz

CONCLUSIONS

- The biological and ecological characteristics of *P. elephas* - slow growth, long life span (> 15 years), low fecundity and small amplitude of adult movements - make the species highly vulnerable to overexploitation.

- *P. elephas* has a high and growing unit value that makes its exploitation profitable even at low population abundance. Presently, most targeted fisheries in the Atlantic have disappeared and populations in the Mediterranean are considered overfished. Viable fisheries remain mainly in archipelagos and islands.

- Seven to nine years after the creation of the Columbretes Islands Marine Reserve *P. elephas* abundance was 5 to 20 times higher than in nearby exploited grounds depending on the season.

- Temporal changes in lobster abundance follow different patterns in the Reserve and in fished grounds. In the Reserve, abundance was highest prior to mating in early summer which may be associated with a proposed inshore reproductive migration. In fished areas, maximum abundance was higher at the end of the 6-month closed season in late winter, demonstrating the effectiveness of the annual closure for rebuilding exploited lobster populations.

- The observed temporal and bathymetric variability in the size and sex structure of the lobster population in the Reserve is consistent with annual onshore-offshore migrations reported for *P. elephas* in other regions and for other temperate spiny lobsters.

- *P. elephas* in the Reserve breeds once a year between June and October with a peak in September. Large females mate and lay eggs earlier in the breeding season than small females. Males copulate and re-charge the gonads repeatedly through the breeding season. Egg incubation lasts about 5 months.

- Female *P. elephas'* physiological and functional maturity in the Reserve occurs at 76-77 mm CL. Males reach physiological maturity at a larger size - 82 mm CL - but at the same age.

- *P. elephas'* individual fecundity in the protected population increases linearly with body size up to the females' maximum size, rejecting the hypothesis of senescence of older females.

- Maximum relative fecundity – eggs per body gram – is reached at intermediate sizes (105-110 mm CL).

- Egg size increases with female size. Based on evidence in other species, large eggs would hatch larger larvae that are able to survive longer under conditions of low food supply.

- For most of the mature female size range, mean individual fecundity in the protected population is higher than in the fished Mediterranean populations studied. It is proposed that the greater availability of large males in the protected population together with their potential greater contribution to reproduction relative to small males cause this difference. The results support neither the hypothesis of density-dependence of spiny lobster fecundity nor that of higher size-specific fecundity following exploitation.

- In the unfished population of the Reserve the size class of breeding females that contributes most to egg production is 105-110 mm CL (or 7-8 years), well above the minimum landing size (MLS, 80 mm CL) and age (3-4 years).

- Newly mature females protected under the MLS may provide only 1% of the unfished population potential egg production and are 20 times less productive than females in the 105-110 mm CL size group.

- Taking the CIMR population as reference, the spawning potential in the Reserve may have increased 6 to 20 times since fishing was banned 10 years ago.

- Over 75% of the fishing sets in the commercial fishery adjacent (within 5 km) to the CIMR occur at less than 1 km from its boundary.

- Commercial CPUE shows a negative relationship with distance from the CIMR boundary up to 4.5 km. The CPUE gradient has a depression at the boundary followed by a plateau and a linear decline as distance increases. The CPUE depression is associated with concentration of effort near the Reserve causing local depletion. The plateau following the depression suggests that export of lobsters from the Reserve is sufficient to maintain stable catch rates up to 1500 m from the boundary.

- Catch per unit area in the adjacent commercial fishery declines linearly with distance from the boundary.

- The negative gradient of lobster catch with distance from the Reserve and the concentration of fishing effort on the boundaries can best be explained by a process of adult export. Tagging data also indicates that the CIMR is supplying the adjacent fishery.

- Lack of data before reserve creation and replicates of the CIMR prevent a true assessment of the its potential benefits of the Reserve.

Picture: Animal's House

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