A behavioural seascape ecology approach to macrophyte herbivory

Jordi Pagès Fauria

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A **behavioural seascape ecology** approach to **macrophyte herbivory**

Jordi Pagès Fauria

Universitat de Barcelona
Facultat de Biologia

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Estudi de l’herbivorisme en macròfits marins des de l’ecologia del comportament i del paisatge

Jordi Pagès Fauria

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Tesi Doctoral

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A behavioural seascape ecology approach to macrophyte herbivory

Memòria presentada per Jordi Pagès Fauria
per optar al Grau de Doctor per la
Universitat de Barcelona

Jordi Pagès Fauria
Centre d'Estudis Avançats de Blanes (CEAB)
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Barcelona, Juny de 2013

La directora de la tesi	El director de la tesi
Dra. Teresa Alcoverro Pedrola	**Dr. Javier Romero Martinengo**
Científica titular	Professor titular
(CEAB-CSIC)	(UB)

Per a la Núria i tots els que
m'heu ajudat a arribar fins aquí.

Agraïments

Sembla impossible que del començament d’aquesta aventura ja en faci més de 4 anys! Quantes coses que hem arribat a aprendre, quantes hores de pensar, escriure, llegir, entendre, de silenci sota l’aigua... I totes aquestes novetats en la manera d’entendre les coses, la natura, la ciència, no haurien estat possibles sense l’ajuda i el suport d’una gran quantitat de persones a qui vull donar les gràcies. De fet, tot i que a la portada només hi aparegui el meu nom, aquesta tesi és una mica de cadascú de vosaltres, fins i tot d’aquells que a causa de la meva tendència a despistar-me oblidi d’anomenar aquí.

Aquesta tesi no hauria estat possible sense la confiança dels meus directors. Teresa i Javier formeu un tàndem fantàstic, una combinació de seny i rauxa única. La gran llibertat que en tot moment m’heu donat per anar afrontant els diferents capítols, tot i que al principi feia una mica de respecte, l’he agraïda molt perquè m’ha permès encarar-me en els temes que m’anaven interessant més. Teresa, moltíssimes gràcies per totes les hores que ens dediques (les visibles i les que no ho són), de xerrades de ciència, de no ciència, per les hores de reunions, els *brainstormings* huracanats, pels dies a l’Índia, per la teva vitalitat i per les moltes coses que vindran! Javier, què dir-ne dels teus correus amb la més fina de les ironies? O dels teus premis en forma de comentaris en els manuscrits revisats (de l’estil "*cáspita, esto se acaba*") que sempre aconsegueixen fer-me somriure? És curiós com des d’aquell primer contacte per demanar-te ajuda per un treball de recerca (quan encara anava a l’escola, devia ser el 2002) hem seguit connectats fins aquí, i la de coses que queden! Així mateix, el suport i la confiança total de la Marta Pérez (tot i que li preocupi la meva falta de gust pel vi, "*usted me preocupa*"), em van ajudar molt a començar en la meva etapa a les catacumbes de la Facultat de Biologia jugant a cuinetes amb el PAM i feixos de *Cymodocea*. En Rohan també ha estat una peça clau, moltes gràcies per les teves reflexions, idees, i sobretot perquè sovint *‘the trip for its own sake is as fulfilling as the destination’*. Un plaer poder conèixer tant la teva versió catalana, com sobretot la teva versió índia!

Si aquesta tesi és una mica de cadascú de vosaltres, hi ha una persona a qui n’hi pertany un tros gegant: l’Alessandro. Ha estat fantàstic poder fer la tesi juntament amb tu! Des del primer dia ens hem ajudat moltíssim i hem estat l’ombra l’un de l’altre. Hem fet el màster, les campanyes del temporal, hem anat a Fenals, a Giverola, amb les gàbies, amb el caçapapallones, punxant eriçons sota una pluja persistent i totalment sols a Medes, ens hem trencat el cap amb els seminaris i ens hem recolzat en el procés d'enclaustrament per escriure aquesta tesi. Moltes gràcies per les mil rialles, els croissants de xocolata, i per entendre'ns tan i tan bé, tant a fora com a dins de l'aigua... de fet, ni tu ni jo som uns grans xerraires (a no ser que jo em prengui un cafè o una cafiaspirina, jeje)!

Un altre tros gros d'aquesta tesi se'l repartiria la resta del nostre gran equip de *posidonios*: Guillem, Simone, Jordi i Yaiza. Cadascú amb les seves peculiaritats: "l'organització especial"d'en Guillem (amb la bogeria a partir de les 18h de la tarda), l'energia inacabable d'en Simone (*quanto sei bella carmine!!*), la curiositat inesgotable d'en Jordi (*coges er movis y lo tiras!*) i la positivitat de la Yaiza (*eh una muhé didna d'admirá!*). No em voldria oblidar de l'Scott, la Donatella, la Sabina, en Vedran, l'Andrea i en Mateo, que han anat passant pel nostre grup durant aquests anys. Tot aquest GRAN grup de gent, alegra qualsevol campanya, totes les hores de despatx, els viatges amb la furgoneta, i la veritat és que és un gust tenir-los al costat!

L'altre meitat d'equip, els de la *cymo*, han estat una altra pota important durant aquests anys. De fet els meus primers passos en aquest món marí van ser amb ells: la Tània, la Neus, l'Oriol, la Sílvia, la Izaskun em van ajudar a entrar al món de les plantes marines, amb les excursions pel delta, triturant *Cystoseira*, muntant experiments fins a altes hores de la nit a sota l'hivernacle, cantant el "cabin fever", inundant la furgoneta amb aigua de mar o a les campanyes anuals a Medes, quin gust! Moltes gràcies a tots i també a l'Aurora que tot i que fa menys que la tenim per aquí porta una empenta!

Una persona que a poc a poc ha anat tenint cada vegada més influència en aquesta tesi ha estat en Fede, que amb la seva passió-bogeria pel comportament (i sobretot pel moviment animal) ha fet que la tesi n'hagi quedat ben impregnada. Moltes gràcies Fede, he après moltes coses de la teva manera de fer i sense voler-ho (o potser volent) m'has donat algun toc d'atenció molt útil per tirar del carro quan les forces començaven a flaquejar! Juntament amb en Fede, l'Aitana, en John i la Liliana m'han anat donant molts cops de mà amb temes que a mi em quedaven una mica més llunyans. Sou uns cracks!

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El capítol 6 no hauria estat possible sense la col·laboració amb en Bernat Hereu. Va ser tota una experiència la campanya de pesca de salpes amb en Miquel Sacanell i l'Àngel López a l'Estartit, moltes gràcies! Igualment, el capítol 8 no hauria estat possible sense la col·laboració de l'Antoni Garcia.

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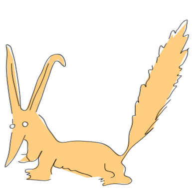
Voldria acabar amb un trosset del Petit príncep dedicat a totes les meves guineus i a totes les persones per a les quals jo sóc una guineu.

> *"Si em domestiques, la meva vida serà com si li toqués el sol, [...] coneixeré un soroll de passos que serà diferent. Els altres passos em fan amagar sota terra. Els teus em cridaran fora del cau [...]. Per començar t'asseuràs una mica lluny de mi. Jo et miraré de reüll i tu no diràs res. El llenguatge és font de malentesos. Però cada dia et podràs asseure una mica més a prop."*



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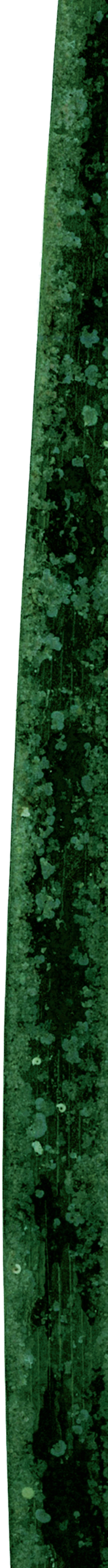

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Resum

1.1 Introducció general

L'organització dels ecosistemes i la importància de les interaccions indirectes

Les comunitats ecològiques estan governades per una complexa xarxa d'interaccions. Un dels principals objectius de l'ecologia és precisament intentar entendre els mecanismes que estructuren aquestes comunitats (Paine, 1980; Polis, 1999). Quantificar la força de les interaccions és crític per tal d'entendre el funcionament dels ecosistemes i l'organització de les comunitats naturals. En aquest sentit, l'anàlisi de xarxes d'interaccions ha estat una eina molt utilitzada, així com els models mecanistícs per valorar les dinàmiques de les poblacions de la comunitat (Ohgushi, 2008). Típicament, aquestes xarxes s'han basat en interaccions tròfiques directes (alimentàries), amb l'assumpció que aquestes són les que determinen més clarament la força de les interaccions. Cada vegada és més reconegut, però, que altres tipus d'interaccions, com les interaccions indirectes i altres interaccions tròfiques i no tròfiques, com l'enginyeria ecosistèmica, poden tenir també grans implicacions a nivell de tota la comunitat (e.g. Pearson, 2010).

La publicació, fa aproximadament 50 anys, de dos articles fonamentals sobre el paper de les interaccions indirectes en les xarxes tròfiques (Hairston et al., 1960; Paine, 1966) va obrir la porta a noves visions, recerca i debats entorn a l'ecologia de comunitats. Aquests estudis pioners subratllaven el paper de les interaccions indirectes, aquelles que s'esdevenen quan l'efecte d'una espècie sobre una altra requereix la presència d'una tercera (Wootton, 1994) (veure Fig. 2.1). La comprensió que aquest tipus d'interaccions poden tenir importants efectes a nivell de tota la comunitat va arribar al gran públic gràcies a l'article de Hairston, Smith & Slobodkin (1960). En aquest article, es proposava que les interaccions tròfiques indirectes poden produir cascades tròfiques, efectes indirectes que explicarien el per què de la relativa dominància dels productors primaris a la majoria d'ecosistemes. La "hipòtesi del món verd", com se l'anomenà més endavant, postulava que els productors, consumidors i descomponedors estan tots limitats pels recursos. Segons aquest model, doncs, la biomassa vegetal s'acumula perquè els depredadors i els paràsits mantenen les poblacions d'herbívors tan baixes que no aconsegueixen fer minvar els seus recursos vegetals. A partir d'aquests estudis pioners, diverses evidències experimentals van semblar confirmar l'existència d'importants efectes indirectes en cascada amb els estudis sobre depredadors claus a la zona intermareal de Paine (1966) i els estudis sobre cascades tròfiques en boscos de kelp d'Estes & Palmisano (1974). Segurament a causa d'aquestes raons històriques, la discussió dels efectes indirectes i en cascada s'ha mirat sempre de dalt a baix (*top-down* en anglès), amb el punt vista centrat en els depredadors (Pringle et al., 2007; Pearson, 2010).

Més recentment, però, els estudis han començat a centrar-se en els mecanismes que determinen la importància relativa de les cascades tròfiques als ecosistemes (Strong, 1992; Shurin et al., 2002), el paper cada vegada més reconegut dels herbívors (Ohgushi, 2005; Pringle et al., 2007) i la importància de tenir en compte els efectes indirectes més subtils com les interaccions provocades per canvis en trets (Werner & Peacor, 2003; Schmitz et al., 2004). En aquest últim cas, les interaccions estan transmeses no per una cadena d'interaccions (Wootton, 1992) (Fig. 2.2a), com en el cas de les cascades tròfiques clàssiques, on una espècie en consumeix una altra i aquest efecte en la densitat de la població implica un efecte en una tercera espècie (per això s'anomenen també interaccions indirectes transmeses per densitat, DMIIs, de les inicials en anglès), sinó a través d'una modificació d'interacció (Wootton, 2002) (Fig. 2.2b). Aquesta modificació pot ser una modificació ambiental (Fig. 2.3) o una modificació a un tret d'una espècie (interaccions indirectes mitjançades per trets, TMIIs, de les inicials en anglès) (Fig. 2.4). Aquest últim tipus d'interaccions indirectes s'ha estudiat a fons durant els últims anys, sobretot en el cas en què el tret modificat és el comportament d'una espècie, que dóna lloc a les conegudes cascades tròfiques de comportament (Schmitz et al., 1997; Werner & Peacor, 2003). Un dels exemples més coneguts d'aquest tipus d'interaccions és l'estudi de la interacció entre llops (*Canis lupus*), cérvols (*Cervus elaphus*) i trèmols (*Populus tremuloides*) al Parc Nacional de Yellowstone (USA) (Ripple & Beschta, 2007). En aquell cas, la reintroducció dels llops al Parc va portar efectes inesperats: el reclutament dels trèmols (*P. tremuloides*), pràcticament absent fins aquell moment, va augmentar significativament. Això va passar sobretot en àrees amb un alt risc de depredació, a causa dels efectes letals dels llops sobre els cérvols, però també dels efectes no letals dels llops sobre el comportament dels ungulats (augment del nivell d'alerta). Altres exemples molt coneguts són els experiments de Schmitz (1998), en què quantificà la importància dels efectes letals i no letals dels depredadors sobre les seves preses en camps abandonats. En aquests exemples, els investigadors van adoptar idees creatives (ex. immobilitzar amb cola les peces bucals dels depredadors) per demostrar que a les xarxes d'interaccions entre plantes, llagostes i aranyes depredadores, els efectes no letals dels depredadors són més importants que els efectes letals en sí mateixos. L'efecte no letal de les aranyes sobre les llagostes va ser un canvi en el comportament de cerca d'aliment en resposta al risc de depredació.

Estudi de les interaccions biòtiques des d'un punt de vista comportamental

Els exemples anteriors posen de manifest la importància de considerar aspectes de comportament en l'estudi de les interaccions biòtiques. Amb tot, l'aproximació a l'ecologia de comunitats a través del comportament havia estat poc utilitzada amb espècies clau fins fa relativament poc temps, i en canvi, l'etologia s'havia centrat a l'estudi d'espècies model (Lima & Zollner, 1996) de poca rellevància ecològica. Aquest fet es deu bàsicament a que els etòlegs i els ecòlegs treballen i pensen generalment a escales completament diferents i amb preguntes diferents. Alguns etòlegs conceben l'ecologia com "l'escenari en el qual els animals han de desenvolupar el seu comportament" (Krebs & Davies, 1993); mentre que des de l'altra banda, fins ben bé la darreria dels anys 1990, el comportament era per a molts ecòlegs una curiositat de les seves espècies d'interès i un aspecte lateral a estudiar. Malgrat això, l'ecologia del comportament estudia aspectes funcionals del comportament; per exemple, com un patró de comportament determinat contribueix a les probabilitats de supervivència i èxit reproductor d'un animal, cosa que pot influir al seu torn a l'estructura i funcionament dels ecosistemes.

La base de bona part de l'etologia gira en torn a la concepció economicista de la presa de decisions animals. De fet, ja MacArthur & Pianka (1966), en un article que va esdevenir fonamental, tenien com a objectiu determinar en quines taques s'alimentaria una espècie determinada i quins aliments formarien part de la seva dieta si l'animal es comportés "de la manera més econòmica possible". Van postular que una activitat s'hauria de continuar produint mentre el benefici resultant, en temps utilitzat per unitat de recurs, fos més gran que les pèrdues per no moure's i canviar de taca. Charnov (1976) va expandir aquesta teoria amb la idea que un depredador hauria d'abandonar la taca en la qual es trobés en aquell moment quan la taxa de captura marginal de la taca (del què queda) fos menor que la taxa de captura de l'hàbitat en general (el famós teorema del valor marginal, Fig. 2.5). Finalment, Emlen (1966) hi va afegir que els animals haurien de ser més selectius en condicions d'aliment abundant, mentre que quan l'aliment fos escàs haurien de ser més indiscriminats en la seva dieta. Aquesta sèrie d'articles constitueixen els fonaments de la teoria d'optimització de la cerca d'aliment. Amb tot, en el seu article inicial, MacArthur & Pianka (1966) ja reconeixien que la seva formulació teòrica seria més útil com a hipòtesi contra la qual testar dades empíriques, que no com una formulació amb valor predictiu. A mesura que aquestes hipòtesis van anar essent testades al camp (e.g. Belovsky, 1978), s'hi van haver d'anar incorporant nous paràmetres, ja que els animals no només han d'optimitzar la cerca d'aliments, sinó que a més han de cuidar de no ser menjats, entre altres aspectes.

De fet, la presa de decisions d'animals en ambients amb risc ha estat un altre dels temes més estudiats en ecologia del comportament des del punt de vista econòmic (e.g. Kacelnik & Bateson, 1997). La valoració del risc és molt important en les interaccions depredador-presa. Les respostes a nivell comportamental de les preses davant els depredadors (o del risc que n'hi hagi) inclouen la redistribució espacial, la selecció d'una estructura d'hàbitat determinada, canvis temporals i/o espacials dels patrons d'activitat, augment de la vigilància i reducció del temps dedicat a l'alimentació, o fins i tot canvis en les mides dels grups (Valeix et al., 2009). Els efectes indirectes dels depredadors s'espera que tinguin, per tant, impactes en l'eficàcia biològica dels individus presa, i per tant en la demografia de les poblacions de preses. Així doncs, el canvi de comportament de les preses en funció de la seva percepció de risc podria ser un tret adaptatiu, i per això la detecció de senyals químiques de depredadors o d'alarma de conespecífics (Hagen et al., 2002) són adaptacions importants en la cursa armamentística entre depredadors i preses. Per exemple, els senyals visuals i acústics són àmpliament utilitzats entre els vertebrats malgrat no permetre la detecció de depredadors a llarga distància o la presència passada d'un depredador (Kats & Dill, 1998). En canvi, els estímuls químics poden ser més fiables per valorar la presència passada de depredadors i per tant poden servir per informar de zones potencialment perilloses (Nishizaki & Ackerman, 2005). Una vegada l'estímul ha estat detectat, l'animal hauria d'emetre una resposta a aquest estímul. En cas que es detecti la presència de depredadors, les respostes més habituals són l'evitació i/o escapada, així com la cerca de refugi. Cadascuna d'aquestes respostes tenen en comú el fet que impliquen un canvi en els patrons de moviment de l'espècie d'interès. Amb tot, tant l'evitació del depredador, com l'escapada, com la cerca de refugi impliquen un cost en forma de menys accés als recursos (Nishizaki & Ackerman, 2005), seria selectivament avantatjós el fet de poder valorar la necessitat d'escapar o buscar refugi d'una manera acurada per mirar de trobar un equilibri òptim entre els riscs potencials (depredació) i els guanys potencials (ex. continuar menjant) (Nishizaki & Ackerman, 2005).

Ecologia del comportament i de paisatge: el paper central del moviment animal

Els models d'optimització de la cerca d'aliment ben aviat van necessitar la incorporació de nous aspectes ecològics, i com hem vist, el risc de depredació va ser un dels més evidents des del primer moment. Un aspecte dels models de cerca d'aliment que cal tenir en compte és que consideren la presència de menjar en taques discretes, repartides pel paisatge. Així doncs, un altre aspecte que ràpidament es va haver d'introduir en aquests models va ser el temps òptim de viatge entre taques, la capacitat de càrrega de recurs òptima en funció de la distància entre les taques i el niu, etc. (ex. Kacelnik, 1984; Schmid-Hempel et al., 1985). La majoria d'aquests models tractaven el moviment animal de manera molt lateral, tenint-lo en compte només com a simple cost per l'animal. Avui en dia, en canvi, el moviment dels animals en paisatges heterogenis es considera un aspecte fonamental en l'ecologia del paisatge. Malgrat això, i tal com hem dit anteriorment, les escales dels experiments de comportament per testar els models d'optimització són en general diferents de les que tenen en compte els ecòlegs de paisatge. Actualment el moviment animal, la dispersió i la selecció d'hàbitats es consideren aspectes especialment importants i determinants de la dinàmica i distribució de les poblacions en paisatges heterogenis (Lima & Zollner, 1996). Paral·lelament, els ecòlegs del comportament també han anat avançant en la comprensió de la presa de decisions dels animals pel què fa al seu moviment, dispersió i selecció d'hàbitat. Per tant, una aproximació al comportament animal tenint en compte el paisatge que l'envolta ens permetria saber quin tipus d'informació té disponible l'animal quan aquest es mou a través de l'ambient, i com aquesta informació s'utilitza en la selecció d'una determinada taca o hàbitat (Lima & Zollner, 1996).

Existeixen tres aspectes fonamentals del moviment animal que són rellevants per a una ecologia del comportament i de paisatge ben fonamentada: el rang de percepció de l'espècie d'interès, els criteris de selecció de taques o hàbitats determinats i els patrons de moviment de les espècies. Aquests tres aspectes comportamentals representen una connexió directa entre l'ecologia del comportament i l'ecologia del paisatge, i en particular es relacionen molt al concepte de connectivitat funcional, que es defineix com el grau amb què el paisatge facilita o impedeix el moviment entre les taques amb recursos (Taylor et al., 1993). A nivell de presa de decisions, diferents rangs de percepció i diferents capacitats de moviment poden implicar majors o menors probabilitats de mortalitat (per depredació o per pertorbacions, per exemple) quan un animal abandona una taca cercant noves zones (veure Fig. 2.6, Lima & Zollner, 1996). De fet, s'espera que els organismes alterin els seus moviments i que experimentin beneficis o costs en la seva eficàcia biològica, en funció de la naturalesa, forma i distribució de les taques d'hàbitat i dels ecotons (Knowlton & Graham, 2010). Així doncs, el rang perceptual i la capacitat de moviment, per raons semblants, poden influenciar aspectes com la connectivitat del paisatge, o l'escala espacial a la qual un organisme interacciona amb un paisatge determinat (Fig. 2.6) (Dunning et al., 1992; Lima & Zollner, 1996; Zollner & Lima, 1997).

Aproximant-nos a l'ecologia des d'una vessant de paisatge i alhora tenint en compte el comportament de les espècies d'interès tindrem una idea més completa de com s'estructuren les poblacions i les comunitats, i de com alguns atributs de paisatge i de comportament poden generar variabilitat en l'abundància i distribució de diferents espècies en funció de les seves capacitats de moviment i la seva selecció d'hàbitats (Ricketts, 2001; Haynes & Cronin, 2003, 2004, 2006; Haynes et al., 2007; Haynes & Crist, 2009). Així mateix, els efectes dels atributs de paisatge també poden tenir efectes sobre els processos ecològics i aquests aspectes continuen essent poc estudiats, amb una majoria d'estudis orientats només a valorar els patrons d'abundància i distribució de les espècies. Mitjançant l'estudi funcional d'espècies claus podem comprendre el funcionament dels ecosistemes, sobretot amb l'estudi de funcions com l'herbivorisme, que impliquen canvis en l'estructura dels hàbitats (Parsons et al., 2013).

La importància de l'herbivorisme en els sistemes ecològics

Tot i que la pressió que exerceixen els depredadors a molt nivells dels ecosistemes és innegable (e.g. Estes & Palmisano, 1974; Terborgh et al., 2001), l'aparent descuit dels herbívors com a potencials iniciadors d'importants efectes indirectes és difícil d'entendre (Pringle et al., 2007). Amb tot, cada vegada més els herbívors estan començant a ésser considerats potencials iniciadors d'interaccions rellevants, ja que s'han demostrat capaços de modificar el seu hàbitat fins el punt de produir efectes en cascada en diversos ecosistemes (Pringle et al., 2007; Huntzinger et al., 2008; Parsons et al., 2013).

En general, s'ha observat que els herbívors són capaços de modificar la producció primària i determinar el reciclatge de nutrients (Abbas et al., 2012; Gera et al., in press), d'influenciar l'estructura de la capçada foliar i les interaccions entre espècies (McNaughton, 1984; Martin et al., 1989; Pringle et al., 2007) o de modificar la composició, diversitat i biomassa de les comunitats (Hobbs, 1996; Knapp et al., 1999), entre d'altres efectes. Les comunitats vegetals fortament modificades pels herbívors es coneixen amb el nom de gespes (*grazing lawns*), un terme encunyat per McNaughton (1984) per descriure els ecosistemes terrestres dominats per grans ramats d'herbívors migradors. L'alta biomassa d'herbívors en aquests ecosistemes, típicament la més alta d'entre els ecosistemes terrestres, implica que l'herbivorisme sigui un dels principals reguladors dels processos ecològics que s'hi desenvolupen. De fet, en els ecosistemes terrestres dominats per herbívors entre un 50 i un 90 % de la producció primària és consumida i transferida a la cadena alimentària via herbivorisme (McNaughton, 1984; Cyr & Pace, 1993; Poore et al., 2012), comparat amb el 9 % de la mitjana global pels ecosistemes terrestres (Frank et al., 1998).

Estudi de l'herbivorisme en les comunitats de macròfits marins a través d'una aproximació d'ecologia del comportament i de paisatge

Les comunitats de macròfits marins presenten diverses característiques que les fan uns sistemes molt interessants per a l'estudi de qüestions de rellevància ecològica, des d'un punt de vista d'ecologia del paisatge. Algunes d'aquestes característiques són: (i) les seves altes taxes d'herbivorisme, que sovint estructuren aquests ecosistemes, (ii) el fet que les interaccions són més intenses en ecosistemes aquàtics que en ecosistemes terrestres, (iii) el fet que les praderes de fanerògames marines i macroalgues són paisatges miniaturitzats amb característiques específiques (veure següents paràgrafs) i (iv) el fet que tenim un coneixement molt limitat del comportament dels seus herbívors.

És ben conegut que en sistemes marins d'esculls coral·lins, praderes de plantes marines o boscos de kelp, els megaherbívors com els peixos, eriçons, tortugues i dugongs exerceixen una forta pressió sobre la producció primària i l'estructura de la comunitat (Burkepile & Hay, 2006). De fet, es considera que els sistemes de fanerògames marines són els ecosistemes marins més anàlegs als ecosistemes terrestres dominats per grans herbívors (Burkepile, 2013; Gruner & Mooney, 2013). Tal com passa en sistemes terrestres dominats per herbívors, en praderes de fanerògames marines els herbívors poden arribar a consumir més del 50 % de la producció foliar en alguns casos (Prado et al., 2007; Christianen et al., 2012; Kelkar et al., in press). A més, tot i que l'impacte dels herbívors en les plantes és segurament equiparable en sistemes marins i terrestres, els controls per depredadors (també anomenat control superior o *top-down* en anglès) i per recursos (també anomenat control inferior o *bottom-up* en anglès) en les poblacions d'herbívors presenta diferències importants entre ambdós ambients (Burkepile, 2013). De fet, les cascades tròfiques són més habituals i intenses en sistemes aquàtics que en sistemes terrestres (Strong, 1992). Això es deu possiblement al menor contingut en nutrients dels vegetals terrestres en comparació als macròfits aquàtics (Cebrian et al., 2009), cosa que pot produir desequilibris en els herbívors terrestres, que fa que aquests es trobin més habitualment limitats pels recursos que no pas els herbívors marins o els d'aigües continentals (Hillebrand et al., 2009). L'estudi de les intenses interaccions i retroalimentacions positives entre plantes aquàtiques i herbívors és doncs cabdal, ja que desacoblar aquestes connexions pot tenir conseqüències per la integritat de l'ecosistema (Burkepile, 2013). Els ecosistemes de macròfits marins sotmesos a importants pressions d'herbivorisme són, doncs, molt atractius des del punt de vista funcional i d'estructuració dels ecosistemes.

A més, els paisatges submarins costaners, tal com passa amb altres paisatges lineals (com els rius, carenes de muntanyes), consisteixen de forma natural en taques més o menys petites d'hàbitat, aïllades entre elles per matrius de diferent naturalesa, i amb tendència a la miniaturització (Goodsell et al., 2007). Aquest tipus d'estructura fa que siguin candidats ideals on estudiar processos ecològics a una escala rellevant pel paisatge (Nally & Quinn, 1998). Malgrat això, s'ha de tenir en compte que els paisatges submarins tenen algunes especificitats. Els paisatges submarins estan generalment més connectats que els paisatges terrestres, això vol dir que les barreres al mar són possiblement més permeables, particularment per a les fases larvàries de molts animals (Tanner, 2006). Amb tot, al mar també podem trobar marges poc permeables entre hàbitats, particularment per les fases adultes d'organismes bentònics poc mòbils com per exemple molts equinoderms (Hereu, 2005) (sovint són marges amb un alt grau de contrast). Aquesta configuració del paisatge, amb marges més o menys permeables i taques més o menys connectades, fa que els animals herbívors no es distribueixin aleatòriament pels mosaics d'hàbitats, sinó que generalment es concentrin en determinades zones de l'espai, cosa que genera heterogeneïtat espacial (Pickett & Cadenasso, 1995; Vergés et al., 2011).

El marc que ofereix l'estudi del comportament, integrant el moviment animal, el risc de depredació i l'adquisició de recursos ha estat útil per a una major comprensió de la presa de decisions dels herbívors a diferents ecosistemes. Amb tot, en ecosistemes marins, l'estudi del comportament dels herbívors ha avançat poc. Només recentment, s'ha començat a estudiar el comportament de grans herbívors com les tortugues (Heithaus & Dill, 2002), els dugongs (Wirsing et al., 2007) i alguns peixos d'esculls de corall (Fox & Bellwood, 2011; Nash et al., 2012). Aquesta tesi és un intent d'enllaçar el comportament i mobilitat animal amb els atributs de paisatge i, eventualment, amb els impactes sobre les comunitats vegetals.

1.2 Objectius

En conjunt, aquesta tesi pretén aproximar-se a l'estudi de l'herbivorisme dels macròfits marins i a l'ecologia de comunitats des d'un punt de vista comportamental i de paisatge. El nostre sistema d'estudi, el paisatge format per praderes de la planta marina *Posidonia oceanica* (L.) Delile barrejades amb àrees de sorra i zones rocoses amb macroalgues, és particularment útil per testar qüestions ecològicament interessants. La comunitat de macroherbívors del sistema està formada en essència per només dues espècies claus, l'eriçó de mar *Paracentrotus lividus* (Lam.) i el peix *Sarpa salpa* (L.). Ambdues espècies són generalistes i s'han demostrat consumidores actives de plantes marines i de macroalgues (Prado et al., 2007), alterant profundament l'estructura dels hàbitats en els què viuen (Tomas et al., 2005b). A més, ambdós animals difereixen en la seva mobilitat i en el risc de depredació a què es troben sotmesos, cosa que motiva preguntes interessants sobre com deuen percebre, utilitzar, respondre i impactar el paisatge que els envolta. *S. salpa* és una espècie altament mòbil (Jadot et al., 2006) amb pocs depredadors coneguts en l'actualitat, mentre que l'eriçó de mar *P. lividus* és una espècie de baixa mobilitat (Hereu, 2005) i amb altes taxes de depredació (Sala, 1997).

Aquesta tesi s'estructura en cinc capítols que se centren en diferents aspectes de l'organització de les comunitats i interaccions ecològiques (**capítol** 4), el moviment animal (**capítols** 5 i 6), valoració del risc i respostes comportamentals dels animals vers el risc (**capítol** 5), selecció d'hàbitats i connectivitat (**capítol** 6), influència dels atributs de paisatge en el comportament de cerca d'aliment i per tant en com els herbívors impacten les poblacions vegetals (**capítol** 7) i en la resposta dels herbívors en termes poblacionals i de comportament enfront a grans pertorbacions (**capítol** 8). Els capítols deriven d'experiments manipulatius (**capítol** 4), de campanyes de mesura al camp (**capítols** 6, 7 i 8) o d'experiments en condicions controlades al laboratori (**capítol** 5).

Els objectius i l'estructura detallada de la tesi és la següent:

- Al **capítol** 4, donat el creixent reconeixement dels impactes directes que té l'herbivorisme en el funcionament de les comunitats de fanerògames marines (Heck & Valentine, 2006), volem analitzar si l'herbivorisme pot modificar a més de la planta en sí, altres processos tròfics a través de vies indirectes. Així doncs, examinem com canvis en l'estructura de la capçada foliar causats per peixos herbívors influencien les interaccions depredador-presa entre un altre herbívor i els seus depredadors.

- Al **capítol** 5 analitzem, en condicions controlades de laboratori, les respostes en els patrons de moviment d'un dels herbívors del sistema (l'eriçó *P. lividus*) sotmès a senyals de depredadors i de llum. Esperem que els eriçons responguin a les senyals químiques dels depredadors canviant els seus patrons de moviment; i que es mouran de la zona il·luminada cap a l'ombra, en l'experiment amb llum heterogènia.

- Al **capítol** 6 ens centrem en el moviment de l'altre herbívor del sistema, el peix *S. salpa*. Volem determinar si aquests peixos són capaços de connectar hàbitats diferents i distants en un mosaic de paisatge compost de plantes marines, sorra i zones rocoses amb macroalgues. A més, pretenem caracteritzar els patrons diaris i la intensitat d'aquestes connexions al llarg de l'any i l'ús de l'hàbitat d'aquesta espècie a través del paisatge.
- Els coneixements obtinguts en els **capítols** 5 i 6, ens permet connectar l'ecologia del paisatge i l'ecologia del comportament de les espècies estudiades amb els patrons d'herbivorisme observats *in situ* al **capítol** 7. En aquest capítol discutim que diferents atributs del paisatge poden afectar de forma diferent el comportament, i per tant les taxes d'herbivorisme, de cadascun dels herbívors del sistema, en funció de la seva mobilitat. Volem saber si darrera dels diferents processos en què interaccionen herbívors i paisatge, existeix algun atribut que determini els patrons espacials d'herbivorisme en els paisatges dominats per plantes marines del Mediterrani, així com intentar dilucidar algun dels mecanismes que provoquen els patrons observats.
- Finalment al **capítol** 8, estudiem si les diferències de mobilitat observades entre els dos herbívors poden implicar també respostes dispars davant de pertorbacions extremes (grans tempestes).

1.3 Discussió general

Conclusions principals

Capítol 4
La pressió de depredació sobre un herbívor clau pot ser modificada tant pel context ambiental en què es troba com per les accions d'un altre herbívor que modifica els trets de la planta que crea aquest context ambiental. Els herbívors, sobretot quan actuen com a espècies enginyeres poden causar increments en el risc de depredació d'altres animals, ja que modifiquen substancialment la complexitat estructural dels hàbitats, amb conseqüències per la disponibilitat de refugis, entre d'altres.

Capítol 5
Els eriçons de mar de l'espècie *Paracentrotus lividus* poden percebre senyals químics de depredadors i respondre escapant mitjançant canvis en els seus patrons de moviment. El risc de depredació, doncs, pot ser tant important en influenciar els moviments dels animals com ho són les estratègies de cerca d'aliment, i per tant, s'haurien de considerar també a l'hora d'analitzar les trajectòries dels animals al camp. Com passa en la cerca d'aliment, alguns patrons de moviment podrien ser evolutivament més òptims per escapar o per la cerca de refugi; i això pot implicar canvis en les poblacions i distribució de les espècies presa.

Capítol 6
El peix herbívor *Sarpa salpa* presenta grans àrees de campeig (*home ranges* en anglès) i té la capacitat de connectar hàbitats distants gràcies a la seva gran mobilitat. Alhora mostren una gran selectivitat per la pradera de *Posidonia oceanica*, que sembla clarament preferida sobre les àrees rocoses i de sorra. Les espècies altament mòbils són capaces de connectar hàbitats distants, i possiblement perceben el paisatge a una escala àmplia. Així doncs, els plans de gestió i les àrees marines protegides haurien de tenir en compte aquests aspectes.

Capítol 7
Els atributs de paisatge poden influenciar els patrons d'herbivorisme en praderes de *P. oceanica*. L'heterogeneïtat espacial observada en el procés d'herbivorisme és produïda, possiblement, per la interacció entre la mobilitat dels dos herbívors principals del sistema (garotes i salpes) i la configuració del paisatge i el risc de depredació.

Capítol 8
Els herbívors de les comunitats de macròfits Mediterranis presenten respostes dispars quan són sotmesos a tempestes extremes. Davant de pertorbacions catastròfiques, la presència de diferents respostes entre els herbívors del sistema pot ser crítica per al manteniment de les funcions ecosistèmiques. Diferències de comportament i en les seves capacitats de moviment poden explicar per què les espècies mòbils (en el nostre cas la *S. salpa*) resisteixen millor les tempestes extremes, mentre que les espècies poc mòbils pateixen grans pèrdues en les seves poblacions, ja que només poden confiar en la complexitat estructural de l'hàbitat en què es troben per intentar passar els temporals.

Els herbívors poden produir importants efectes a nivell de tota la comunitat

El paper dels depredadors s'ha considerat sempre central per entendre gran part de l'ecologia de comunitats i les interaccions biòtiques, relegant els herbívors a un paper secundari. Tot i que era ben conegut que els herbívors terrestres podien ser importants en alguns ecosistemes concrets, el paper d'iniciadors d'efectes en cascada es reservava als depredadors. Amb tot, en els últims anys, els herbívors també s'estan començant a tenir en compte com a possibles iniciadors d'importants interaccions ecològiques (Pringle et al., 2007). Hi ha hagut dos camps molt importants per la reconsideració de la importància dels herbívors en l'estructuració dels ecosistemes: l'estudi dels megaherbívors (ex. ungulats) com a espècies enginyeres (Pringle et al., 2007; Huntzinger et al., 2008; Parsons et al., 2013) i l'estudi de les modificacions d'interaccions transmeses per trets (TMIIs, de les sigles en anglès *trait-mediated indirect interactions*) iniciades per insectes fitòfags (Karban & Baldwin, 1997; Ohgushi, 2005, 2008). El nostre estudi dels efectes indirectes generats per peixos herbívors en praderes de *P. oceanica* (**capítol** 4) combina els dos camps anteriors, i enllaça amb el creixent reconeixement que els herbívors poden tenir un paper rellevant en l'estructuració de les comunitats a través d'efectes indirectes. Els resultats del **capítol** 4 mostren com els herbívors, especialment quan actuen com a enginyers, poden produir efectes a nivell de tota la comunitat mitjançant la modificació de l'ambient creat per la vegetació, en el qual altres interaccions complexes poden ocórrer. A la nostra zona d'estudi, el canvi d'alçada de la capçada foliar produït per l'herbivorisme de *S. salpa* modifica la interacció depredador-presa entre l'eriçó de mar *P. lividus* i els seus depredadors. La interacció descrita és interessant pel fet que és un herbívor el que modifica el risc de depredació d'un altre herbívor i potencial competidor.

Passant a un terreny més especulatiu, al **capítol** 7, hem mostrat també que els atributs de paisatge, com la composició de la matriu d'hàbitats o la posició de les plantes a la pradera, poden influir en la pressió d'herbivorisme que rep un determinat feix de posidònia. És per tant possible, que l'heterogeneïtat espacial en el procés d'herbivorisme doni lloc a praderes amb una alçada de fulles variable, en funció d'atributs del paisatge i, per tant, doni lloc a un paisatge variable pel què fa al risc de depredació de les garotes que viuen entre els feixos de posidònia. Finalment, i enllaçant amb el **capítol** 8, és possible a més que aquesta heterogeneïtat espacial en l'herbivorisme, fins i tot tingui implicacions en la capacitat dels eriçons de resistir pertorbacions, ja que les praderes amb menor capçada foliar atenuen pitjor els impactes de les onades (Koch et al., 2006).

En resum, la modificació de la complexitat estructural de l'hàbitat per part de *S. salpa* (**capítol** 4), que a la vegada depèn dels atributs del paisatge (**capítol** 7), pot influir en els altres herbívors del sistema a través de dues vies almenys: primer, a través d'un augment en el seu risc de depredació a causa d'un parell de modificacions d'interacció (una mitjançant un canvi en un tret i l'altra per un canvi en l'ambient) (**capítol** 4); i segon, reduint la capacitat d'atenuació hidrodinàmica de la capçada foliar de la pradera, que els eriçons utilitzen com a refugi (**capítol** 8).

Així doncs, tot i que als objectius presentàvem el nostre sistema d'estudi com un sistema senzill, amb un sol productor, dos herbívors i un grup de depredadors, la imatge potser ara és més completa, però també força més complexa. Si una xarxa aparentment tan senzilla es pot arribar a complicar tant, és difícil d'imaginar la quantitat infinita d'interaccions entre espècies, comportament, paisatge i pertorbacions, en comunitats molt més complexes com les d'herbívors de les selves tropicals (ex. Morris et al., 2004).

Patrons de moviment dels dos herbívors principals

Al **capítol** 6, hem mostrat com el peix herbívor *S. salpa* és una espècie molt mòbil, que presenta unes grans àrees de campeig (*home ranges*) i amb capacitat per connectar hàbitats diferents i distants. Estudis anteriors, també amb telemetria acústica, ja assenyalaven una gran mobilitat a curt termini per aquesta espècie (seguiments d'aproximadament un mes); però el nostre estudi confirma que aquesta gran mobilitat es manté al llarg de l'any, cosa que fa de les salpes una de les espècies demersals més mòbils de les observades fins ara al Mediterrani. Aquesta mobilitat també s'observa a petita escala espacial i temporal, i al llarg de tot el període de seguiment, amb una majoria de peixos marcats que passen la nit a la zona profunda de la pradera, a prop del límit, movent-se a àrees més someres durant el dia (segurament per alimentar-s'hi). En conjunt, aquests resultats no concorden amb la hipòtesi de Verlaque (1990), segons la qual les salpes durant l'hivern migren de les zones someres on s'alimenten durant l'estiu, a zones més profundes per reproduir-se i refugiar-se. Tot i això, tal com hem vist al **capítol** **8**, en dies de tempesta els peixos es mouen de les seves zones preferides (on passen un percentatge més alt del temps, zones someres de pradera) a àrees més profundes, molt probablement per refugiar-se de l'efecte de les onades. Com que l'hivern és l'època de l'any amb més tempestes (veure Fig. 8.5a, **capítol** **8**), és lògic pensar que les salpes deuen passar més temps a aigües profundes durant l'hivern. Malgrat que aquest comportament es produeix cada vegada que hi ha temporals amb onades màximes per sobre els 2 m, els peixos retornen al seu rang de profunditats normals a les poques hores o dies. Per tant, aquestes modulacions del comportament en funció de les pertorbacions no es poden considerar migracions per reproduir-se.

A una altra escala, més rellevant pels patrons de moviment de les garotes, hem observat que els moviments d'aquests equinoderms en un ambient sense estímuls de depredadors i llum homogènia eren molt variables, però en general superdifusius (**capítol** **5**). Aquest tipus de moviments són òptims per a la cerca de recursos distribuïts a l'atzar i de forma esparsa (Bartumeus et al., 2005). També hem identificat que la presència a l'aigua de senyals químics d'un dels seus principals depredadors (un gasteròpode) produeixen un canvi en els patrons de moviment dels eriçons. En aquests casos, els *P. lividus* reaccionen amb moviments més ràpids i rectilinis que en situacions control. Aquest estudi, per tant, subratlla la importància de tenir en compte el risc de depredació a què estan sotmesos els animals al camp, ja que això pot determinar l'escala a la qual l'animal percep el paisatge. Aquest aspecte és de gran importància per a l'estudi de l'herbivorisme en comunitats de macròfits des d'un punt de vista de comportament i de paisatge (vegeu la següent secció i **capítol** **7**).

Interacció entre el moviment dels herbívors i els atributs de paisatge

El **capítol** **6** subratlla la importància d'analitzar el moviment animal a l'hora d'intentar entendre com els animals perceben el paisatge, per intentar examinar la connectivitat funcional de les espècies. En general, s'espera que animals molt mòbils percebin el paisatge com a més connectat que les espècies menys mòbils (Lima & Zollner, 1996). D'aquesta manera, la gran mobilitat observada en el peix herbívor *S. salpa* pot explicar per què, en el **capítol** **7**, no vam trobar diferències en els nivells d'herbivorisme entre taques de posidònia a prop o lluny de zones de roca. Els nostres resultats contrasten amb altres estudis, sobretot en zones tropicals, que han observat altes taxes d'herbivorisme en macròfits marins a prop d'esculls de corall (fins i tot amb la formació d'halos), però amb una clara disminució de la pressió d'herbivorisme a mesura que s'incrementa la distància respecte els esculls (Valentine et al., 2007; Vergés et al., 2011). Això suggereix que les espècies responsables d'aquests patrons d'herbivorisme, segurament presenten unes àrees de campeig molt limitades i una gran fidelitat a la seva àrea preferida. De fet, això és el que s'ha trobat per la majoria d'espècies de peixos demersals (Chapman & Kramer, 2000; Topping et al., 2005; Alós et al., 2012), amb unes àrees de campeig molt petites, especialment pels peixos d'esculls coral·lins (Welsh & Bellwood, 2012a,b).

La integració, en el **capítol 6**, de l'ús espacial i temporal dels hàbitats juntament amb la mobilitat observada de les salpes i la configuració del paisatge identifica aquest peix herbívor com a potencial organisme enllaç (*mobile link* en anglès). Mentre que estudis anteriors han demostrat separadament que les salpes són peixos herbívors clau en praderes de posidònia i en zones rocoses amb macroalgues (Prado et al., 2007; Vergés et al., 2009), els nostres resultats connecten l'ús dels dos hàbitats per part dels mateixos individus o bancs de peixos. De fet, considerem l'espècie *S. salpa* un organisme enllaç ja que és capaç de moure's entre hàbitats diferents, i com que és generalista, és capaç d'alimentar-se (i probablement de defecar, amb la conseqüent transferència d'energia) tant en zones de macroalgues com de posidònia. Això vol dir que, possiblement, proporciona la seva funció d'herbívor en els diferents hàbitats inclosos en el mosaic de paisatge sense la percepció de barreres entre ells. De fet, en el paisatge estudiat al **capítol 7** hem trobat que les salpes són capaces d'impactar fins a tres vegades més les praderes incloses en matrius de roca que en matrius de sorra. Aquest patró pot ser degut a les hipòtesis de complementació o suplementació de la dieta (Dunning et al., 1992), cosa que subratllaria encara més el paper de les salpes com a potencials organismes enllaç i la seva percepció del paisatge a una escala àmplia. De fet, un estudi amb papallones va trobar resultats semblants (Ricketts, 2001): per les papallones més vàgils les taques d'hàbitat separades per diferents matrius eren percebudes com a connectades, mentre que les papallones menys vàgils percebien les taques com a aïllades (Ricketts, 2001). En funció de la naturalesa, de la forma, del tipus de marges i de la disposició en el paisatge de les taques d'hàbitat s'espera que els organismes modifiquin els seus moviments, i que en conseqüència experimentin costs o beneficis en la seva eficàcia biològica. Per tant, la connectivitat funcional d'un paisatge és probablement depenent de l'espècie i del paisatge en qüestió (Belisle, 2005). Els nostres resultats demostren que per *S. salpa* la connectivitat funcional del paisatge és alta. De fet, en el **capítol 6** hem observat que aquesta espècie és capaç de fer excursions de llarga distància (aproximadament 2 km) fins i tot creuant grans extensions de sorra (hàbitat no favorable per les salpes), malgrat que la majoria d'animals generalment no creuen aquest tipus de marges tan contrastats (entre roca-sorra o pradera-sorra, coneguts com a marges durs) (Chapman & Kramer, 2000; Haynes & Cronin, 2006).

La connectivitat, entesa com el grau de permeabilitat entre els hàbitats d'un paisatge per a una espècie determinada, és segurament alguns ordres de magnitud més alta pels peixos herbívors *S. salpa* que no pas pels eriçons de mar *P. lividus* adults, ja que només es mouen de l'ordre de desenes de metres (Hereu, 2005), fins i tot a llarg termini (Palacin et al., 1997). A més, se sap que els eriçons adults es poden veure influenciats per barreres i marges de tipus dur (ex. pradera-sorra, Dance, 1987), cosa que limita encara més el seu moviment entre hàbitats. Malgrat tot, la seva dificultat per creuar marges durs possiblement no es deu només a una baixa capacitat de moviment, sinó també als riscos associats a creuar hàbitats amb poca complexitat estructural (ex. sorra nua) i per tant amb poca protecció contra els depredadors. A nivell de presa de decisions, diferents rangs de percepció i diferents capacitats de moviment poden significar major o menor risc de mortalitat (per depredadors, com hem vist al **capítol 5**; o a causa de pertorbacions, com hem vist al **capítol 8**) a l'hora de abandonar una taca per cercar noves àrees (Lima & Zollner, 1996). Pels *P. lividus*, aquesta limitada capacitat d'exploració del paisatge, pot ser en part compensada per la fase planctònica dispersiva que tenen els eriçons. De fet, al **capítol 7** no hem trobat diferències en l'abundància d'eriçons comparant taques a prop o lluny de zones rocoses, cosa que subratlla la importància de la fase planctònica d'aquesta espècie i del coll d'ampolla en el reclutament d'aquest equinoïdeu (Prado et al., 2012), ja que és improbable que els eriçons adults es moguin de les zones rocoses cap a les taques de posidònia creuant desenes de metres de sorra nua. En canvi, i com també hem vist al **capítol 7**, és molt possible que els eriçons creuin els marges tous (poc contrastats) entre les praderes de posidònia i les zones rocoses de macroalgues. De fet, està ben establert que els eriçons són capaços de creuar els marges entre zones rocoses i zones de pradera (Ceccherelli et al., 2009). Això es podria explicar per almenys dos motius: (i) denso-dependència en la migració, a causa de l'alta taxa de reclutament en zones de roca (Prado et al., 2012); o bé perquè (ii) els eriçons podrien necessitar complementar o suplementar la seva dieta amb fulles de posidònia (o dels seus epífits, Tomas et al., 2005a) creuant el marge roca-posidònia. Sigui quina sigui la raó, aquests aspectes podrien explicar encara més les taxes d'herbivorisme dispars entre les taques de posidònia en matriu de sorra i les taques en matriu de roca (**capítol 7**). De fet, el tipus de matriu s'ha observat que afecta el comportament dels organismes a l'hora de creuar un marge entre l'hàbitat i la matriu, així com les taxes de migració de diverses espècies (Ricketts, 2001; Haynes & Cronin, 2003, 2006). Aquest fet s'ha atribuït a diferències en el risc de depredació en funció del tipus de matriu en la qual es troba l'animal.

La connectivitat i l'escala de transmissió de les funcions ecosistèmiques

Com hem vist, els dos herbívors més importants del Mediterrani occidental, la garota *P. lividus* i el peix *S. salpa*, perceben el paisatge i responen a la seva configuració espacial a escales totalment diferents. Aquestes diferències de mobilitat entre ambdues espècies impliquen també diferents escales de transmissió de les seves funcions (ex. herbivorisme). Malgrat això, apart de l'escala i de la capacitat de moviment, la selecció dels hàbitats és també d'importància a l'hora de considerar els impactes de les espècies en el paisatge. Per exemple, tot i que *S. salpa* és una espècie generalista amb suficient mobilitat com per impactar diferents hàbitats, presenta una gran selectivitat per la posidònia (ex. en el nostre estudi del **capítol 6**, l'ús arribava al 90 % del temps). Això suggereix que aquests peixos deuen impactar més les praderes de posidònia que no pas les comunitats algals, cosa que enllaça amb els resultats obtinguts en altres estudis fets al mateix lloc (Tomas et al., 2005b; Hereu et al., 2008). Per tant, per a una comprensió completa de com es distribueixen els impactes dels herbívors en funció del paisatge és important no només entendre les taxes de consum, les dietes i les preferències de l'espècie en el sistema, sinó també el comportament dels herbívors. És important tenir en compte, doncs, el moviment i la selecció d'hàbitats en el temps i l'espai, al llarg de tot el mosaic de paisatge.

Per altra banda, les pertorbacions generalment operen en un rang limitat d'escales, és a dir, fins a una determinada profunditat, o en un tram de costa concret. Si espècies diferents dins un mateix grup funcional operen a diferents escales (si per exemple una espècie pot nedar a profunditats majors, o pot escapar-se amb moviments de llarga distància horitzontals), poden contribuir a reforçar mútuament la resiliència de la funció, i al mateix temps minimitzar la competència entre elles (Peterson et al., 1998; Elmqvist et al., 2003). Aquest fenomen s'anomena redundància a nivell d'escala i com hem apuntat al **capítol 8** és possible que es produeixi en la comunitat de macroherbívors mediterranis, donades les diferències de mobilitat i de comportament que hem observat entre *P. lividus* i *S. salpa* als **capítols 5** i **6**. Així mateix, la seva resposta diferencial davant les tempestes (**capítol 8**) es coneix com a diversitat de resposta i pot ser de gran importància pel manteniment de les funcions ecosistèmiques i la resiliència en ambients sotmesos a pertorbacions (Elmqvist et al., 2003). Tot i que al **capítol 8** no vam mesurar si la funció que proporcionen *S. salpa* o *P. lividus* (herbivorisme) va canviar a causa de la pertorbació extrema estudiada, és ben sabut que els dos herbívors són elements funcionals importants dels ecosistemes de macròfits marins mediterranis (Palacín et al., 1998; Vergés et al., 2009; Pagès et al., 2012). En el nostre sistema, donada la seva baixa riquesa d'espècies herbívores, la funció d'herbivorisme podria veure's erosionada fàcilment si els dos herbívors principals s'haguessin vist greument afectats per la tempesta. Malgrat això, fins i tot davant de grans pertorbacions de baixa freqüència, com el temporal de Sant Esteve del 2008, hem observat que almenys una de les dues espècies d'herbívors del sistema (*S. salpa*) seria capaç de mantenir la funció d'herbivorisme.

L'estudi no només de l'abundància o distribució de les espècies, sinó també de processos com l'herbivorisme, pot ser cabdal per enllaçar l'ecologia del comportament i l'ecologia del paisatge. Tal com mostrem al **capítol** 7, això és pel fet que els estudis d'abundància-distribució d'espècies poden no són suficients per a una comprensió completa dels processos ecològics en diferents paisatges, ja que àrees amb abundàncies d'herbívors similars poden presentar grans diferències en quant a taxes d'herbivorisme a causa de comportaments en les espècies d'herbívors dependents de la configuració del paisatge. Aquestes aproximacions diverses a l'estudi del funcionament dels ecosistemes pot ser fonamental per predir l'heterogeneïtat espacial en els processos ecològics, que en el cas de l'herbivorisme, poden influenciar en últim terme la producció primària, reciclatge de nutrients, èxit reproductor de la planta, interaccions biològiques i vies tròfiques del sistema. Els resultats d'aquesta tesi subratllen les perspectives que l'estudi del comportament i dels patrons de moviment d'espècies clau del sistema poden aportar en l'estudi de funcions ecològiques integrades en el paisatge.

Perspectives de futur

Les interaccions indirectes descrites al capítol 4 són realment comunes?

La xarxa d'interaccions que descrivim al **capítol** 4 és altament negativa per la població de garotes. De fet, en el nostre lloc d'estudi la població de garotes es troba pràcticament extingida (Romero et al., 2012). Tot i que és obvi que les salpes (*S. salpa*) modifiquen l'alçada de la capçada foliar de la majoria de praderes de posidònia de la costa catalana (Prado et al., 2007), són realment comuns els potents efectes indirectes que hem trobat en l'àrea protegida de les Illes Medes? Els resultats del **capítol** 4 fan pensar que a qualsevol herbei on les salpes redueixin l'alçada de capçada foliar per sota de 25 cm és possible trobar-hi aquests tipus d'interaccions. Per això seria interessant correlacionar les alçades de fulles de diferents praderes amb les abundàncies de garotes que presenten. Amb tot, l'abundància i biomassa de depredadors que trobem la zona de les Illes Medes és varis ordres de magnitud més alta que en la majoria de zones de la Mediterrània (Sala et al., 2012). Per tant, possiblement sigui difícil de detectar aquest tipus d'interaccions fora d'àrees marines protegides. En qualsevol cas, els nostres resultats emfatitzen que només tenir en compte les interaccions més òbvies pot ser perillós per a la gestió d'àrees protegides, ja que ens podem trobar amb resultats inesperats a llarg termini per la interacció entre diferents efectes indirectes. Això és especialment cert quan tant els depredadors com altres espècies iniciadores d'efectes indirectes es troben igualment afectades per les mesures de conservació, ja que poden interaccionar en retroalimentacions positives.

Moviments dels eriçons i estímuls lluminosos i químics

Al **capítol** **5** hem mostrat que els eriçons de mar responen a la presència de senyals químics de depredadors canviant els seus patrons de moviment, però que en canvi, no responen a diferències de llum. Durant el temps que durà l'experiment se'ns van acudir un bon nombre d'altres possibles estudis, que no es van poder dur a terme per limitacions de temps. Per exemple, ens interessaria saber si aquesta espècie respondria amb el mateix tipus d'estratègies d'escapada si la senyal química no fos d'un depredador bentònic lent sinó d'un depredador amb alta capacitat mòbil, com un peix. També ens agradaria saber si les garotes d'aquesta espècie (*P. lividus*) són capaces de detectar diferències de llum-ombra més contrastades que les utilitzades als experiments del **capítol** **5**, si buscarien refugi amb estratègies diferents en presència i absència de depredadors, com variarien els seus patrons de moviment en presència d'aliment, etc. Cadascun d'aquests experiments es podria complementar amb diferents mides d'eriçons i amb diferents nivells de sacietat. A més, seria interessant fer el salt del laboratori al camp, i d'experiments d'aproximadament una hora de duració, a experiments amb tot un cicle diari (24h) o més. Això implicaria alguns reptes metodològics, com per exemple fotografiar les garotes durant la nit (quan són més actives, Dance, 1987; Hereu, 2005).

Com es comporten les salpes que viuen en zones sense praderes de posidònia?

Al **capítol** **6**, hem mostrat la gran mobilitat que presenten les salpes i la seva capacitat per moure's entre hàbitats distants i diferents. Amb tot, també ha quedat molt palesa la seva gran preferència de les praderes de posidònia sobre tots els altres hàbitats. Per tant, la pregunta seria: com es comporten aquests peixos herbívors quan viuen en àrees sense praderes? Presenten en aquestes altres configuracions del paisatge el mateix tipus de cicles diaris que hem observat a la zona de pradera? O al revés, en un paisatge amb vàries praderes de posidònia dins la seva àrea de campeig, com es mourien? Serien fidels a una pradera en concret o repartirien el temps entre les diferents praderes?

Estacionalitat, herbivorisme en praderes de posidònia i patrons de moviment de *S. salpa*

Al **capítol 6** vam mostrar que les salpes presenten patrons de moviment similars al llarg de les diferents estacions de l'any. En canvi, l'herbivorisme a què estan sotmeses les fanerògames al Mediterrani és clarament estacional, amb un pic evident durant l'estiu i taxes molt baixes durant l'hivern (Prado et al., 2007). Si la salpa, que és el principal herbívor de les praderes de posidònia (Prado et al., 2007), no migra a zones més profundes a l'hivern (com diem al **capítol 6**), com es produeixen aquests patrons estacionals en l'herbivorisme? La nostra sospita és que l'activitat de les salpes podria ser altament dependent de la temperatura, com s'ha demostrat per altres espècies de peixos (Smith, 2008). La nostra experiència al camp durant aquests anys, ens indica que l'herbivorisme de les salpes no sol ser massa important fins que l'aigua arriba a uns 19-20ºC. Però, això és realment així? I en cas afirmatiu, els períodes amb altes taxes d'herbivorisme són, doncs, més llargs en la zona sud del Mediterrani (ex. nord d'Àfrica)? Així doncs, les praderes en aquestes zones estan sotmeses a altes taxes d'herbivorisme durant més mesos que a la zona nord del Mediterrani, amb les implicacions a nivell de planta i de tota la comunitat que això comporta (en la línia del **capítol 4**)? Encara estirant una mica més aquest argument, en un context de canvi climàtic (amb increments en la temperatura de l'aigua de mar) podem esperar un increment generalitzat en la pressió d'herbivorisme sobre els macròfits marins?

Una altra explicació per les menors taxes d'herbivorisme observades durant l'hivern serien canvis estacionals en les preferències alimentàries de les salpes, o l'eixamplament de la dieta de les salpes a l'hivern, com s'ha trobat per altres espècies de peixos (Horn, 1983). De fet, els nostres resultats en l'ús de l'hàbitat per part de les salpes (**capítol 6**) apuntaven en aquesta direcció, amb un augment en l'ús de l'hàbitat de roca durant l'hivern comparat amb pràcticament un 100 % d'ús de la pradera a l'estiu, tot i que no ho podem afirmar amb seguretat ja que només un peix continuava transmetent senyals durant l'estiu ($n = 1$). Per tant, estudis en aquesta direcció poden ajudar a entendre els patrons de comportament alimentari dels peixos herbívors al llarg de les estacions, cosa que pot tenir implicacions en com les espècies d'algues i de plantes marines s'adapten als nivells d'herbivorisme variable produïts per les salpes.

L'heterogeneïtat espacial en l'herbivorisme, que alhora depèn dels atributs de paisatge, provoca diferències en la producció de la planta o en l'èxit reproductor d'aquesta?

Les taxes d'herbivorisme en la posidònia d'algunes àrees del paisatge estudiat al **capítol** **7** estaven clarament per sobre de les taxes de producció en aquell moment de l'any. Tot i això, no vam trobar efectes d'aquest desequilibri en forma de reduccions en la producció primària, com sí que s'ha trobat en altres casos (ex. Gera et al., in press). Amb tot, és possible que tot i no haver trobat diferències en l'època de l'any en què vam fer les mesures (principi d'estiu), sí que es produeixin efectes en altres èpoques de l'any, com per exemple al setembre, després d'haver passat tot l'estiu amb una menor superfície fotosintètica (Gera et al., in press). De fet aquests desequilibris producció-herbivorisme fins i tot poden provocar un augment o disminució dels recursos destinats a la reproducció (flors), tal com s'ha vist en praderes sotmeses a grans taxes d'herbivorisme dins d'àrees marines protegides (Planes et al., 2011).

Els macroherbívors de les comunitats bentòniques del Mediterrani exhibeixen diversitat de respostes i compensació funcional davant de les pertorbacions?

Al **capítol** **8** hem trobat que *S. salpa* i *P. lividus* presenten respostes contrastades davant de grans pertorbacions en forma de tempesta: les salpes van resistir sense pràcticament pèrdues i en canvi el eriçons van perdre més del 50 % dels seus efectius en alguns casos. Creiem que això pot implicar que la funció de l'herbivorisme es mantingui a través de les salpes, fins i tot després de tempestes catastròfiques, i gràcies al fet que aquests peixos tenen mecanismes comportamentals i la capacitat de moviment suficient per escapar dels excessos d'hidrodinamisme. Malgrat els indicis que tenim, però, per testar realment si la funció es manté gràcies als mecanismes esmentats hauríem de comparar les taxes d'herbivorisme en diferents zones abans i després d'una gran tempesta. En aquest cas podríem realment comparar ambdues taxes i saber si la funció es manté i qui la manté.

En conjunt, estem convençuts que la unió dels diferents punts de vista que ens aporten l'ecologia del comportament i l'ecologia del paisatge poden resultar en una millor i més completa comprensió de funcions ecològiques com l'herbivorisme, en les quals almenys dues espècies interaccionen incloses en un paisatge determinat.

Informe dels directors

Els directors de la present tesi, la Dra. Teresa Alcoverro Pedrola i el Dr. Javier Romero Martinengo certifiquen que en Jordi Pagès Fauria ha participat activament en el desenvolupament de la feina associada a cadascun dels articles presentats en aquesta Tesi Doctoral, així com en la seva elaboració.
En concret, la seva participació en cadascun dels articles ha consistit en:

- Plantejament dels objectius.
- Planificació i execució dels experiments, tant pel què fa a feina de camp com al laboratori.
- Processat i anàlisi de les mostres obtingudes.
- Redacció dels articles i seguiment del procés de revisió dels mateixos.

Finalment, certifiquen que cap dels coautors dels articles presentats a continuació i que formen part de la Tesi Doctoral d'en Jordi Pagès Fauria utilitzarà implícitament o explicita aquests treballs per a l'elaboració d'una Tesi Doctoral.

La directora de la tesi
Dra. Teresa Alcoverro Pedrola
Científica titular
(CEAB-CSIC)

El director de la tesi
Dr. Javier Romero Martinengo
Professor titular
(UB)

Llistat d'articles publicats, enviats o en preparació

Capítol 4
Pagès, J.F., Farina, S., Gera, A., Arthur, R., Romero, J. & Alcoverro, T. (2012) Indirect interactions in seagrasses: fish herbivores increase predation risk to sea urchins by modifying plant traits. *Functional Ecology*, **26**, 1015-1023. **Factor d'impacte:** 4.567

Capítol 5
Pagès, J.F., Bartumeus, F., Romero, J. & Alcoverro, T. (en preparació) Sea urchin movement responses to predator cues and non-homogeneous light.

Capítol 6
Pagès, J.F., Bartumeus, F., Hereu, B., López-Sanz, A., Romero, J. & Alcoverro, T. (en revisió) Identifying a key herbivorous fish as a potential mobile link using Bownian Bridges: spatio-temporal habitat use. *Marine Ecology Progress Series*. **Factor d'impacte:** 2.711

Capítol 7
Pagès, J.F., Gera, A., Romero, J. & Alcoverro, T. (en preparació) Seascape attributes influence seagrass-herbivore interactions.

Capítol 8
Pagès, J.F., Gera, A., Romero, J., Farina, S., Garcia-Rubies, A., Hereu, B. & Alcoverro, T. (2013) The Mediterranean benthic herbivores show diverse responses to extreme storm disturbances. PLoS ONE, 8, e62719. **Factor d'impacte:** 4.092

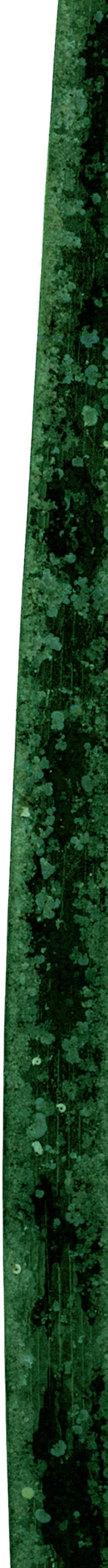
Alcoverro, T., Bartumeus, F., Farina, S., Garcia-Rubies, A., Gera, A., Pagès, J.F. Centre d'Estudis Avançats de Blanes (CEAB-CSIC), c/ d'accés a la cala Sant Francesc, 14, 17300, Blanes.

Alcoverro, T., Arthur, R. Nature Conservation Foundation (NCF), 3076/5, 4th Cross, Gokulam Park, 570 002, Mysore, Karnataka, India.

Hereu, B., Romero, J. Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona (UB), Av. Diagonal, 645, 08028, Barcelona.

López-Sanz, A. Institut de Ciències del Mar (ICM-CSIC). Passeig Marítim de la Barceloneta, 37-49. 08003 Barcelona.

A behavioural seascape ecology approach to macrophyte herbivory



2

General introduction

2.1 Ecosystem organization and the relevance of indirect effects

Ecological communities are governed by a complex network of interactions. The unravelling of the causal mechanisms underlying such structure has been a central issue in ecology (Paine, 1980; Polis, 1999). Quantifying the strength of these interactions is critical to understand how natural communities are organised and how ecosystems function. Network analysis has been widely used to decipher the structuring of communities and mechanistic models have been designed in order to assess population dynamics within the community (Ohgushi, 2008). Typically, these networks are based on direct trophic interactions (feeding), with the assumption that they are the major determinants of interaction strength. Increasingly, however, there is a growing recognition that indirect trophic interactions and other trophic and non-trophic interactions, such as ecosystem engineering, may also have fundamental community-wide implications (e.g. Pearson, 2010).

The publication 50 years ago of two seminal papers on the role of indirect interactions in food webs (Hairston et al., 1960; Paine, 1966) opened the field for new views in community ecology and originated an immense amount of research and debate. These early studies stressed the role of indirect interactions, which arise when the effect of one species on another requires the presence of a third (Wootton, 1994) (see Fig. 2.1). The realization that these interactions could have community-wide influences found large audience with the paper by Hairston, Smith & Slobodkin (1960), who proposed that indirect

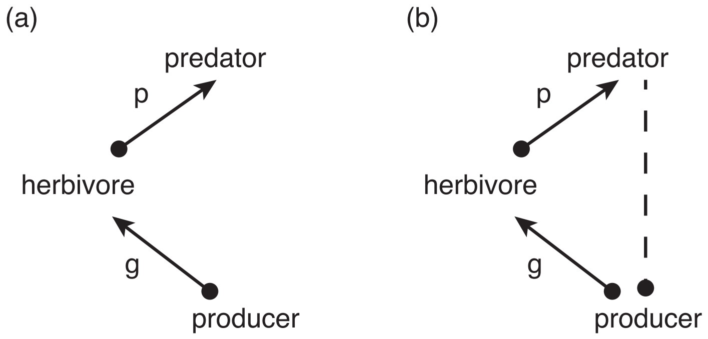


Figura 2.1: (a) Direct trophic interactions (feeding), p stands for predation and g for grazing. (b) Chain of direct interactions (solid lines) and indirect interaction (dashed line) of predators on producers through their effects on herbivores. This is an example of a trophic cascade. Note the arrows point the direction of the flux of energy.

trophic interactions could drive trophic cascades resulting in ecosystems that are relatively dominated by primary producers. *The green world hypothesis*, as it was called, postulated that producers, consumers and decomposers are all resource limited. According to this model, plant biomass accumulates because predators and parasites keep herbivore numbers so low they cannot deplete their plant resources. Experimental evidence on trophic cascades came early from the rocky intertidal with studies on keystone predation by Paine (1966) and further evidence provided by Estes & Palmisano (1974). Perhaps in part for these historical reasons, the discussion of indirect or 'cascading' effects in community ecology has remained largely top-down and predator-centric (Pringle et al., 2007; Pearson, 2010).

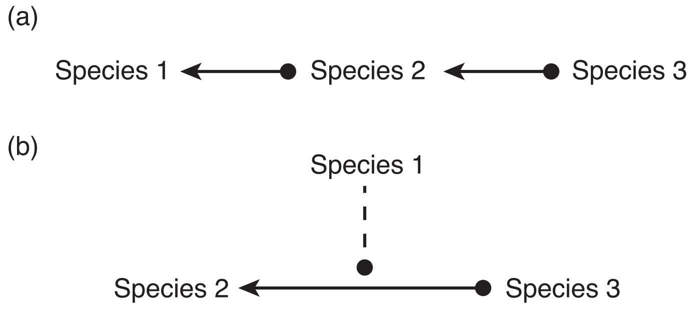


Figura 2.2: Schematic representation of the two different types of indirect interactions. (a) An interaction chain, where indirect effects arise by linking two or more direct effects together via a species involved in both interactions. (b) An interaction modification, where indirect effects arise when a species modifies the interaction between individuals of other two species. Note the arrows point the direction of the flux of energy.

More recently however, research has begun to focus on the mechanisms that determine the relative strength of trophic cascades across ecosystems (Strong, 1992; Shurin et al., 2002), the increasingly acknowledged role of herbivores (Ohgushi, 2005; Pringle et al., 2007) and the importance of other more nuanced and subtle indirect effects such as trait-mediated interactions (Werner & Peacor, 2003; Schmitz et al., 2004). In this latter case, the indirect effects are transmitted not within an interaction chain (Wootton, 2002) (Fig. 2.2a), such is the case of classical trophic cascades, where a species consumes another one, and this density effect cascades down to a third (for this reason they are also called density-mediated indirect interactions, DMIIs), but through an interaction modification (Wootton, 2002) (Fig. 2.2b). This modification may be a modification in the environment (see Fig. 2.3) or in a trait of the species involved (trait-mediated indirect interaction, TMII) (Fig. 2.4). This latter case of indirect interactions has been widely studied in recent years, with the focus on behavioural trait modifications: the so-called behaviourally-mediated trophic cascades (Schmitz et al., 1997; Werner & Peacor, 2003). One of the best known examples of this kind of interactions is the study with wolves (*Canis lupus*), elks (*Cervus elaphus*) and aspen (*Populus tremuloides*) in Yellowstone National Park (USA) (Ripple & Beschta, 2007) (see Fig. 2.4). In that case, the reintroduction of wolves in the Park had unexpected community-wide effects: aspen recruitment (*Populus tremuloides*), nearly absent until then, increased significantly specially in areas of high predation risk due to lethal but also non-lethal effects of wolves on herbivores, such as an increased elk vigilance. Other well-known examples are experiments quantifying the importance of lethal and non-lethal effects of predators on their prey. With creative experimental approaches like gluing predators' mouthparts, Schmitz (1998) demonstrated that in old field systems with an interaction web involving grasshoppers, plants and spider predators; predator indirect effects on plants were propagated by a trait-mediated effect (i.e. nonlethal effect) rather than by a density-mediated effect (i.e. actual lethal predation). The trait-mediated effect was a shift in grasshopper foraging behaviour in response to predation risk.

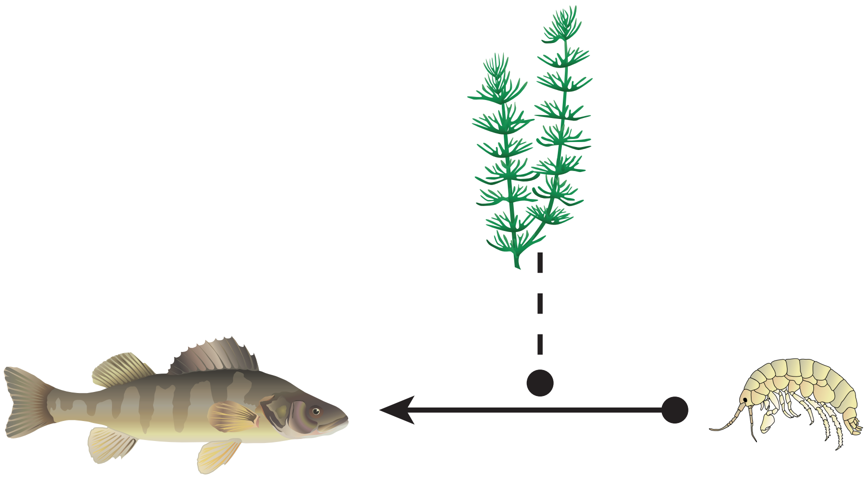


Figura 2.3: Example of an environment-mediated interaction modification described in Crowder & Cooper (1982). In the example, a macrophyte species modifies the environment (i.e. increases habitat structure), and thus changes the outcome of the predator-prey interactions between fishes and amphipods (the macrophyte provides shelter to the mesograzer). Note the arrows point the direction of the flux of energy. Symbols from the IAN, University of Maryland, Center for Environmental Science (`ian.umces.edu/imagelibrary/`).

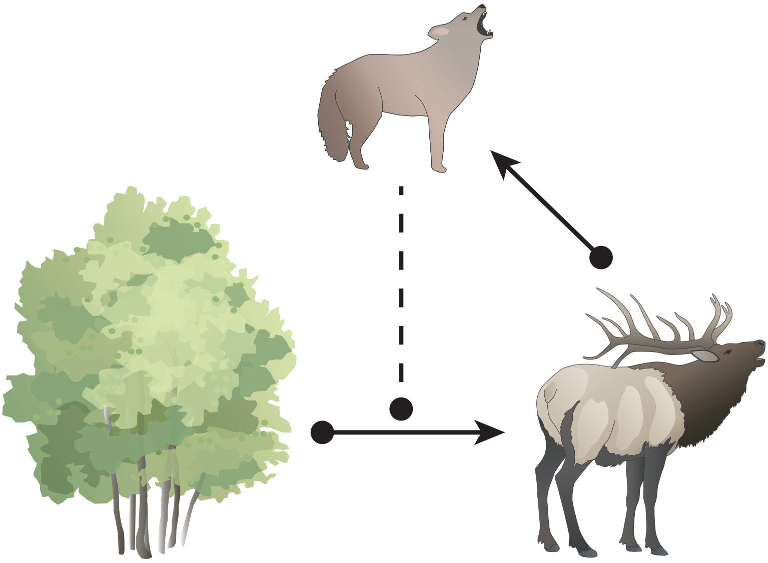


Figura 2.4: Example of a trait-mediated interaction modification. In this case, the trait changed is the behaviour of an herbivorous species, and is one example of the so-called behaviourally-mediated trophic cascades. In this case, described by Ripple & Beschta (2007), "wolves (*Canis lupus*) are saving Yellowstone aspens (*Populus tremuloides*)" with lethal but also with their non-lethal predator effects on elks (*Cervus elaphus*), i.e. increased vigilance, and thus less time allocated to foraging. Note the arrows point the direction of the flux of energy. Symbols from the IAN, University of Maryland, Center for Environmental Science (`ian.umces.edu/imagelibrary/`).

2.2 A behavioural approach to the study of biotic interactions

The examples above emphasise the perspective that behavioural ecology can add to the study of biotic interactions. Indeed, a behavioural approach to community ecology had seldom been used with key species until recently, and rather, behaviourists had been limited to the study of model species (Lima & Zollner, 1996) with limited ecological importance. This is because behaviourists and ecologists usually work and think at completely different scales and with different questions. Some behaviourists have thought of ecology "as setting the stage in which animals must perform their behaviour" (Krebs & Davies, 1993); and from the other side, until late 1990s, behaviour for most ecologists was a curiosity of each species of interest and a lateral issue to regard. However, behavioural ecology is concerned with functional questions about behaviour, namely how a particular behaviour pattern contributes to an animal's chances of survival and its reproductive success (Krebs & Davies, 1993), which may contribute to structure a given ecosystem and to influence ecosystem functioning.

The basis of a great amount of behavioural knowledge emerges from an economic view of animal decision-making. Indeed, in the seminal paper by MacArthur & Pianka (1966) their aim was to determine in which patches a species would feed and which items would form its diet if the species acted in "the most economical fashion". They postulated that an activity should be enlarged as long as the resulting gain in time spent per unit food exceeded the loss. Charnov (1976) expanded this theory with the idea that a predator should leave the patch it was at the moment when the marginal capture rate in the patch dropped to the average capture rate for the habitat (i.e. the so-called marginal value theorem, Fig. 2.5). And Emlen (1966) further added that animals should be more selective in their choice of foods when satiated or when food was common; more indiscriminate when starved or when food was scarce. This series of papers constituted the foundations of optimal foraging theory. However, in their first paper, MacArthur & Pianka (1966) already acknowledged that their theoretical formulation should be used as hypotheses against which testing empirical findings, rather than a formulation with predictive value. And as these hypotheses began to be empirically tested (e.g. Belovsky, 1978), new parameters had to be introduced into the models since animals not only trade for food but also for the risk of being preyed upon, among others.

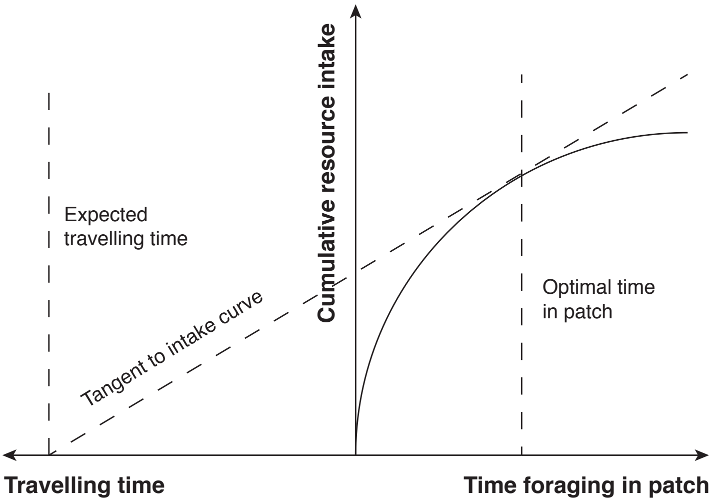


Figura 2.5: Schematic description of the Marginal Value Theorem, modified from Charnov (1976). The tangent to the resource intake curve that departs from the expected transit time value gives the optimal time spent in a patch.

Indeed, animal decision-making in risky environments has also been thoroughly studied within an economic point of view in behavioural ecology (e.g. Kacelnik & Bateson, 1997). And of great importance is risk assessment in predator-prey interactions. Behavioural responses of prey to predation include spatial redistribution, selection of specific habitat structure, temporal and spatial changes in activity patterns, increased vigilance and reduced foraging time, or changes in group size (Valeix et al., 2009). Indirect effects of predation are thus expected to have an impact on the fitness of prey individuals, and hence on prey demography. It would therefore be adaptive for prey to vary its behaviour in accord with perception of risk, and for this reason the detection of predator cues or alarm cues from conspecifics (Hagen et al., 2002) are important adaptations in the arms race between predators and prey. For example, visual and acoustic cues are widely used among vertebrates but they may not allow an organism to detect a predator over large distances, or the past presence of a predator (Kats & Dill, 1998). Conversely, chemical cues may be more reliable to assess the presence of predators while providing advance warning of danger (Nishizaki & Ackerman, 2005) since they are more integrative. Once the cue is detected a behavioural reaction should be triggered. In the case of predator detection, avoidance and/or escape (i.e. fleeing) and refuge seeking are amongst the most common responses and involve changes in the movement patterns of the species of interest. However, and since predator-avoidance, or shelter seeking behaviours incur in a cost in the form of lower access/use of resources, it would be a selective advantage to assess the need to escape or shelter in an accurate manner to optimally balance potential risks (predation) with potential gains (food intake) (Nishizaki & Ackerman, 2005).

2.3 Behavioural landscape ecology: the central role of animal movement

Optimal foraging models very early needed the incorporation of new ecological aspects, and as seen, predation risk was one of the obvious from the beginning. However, optimal foraging theory considered the presence of food in discrete patches within the landscape, and several models on the optimal travelling time, load capacity and distance to the nest were formulated in few years (e.g. Kacelnik, 1984; Schmid-Hempel et al., 1985). Most of these models dealt with animal movement only laterally, viewing it as a mere cost for the consumer. Nowadays, animal movement in heterogeneous landscapes is acknowledged to be a key aspect of landscape ecology. Nevertheless, as previously said, the scales of behavioural experiments to test optimal models are usually different to those of interest to landscape ecologists. Ecologists have identified animal movement, dispersal and habitat selection as particularly important determinants of the dynamics and spatial distribution of population in heterogeneous landscapes (Lima & Zollner, 1996) and behavioural ecologists have also long been interested in animal decision-making regarding movement, dispersal and habitat selection. Thus, a 'landscape conscious' behavioural approach would allow us to understand the sort of information available to an animal as it moves through its environment, and how this information is used in selecting a patch or habitat (Lima & Zollner, 1996).

Three key aspects of animal movement are relevant for sound behavioural landscape ecology: the perceptual range of the species of interest, the criteria for habitat and/or patch selection and the movement patterns of the species. These three behavioural aspects represent a direct link to landscape ecology, and in particular to functional connectivity, which, in this context, is defined as the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al., 1993). At the level of behavioural decision-making, different perceptual ranges and movement capabilities may mean elevated or lowered mortality risk (i.e. from predators, or from disturbances) when leaving a patch in search of new grounds (see Fig. 2.6, Lima & Zollner, 1996). In fact, organisms are expected to alter their movements, as well as experience differential fitness benefits or costs, according to the nature, form, and spatial arrangement of habitat patches and ecotones (Knowlton & Graham, 2010). For instance, the perception and response of individuals to landscape structure will be influenced by their state and their motivation, which will dictate their needs, how much risk they are willing to take in order to fulfil those needs, and possibly their specific destinations. It follows that the functional connectivity of a landscape is likely to be both species and context-dependent (Knowlton & Graham, 2010). Thus, perceptual range and movement capacity, for similar reasons, may be a determinant of landscape-level attributes such as connectivity, or the spatial scale at which an animal interacts with a given landscape (see Fig. 2.6, Dunning et al., 1992; Lima & Zollner, 1996; Zollner & Lima, 1997).

From the behavioural landscape ecology approach we have learnt that landscape attributes can strongly influence population structure and community composition, and generate variability in the abundance and distribution of different species according to their movement capacities and their habitat selection (Ricketts, 2001; Haynes & Cronin, 2003, 2004, 2006; Haynes et al., 2007; Haynes & Crist, 2009). However, the effects of landscape attributes on ecosystem processes have been largely disregarded, with most studies mostly oriented at assessing patterns of abundance-distribution. By working with key organisms, we may gain knowledge on ecosystem functioning, specially with the study of functions that can imply changes in habitat structure (Parsons et al., 2013), such as herbivory.

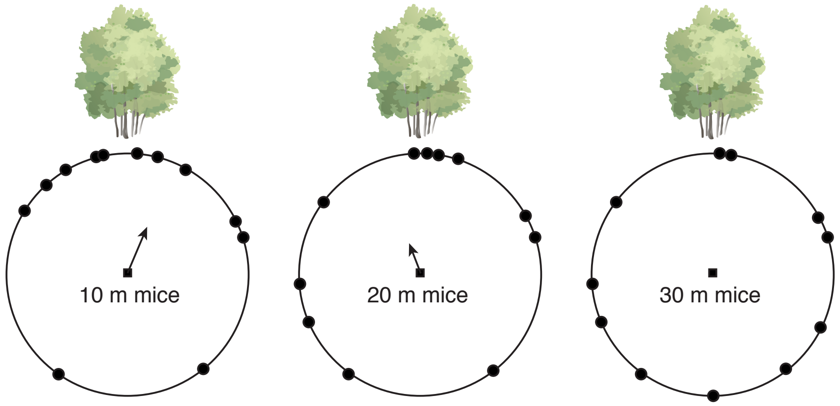


Figura 2.6: Perceptual range test to assess the scale at which animals perceive the landscape. In a pioneer experiment on perceptual ranges, Zollner & Lima (1997) tested the orientation of mice left on bare ground at 10 m, 20 m and 30 m from a forest edge. Mice left farther than 20 m were unable to orient towards the forest. The arrows represent significant orientations. Symbols from the IAN, University of Maryland, Center for Environmental Science (`ian.umces.edu/imagelibrary/`).

2.4 The importance of herbivory in ecological systems

Although the importance of predators in exerting substantial pressure at different levels of ecosystems is undeniable (e.g. Estes & Palmisano, 1974; Terborgh et al., 2001), the apparent neglect of herbivores as potential initiators of relevant indirect effects is troubling (Pringle et al., 2007). Increasingly, however, herbivores are being seen as potential strong interactors, since they have been shown to be able to engineer their habitat producing cascading implications in several ecosystems (Pringle et al., 2007; Huntzinger et al., 2008; Parsons et al., 2013).

In general, herbivores are known to influence plant primary production and nutrient cycling (Abbas et al., 2012; Gera et al., in press), to influence canopy structure and species interactions (McNaughton, 1984; Martin et al., 1989; Pringle et al., 2007) or community composition, diversity and biomass (Hobbs, 1996; Knapp et al., 1999) among others. Plant communities strongly modified by herbivores are known as grazing lawns, a term coined by McNaughton (1984) to describe terrestrial ecosystems dominated by large herds of migratory herbivores. The high biomass of herbivores in these ecosystems, typically the highest among terrestrial systems, results in herbivory being an important regulator of ecosystem processes with >50 % of primary production removed as compared to *c.* 9 % removal, on average, for other terrestrial ecosystems (Frank et al., 1998). Across grazing ecosystems 50-90 % of primary production gets passed up the food chain via herbivory (McNaughton, 1984; Cyr & Pace, 1993; Poore et al., 2012).

2.5 A behavioural seascape ecology approach to the study of herbivory in macrophyte communities

Several features of marine macrophyte communities make them interesting systems to test ecologically relevant questions on herbivory, from a behavioural seascape ecology perspective, namely: (i) the potentially high herbivory rates that structure these ecosystems, (ii) the fact that interactions are stronger in aquatic than in terrestrial systems, (iii) the fact that seagrass meadows and macroalgal stands are miniaturised seascapes with specific features (see below) and (iv) the limited knowledge about of their herbivores behaviour, largely understudied up to now.

In marine systems, it is accepted that, generally large herbivores such as fishes, sea urchins, turtles and dugongs have strong influence in primary production and community structure (Burkepile & Hay, 2006). This has been reported for coral reefs, seagrass beds, and kelp forests. Indeed, seagrass beds may be the best analogs to terrestrial grazing ecosystems (Burkepile, 2013; Gruner & Mooney, 2013), and herbivores can graze there more than 50 % of foliar production in some cases (Prado et al., 2007; Christianen et al., 2012; Kelkar et al., in press). Moreover, although the impact of herbivores on plants may be similar across terrestrial and aquatic ecosystems, the relative effects of top-down and bottom-up forces on herbivore populations shows fundamental differences between both (Burkepile, 2013). Trophic cascades appear to be more preeminent in aquatic than terrestrial systems (Strong, 1992). This may be caused by a relatively lower nutrient content in terrestrial primary producers compared to marine or freshwater producers (Cebrian et al., 2009). The subsequent nutrient imbalance in terrestrial herbivores may mean they are more often limited from the bottom-up than would be marine or freshwater herbivores (Hillebrand et al., 2009). Hence, it is important to study the strong interactions and positive feedbacks between aquatic plants and herbivores, since disrupting these connections may have severe consequences for ecosystem integrity (Burkepile, 2013). From the ecosystem structuring (i.e. control) and functional point of view, marine grazing ecosystems are thus appealing.

Underwater landscapes in the coastal zone (seascapes), as many other linear ones (such as those along rivers, or tops of mountain chains), naturally consist of relatively small patches of habitat isolated one another by matrices of different nature and with a tendency of being miniaturized (Goodsell et al., 2007). This type of structure makes them ideal candidates to study ecosystem processes at a scale that is relevant for the seascape (Nally & Quinn, 1998). However, it has also to be taken into account that seascapes have specificities. They are generally more connected than terrestrial systems, and this may mean that some seascape barriers could be less important, particularly during the larval phases (Tanner, 2006). However, hard edges also exist in the sea, particularly for the adult phase of animals with restricted movement patterns (e.g. echinoderms, Hereu, 2005). Therefore, herbivores do not distribute randomly across the mosaic of habitats, and often concentrate or dilute in space as a function of the seascape configuration, generating spatial heterogeneity (Pickett & Cadenasso, 1995; Vergés et al., 2011). Thus, the understanding of ecological functions at a landscape level seems also relevant.

A behavioural framework integrating animal movement, predation risk and resource acquisition has been useful across ecosystems for understanding herbivore foraging decisions, but in marine systems, herbivores' behaviour has been understudied. Only recently, the behaviour of megaherbivores such as turtles (Heithaus & Dill, 2002), dugongs (Wirsing et al., 2007) and coral reef fish species has began to be studied (Fox & Bellwood, 2011; Nash et al., 2012). This thesis is an attempt to link this movement behaviour to seascape patterns and eventually to the impacts on plant communities.

3

Objectives

Overall, this thesis aims at approaching macrophyte herbivory and community ecology from a behavioural seascape perspective. Our study system, the seascape mosaic of *Posidonia oceanica* (L.) Delile seagrass meadows interspersed with sand patches and rocky areas with macroalgal cover, is particularly useful to test sound ecological questions. In essence, the macroherbivore community is made up of just two key species, the sea urchin *Paracentrotus lividus* (Lam.) and the fish *Sarpa salpa* (L.). Both species are generalists and have been found to actively consume seagrass and macroalgae (Prado et al., 2007), profoundly altering habitat structure (Tomas et al., 2005b). Moreover, both animals differ in their mobility and in the predation risk they are subjected to, which poses interesting questions on how they will perceive, use, respond to and impact their surrounding seascape. *S. salpa* is a highly mobile species (Jadot et al., 2006) with few known extant predators, while the sea urchin *P. lividus* is a low mobility species (Hereu, 2005) with high rates of predation (Sala, 1997).

The thesis is structured in five chapters that focus on different aspects of community organization and ecological interactions (**chapter** 4), animal movement (**chapters** 5 and 6), animal risk assessment and behavioural responses to predation risk (**chapter** 5), habitat selection and connectivity (**chapter** 6), influence of seascape attributes on herbivore foraging and thus on herbivores' impacts on plants (**chapter** 7) and herbivores' responses in terms of population and behaviour to disturbances (**chapter** 8). Chapters derive from field manipulative experiments (**chapter** 4), field mensurative campaigns (**chapters** 6, 7 and 8) or controlled experiments in the laboratory (**chapter** 5).

The detailed objectives and the structure of the thesis are given below:

- In **chapter** 4, given the increasing recognition of the direct impact herbivory has to the functioning of seagrass ecosystems (Heck & Valentine, 2006), we aim at assessing whether herbivory can additionally influence other trophic processes, through indirect pathways. We examine how changes in seagrass structure caused by an herbivorous fish influence the predator-prey interaction between another herbivore and its predators.

- In **chapter** 5 we assess, under controlled conditions (in the laboratory), the behavioural responses in terms of movement patterns of one of the herbivores of the system (the sea urchin *P. lividus*) subjected to predator and light cues. We expect that sea urchins will respond by switching their movement patterns in the presence of predator cues and they will choose to move from light to shadows in the heterogeneous light experiment in the search of a refuge.

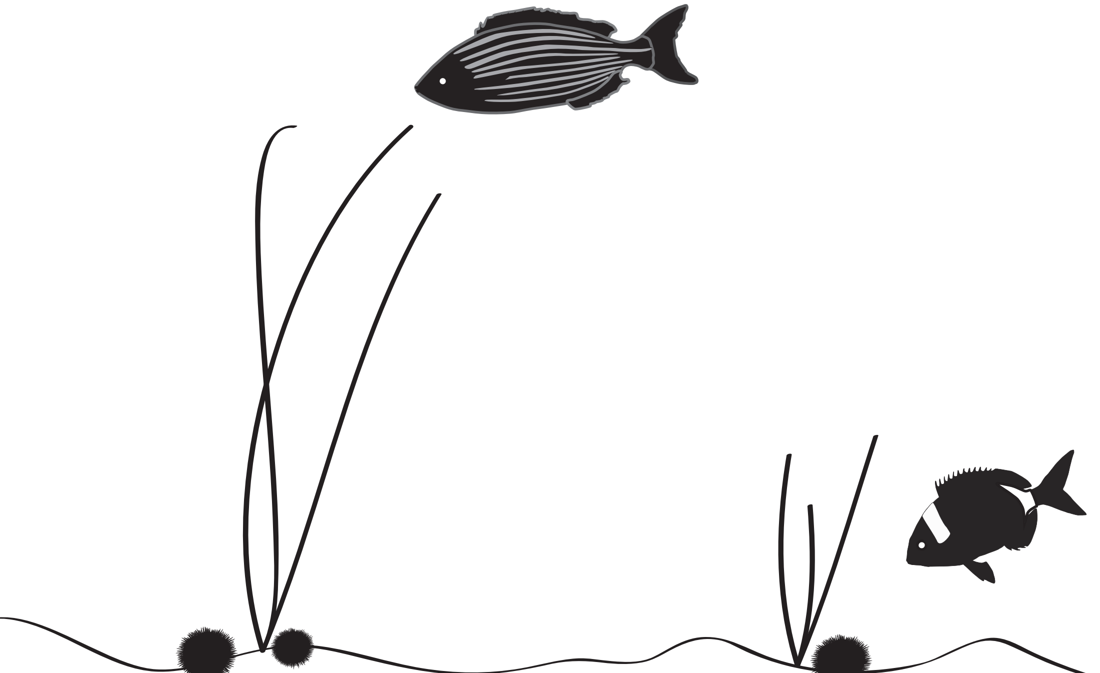
- In **chapter** 6 we focus on the movement patterns of the other herbivore of the system, the fish *S. salpa*. We want to determine whether these fishes are capable of connecting different distant habitats in a seascape mosaic composed of seagrass meadows, sand and rocky areas. Moreover, we characterise on a diel basis and over an annual period the strength of these links and the habitat use of this species across the seascape.

- The knowledge obtained in **chapters** 5 and 6, on the behaviour and movement ecology of the two key herbivores of the system, allows us to bridge seascape and behavioural ecology with herbivory patterns in **chapter** 7. In this chapter we argue that different seascape attributes will differently affect each herbivores' behaviour, and thus their herbivory rates, according to their mobility. We want to test if behind the multiple herbivore-mediated processes interacting with the seascape, there is any generalised attribute that can determine the spatial patterns of herbivory in seagrass-dominated seascapes in the Mediterranean, and try to elucidate some of the mechanisms behind them.

- In **chapter** 8 we finally assess whether the observed differences in mobility of both herbivores may also lead to distinct responses when faced with extreme storm disturbances.

4

Indirect interactions in seagrasses: fish herbivores increase predation risk to sea urchins by modifying plant traits



Resum

1. El paradigma dominant que considera que les comunitats ecològiques tenen un control superior mitjançant interaccions tròfiques directes, es complica per la comprensió cada cop més gran de les interaccions indirectes, que tot i més subtils, poden tenir sovint papers cabdals en l'estructuració de les comunitats. De fet, molt possiblement, les interaccions indirectes tròfiques i no tròfiques poden actuar alhora en un sistema, i la combinació dels seus efectes pot ser sinèrgica.
2. En aquest treball vam estudiar les interaccions indirectes que s'esdevenen en una xarxa tròfica relativament senzilla, que comprèn un sol productor, dos herbívors i una comunitat de depredadors. Específicament, vam analitzar si (1) l'herbívor principal del sistema, el peix *Sarpa salpa*, és capaç de modificar a través de l'herbivorisme un tret de la planta, l'alçada de la capçada foliar; i (2) si aquesta alteració de l'hàbitat, causada per l'herbivorisme del peix, pot implicar una modificació d'interacció mediada per l'ambient de la interacció entre l'altre herbívor del sistema, la garota *Paracentrotus lividus*, i els seus depredadors.
3. Aquestes hipòtesis les vam testar mitjançant experiments de camp amb gàbies d'exclusió d'herbívors (per avaluar la capacitat de *S. salpa* de modificar les praderes), i amb experiments de depredació amb garotes marcades en zones de la pradera amb diferent alçada de capçada foliar.
4. L'efecte de l'herbivorisme de *S. salpa* va ser molt significatiu. La capçada a les àrees d'exclusió d'herbívors va ser 3.5 vegades més alta que a les àrees control amb presència d'herbívors. A més, el risc de depredació de les garotes adultes fou de 4-5 cops més alt en les àrees amb les fulles més curtes (més herbivorisme) respecte a les àrees amb la capçada foliar més alta. En canvi, el risc de depredació de garotes juvenils no es va veure influït per l'alçada de fulles.
5. Els nostres resultats mostren com la depredació sobre un herbívor clau es pot veure afectada tant pel context ambiental en què es desenvolupa la interacció depredador-presa, com per l'acció d'altres herbívors que modifiquen els trets de la planta que crea aquest context ambiental. Ambdós processos actuen com a dues vies discretes que poden interaccionar generant patrons no linears en el control superior d'aquestes comunitats. Els herbívors, particularment quan actuen com a espècies enginyeres, poden alterar el risc de depredació d'altres espècies, ja que modifiquen l'estructura de l'hàbitat (cosa que pot tenir conseqüències en la disponibilitat de refugis, entre d'altres). Examinar aquestes interaccions indirectes és important no només per entendre el funcionament dels ecosistemes, sinó també de cara a la seva gestió i conservació.

Abstract [1]

1. The dominant paradigm of top-down control of ecological communities through direct consumption pathways is giving way to a more nuanced understanding of trophic interactions with the recognition that subtler indirect effects can often play an important role in structuring communities. Direct and indirect trophic and non-trophic processes could well be acting simultaneously within the same food web, and their overall effects may even interact with each other.
2. We studied indirect interactions in a relatively simple trophic system comprising a single producer, two herbivores and a guild of predators. In particular, we assessed if (1) the principal herbivore fish, *Sarpa salpa*, is capable of modifying a seagrass trait, canopy height, by grazing; and (2) if grazing-induced habitat alteration can trigger an environment-mediated modification of the interaction between herbivorous sea urchins *Paracentrotus lividus* and their predators.
3. We tested these hypotheses with field experiments including fish herbivore exclusion experiments (to examine the ability of *S. salpa* to modify seagrass habitats), and predation experiments using tethered sea urchins in a meadow with varying canopy heights (to test if habitat modification can mediate urchin predation risk).
4. The effect of *S. salpa* herbivory was highly significant. Canopy height in herbivore-excluded plots was more than 3.5 times higher than in uncaged control plots. In addition, adult sea urchin predation risk in the most highly grazed plots was 4 to 5 times higher than plots with higher canopy heights. In contrast, predation risk on juvenile urchins was not influenced by canopy height.
5. Our results show that predation pressure on a key herbivore can be modified both by the environmental context within which it finds itself, as well as by the actions of another herbivore that modifies the plant traits that create this environmental context. These act as two discrete pathways that interact in potentially non-linear ways, mediating top-down control in these ecosystems. Herbivores, particularly when acting as ecosystem engineers, may have the potential to mediate and increase predation risk, since they substantially modify habitat structure, with consequences for refuge availability, among others. Assessing these indirect interactions is not just important to understand the functioning of the system itself but may have important management and conservation consequences.

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[1] See original publication in Pagès et al. (2012).

4.1 Introduction

Ecological communities are structured by a complex interaction of their trophic elements, and understanding the causal mechanisms through which they operate has been a central issue in ecology (Paine, 1980; Polis, 1999). Quantifying the strength of these interactions is critical to understanding how natural communities are organized, and how they may respond to human interference (Bascompte et al., 2005). Interaction networks have been widely used to decipher the structuring of ecological communities (Polis & Winemiller, 1995; Ohgushi, 2008). Typically, these networks are built on direct trophic interactions (feeding), with the assumption that they are the major determinant of interaction strength. Increasingly, however, there is a growing recognition that indirect trophic interactions (e.g. trophic cascades) and other trophic and non-trophic interactions, such as ecosystem engineering, may also have fundamental community-wide implications (e.g. Pearson, 2010, and references therein). Direct and indirect trophic and non-trophic processes could well be acting simultaneously within the same food web, and their overall effects may even be synergistic (Jones et al., 1997; Golubski & Abrams, 2011).

Indirect interactions are powerful forces shaping ecological systems (Abrams et al., 1996). They arise when the effect of one species on another requires the presence of a third (Wootton, 1994). The realization that these interactions could have community-wide influences arose with the publication of the seminal paper by Hairston, Smith & Slobodkin (1960), who proposed that indirect trophic interactions could drive trophic cascades resulting in ecosystems that are relatively dominated by primary producers ("the green world hypothesis", as it was later called). Experimental evidence on trophic cascades came early from the rocky intertidal with studies on keystone predation by Paine (1966) and further evidence provided by Estes & Palmisano (1974). From then on, top down control, trophic cascades, and particularly, the study of tri-trophic food chains (TFCs, e.g. Bascompte et al., 2005) with a focus on predator-consumer-producer interactions, have dominated much of the research in community ecology. These have been termed 'interaction chains' and they arise by linking two (or more) direct effects together via a species involved in both interactions (Wootton, 1993, 2002). Given that linked direct effects often imply that densities of the intermediary species change, these interactions have also been described as 'density-mediated indirect interactions (DMIIs)' (Abrams et al., 1996).

While interaction chains are now relatively well studied, our understanding of other indirect interactions is much patchier, even though they may be as important in their ecosystem consequences. It has been shown, for instance, that when a species modifies the interaction between two other species (’interaction modification’ Wootton, 1993), it results in sometimes significant community-wide consequences (e.g. Kauffman et al., 2010). Species in an ecosystem can modify an interaction in at least two separate pathways. For one, a species can change the environmental context in which two other species interact, thereby modifying the interaction between them. These interactions have been labelled ‘environment-mediated interaction modifications’ (Wootton, 1993) and generally involve the participation of a foundation species (e.g. macrophytes reducing predation pressure on prey by providing hiding places Crowder & Cooper, 1982).

The second way, by which interaction modification may arise, occurs when one species changes the traits (i.e. a particular property of individual organisms) of another species, and these altered traits modify how the second species interacts with the third (Wootton, 1993). These so-called ‘trait-mediated indirect interactions (TMIIs)’ (Abrams et al., 1996) may be behavioural (in which there has been much interest in recent years, see Werner & Peacor, 2003, for a review), morphological, chemical, etc. Non-behavioural TMIIs have been recently reassessed, particularly for plant communities (Ohgushi, 2005; Pringle et al., 2007; Caccia et al., 2009; Pearson, 2010). Ohgushi (2008) argues that it is critical to account for the impact of these lesser explored interactions in analyzing interaction webs because they are likely more common and important in a wide variety of ecosystems than earlier considered, where they influence community structure and, ultimately, species diversity. Among them, nonlethal herbivory plays a central role in many indirect interactions (Ohgushi, 2005; Huntzinger et al., 2008; Pringle, 2008). In effect, herbivores can induce a great variety of responses on plants (Karban & Baldwin, 1997), some of which alter their traits resulting in trait-mediated indirect interactions (TMIIs).

Nonlethal herbivory is more frequent in terrestrial systems than in aquatic ones. This is because terrestrial herbivores usually feed on a part of the plant, whereas marine herbivores tend to consume the producer as a whole (e.g. zooplankton feeding on phytoplankton) or almost in entirety (e.g. sea urchins feeding on algae). Marine herbivores remove 51% of primary production on average, three times higher than their terrestrial counterparts (Cyr & Pace, 1993). Aquatic vascular plants represent an exception to this pattern, with removal rates similar to that of terrestrial vegetation (Cyr & Pace, 1993), making TMIIs much more likely in these systems. It has recently been shown that seagrasses can endure substantial herbivory pressure without lethal impacts (Prado et al., 2007; Planes et al., 2011). This, together with the fact that they are relatively simple systems (with few trophic links) makes seagrass meadows an excellent model system to explore indirect interactions. Evolutionarily derived from terrestrial plants, these species have several morphological adaptations (meristemic growth, protected rhizomes, mechanical defences, etc. Heck & Valentine, 2006), as well as physiological responses (compensatory growth, chemical defences; Vergés et al., 2008; Planes et al., 2011) to deal with the impacts of herbivory. Given the increasing recognition of the direct impact herbivory has to the functioning of these ecosystems (Heck & Valentine, 2006), it is vital to understand if herbivory can additionally influence other trophic processes through indirect pathways. We examined how changes in seagrass structure by an herbivorous fish influenced predation risk of other species. We tested this main question by attempting to separately assess the interactions present in the system: (i) Are fish herbivores capable of changing canopy structure, a seagrass trait? And if so, (ii) does this habitat structure modification affect another herbivore, a sea urchin, by triggering a change in its size-specific predation risk?

4.2 Materials and methods

Study system and experimental design

Posidonia oceanica (L.) Delile, an endemic seagrass species in the Mediterranean sea, forms extensive monospecific meadows along the coasts of the whole basin (Procaccini et al., 2001). It is a habitat-forming seagrass that provides shelter, food and substrate to a great number and variety of species (Mazzella et al., 1989; Francour, 1997; Martinez-Crego, 2008). It has two principal herbivores, the fish *Sarpa salpa* (L.) and the sea urchin *Paracentrotus lividus* (Lam.) (Prado et al., 2007). Both together have been reported to remove 50% of the annual plant primary production on average (Prado et al., 2007), despite most of this grazing is exerted by *S. salpa*, which is even capable of causing overgrazed patches in certain meadows (Tomas et al., 2005b). Trophic interactions in sea urchins, as in many age- or size-structured populations, change considerably with the stage of their life cycle as their vulnerability to particular predators varies (Sala, 1997; Hereu et al., 2005). The principal predator of juvenile *P. lividus* (<1 cm Test Diameter without spines, TD) is the labrid fish *Coris julis* while other species are of secondary importance (in order of relevance: *Diplodus sargus*, *Thalassoma pavo*, *Labrus merula*, *Diplodus vulgaris*; Hereu et al., 2005). For adult sea urchins, the sparid *Diplodus sargus* is by far the principal predator (Sala, 1997), although *Sparus aurata* has also been observed frequently preying on them (personal observations).

In this study we tested the existence of interaction modifications in seagrass meadows. We first assessed if the herbivore *S. salpa* can modify seagrass-traits through herbivory (trait-mediated interaction modification), which in turn, can modify the environment in which a predator-prey interaction takes place (between the sea urchins and their predators). To assess these interactions, we conducted two different experiments. The first was an herbivore-exclusion experiment to test the capacity of *S. salpa* to modify a morphological plant trait. The second one was designed to test the relationship between size-specific predation risk and plant traits. These experiments were conducted separately for different urchin size classes to test whether indirect effects detected were modulated by individual size.

All field experiments were carried out in the Medes Islands Marine Protected Area in the northern part of the Catalan coast (42° 2′ N, 3° 13′ E), where fishing has been prohibited since 1983 and fish abundance is very high (García-Rubies & Zabala, 1990; Hereu et al., 2005). The region has a large continuous *P. oceanica* meadow extending from 3 m to 14 m depth. Our experiments were conducted in summer, from August – September 2010, after a grazing peak that takes place in July – August (Prado et al., 2007) and corresponding to a seasonal peak in predatory fish activity (García-Rubies, 1997).

Experiment 1: Habitat structure modification

In order to test the first hypothesis ("herbivorous fishes are able to modify plant traits and habitat structure"), we established herbivory exclosures by fencing off areas of the seagrass meadow and compared these to the surrounding, exposed habitat. We deployed three exclosures in the meadow (*c.* 5 m depth) a month before the beginning of the summer grazing peak (i.e. in May 2010). Each cage consisted of a plastic mesh (cage size 150 × 150 × 100 cm, length × width × height) attached to four metal stakes, with a transparent nylon net on the top in order to protect the leaves and reducing light as little as possible. Mesh openings were sufficiently large (2 × 2 cm) to allow free movement of small fish and invertebrate mesofauna, but small enough to prevent the entrance of *S. salpa* fish. Cages were maintained for two months, during which natural leaf elongation was possible (Alcoverro et al., 1995), without suffering any losses to herbivory. The areas outside the cages were subject to intense *S. salpa* grazing. After two months, we compared habitat structure inside and outside the cages by measuring canopy height in the three experimental plots and three additional plots selected at random in adjacent areas of the meadow. To measure canopy height, we grabbed a large handful of plants, extended the leaves to their maximum height, and ignoring the tallest 20% of leaves, measured from the sediment to the height of the top of the remaining 4/5 of this bundle (80% of the leaves) (Duarte & Kirkman, 2001).

Experiment 2: Size-specific predation risk

In order to test the relationship between the size-specific predation risk and habitat structure we took advantage of the heterogeneous canopy height caused by the foraging behaviour of the herbivore fish *S. salpa*, which is known to produce small scale variability in meadow canopy height (i.e. on the order of tens of meters, see Tomas et al., 2005b). We used two complementary approaches, one categorical and one continuous. For the first approach, three different treatments (i.e. canopy height, conditions of sea urchins' exposure) were selected: 'mowed' (canopy height = 7 ± 1 cm); 'short' (canopy height = 26 ± 0.2 cm); and 'long' (canopy height = 47 ± 3 cm). Shoot density differed slightly between treatments (*P*-value < 0.05, Table 4.1). Shoot density was 490 ± 36, 589 ± 58 and 353 ± 10 shoots m^{-2} in mowed, short and long treatments respectively. A total of nine plots per category were chosen for each treatment and assigned randomly to three different sea urchin size classes (juveniles, $\leq$1 cm TD, young adults, 3-5 cm TD, and adults, >5 cm TD), resulting in a total of three replicate plots for treatment and urchin size. Each replicate (plot) was 150 $\times$ 150 cm in size, marked with metal stakes and with a plastic mesh surrounding its perimeter (20 cm height, 2 cm mesh openings). This was carried out to exclude potential benthic predators, since our objective was to assess only visual predation (i.e. by predatory fish). Although the fences could have drawn attention of visual predators to the urchins, potentially leading to artifactual predation rates, predation rates on this experiment were very similar (for a given canopy height) to those in the gradient-based continuous approach (without fences, see below and results). Plots were deployed in areas where rhizomes were covered with sand (to avoid the potential shelter rhizomes can offer to urchins, which would obscure our results; Farina et al., 2009). All plots were located at the same depth (*c.* 5 m), within tens of meters of each other, and within an area <20 $\times$ 20 m. We can therefore safely assume that every plot was exposed to the same predator fish community.

Sea urchins were collected from rocky substrates using SCUBA. For each experimental plot, 10 individuals of the same size class were pierced through the test with a hypodermic needle, threaded with monofilament line (nylon, 30 cm length) and tied to metal pegs. Each tethered urchin was uniquely identified with a number and placed randomly inside the plot, after verifying that the plot was free of bottom predators. While it is true that this is a rather invasive method, given that it implies the perforation of the test, most studies acknowledge very few detrimental effects (e.g. McClanahan & Muthiga, 1989; Aronson & Heck, 1995; Sala & Zabala, 1996). Indeed, tethering has been effectively applied to estimate predation rates on sea urchins in coral reefs, rocky reefs and seagrass habitats (McClanahan & Muthiga, 1989; Sala & Zabala, 1996; Shears & Babcock, 2002; Farina et al., 2009). We attributed sea urchin mortality to two sources: (i) predation by fish (characterized by missing sea urchin tests with an intact nylon loop or broken tests with firmly attached spines), and (ii) mortality due to manipulation-induced stress (intact test with loosely attached spines and faded test colour) (Bonaviri et al., 2009). Mortality due to the tethering manipulation itself was 2.5% (similar to rates found in other studies, e.g. Sala & Zabala, 1996). These individuals were removed from any further analysis. Urchins were monitored everyday to correctly attribute sea urchin mortality to one of the sources above.

In addition to the 27 treatment plots inside the meadow (three treatments × three urchin sizes × three replicates), three more plots (one for each size-class) were established on a bare sand patch as a time control, with the urchins totally exposed, to determine the endpoint of the experiment. Complete urchin predation in the sand patch took place within 5 days, after which pegs were removed and the remaining sea urchins counted in all plots.

For the gradient-based, continuous approach, 20 tethered urchins of each size class (namely: juveniles, young adults and adults) were distributed randomly (as independent replicates) on a large area inside the meadow (outside the fences, *c.* 250 m^2) with the aim of capturing the heterogeneity of canopy heights in which urchins might shelter. These urchins were visited daily to assess their survival time (in days). The total number of urchins per size class was $n = 30$, because, in addition to these 20 urchins, one urchin from each experimental and sand plot was also used in the analyses.

Statistical analyses

All calculations were performed using the open-source statistical software R (R Development Core Team, 2012).

For both categorical experiments, we treated each plot as the experimental unit with three replicates each. The variables canopy height and shoot density were evaluated with a one-way ANOVA with 'canopy height' as a fixed factor with 3 levels (mowed, short, long). The variables percent of juveniles preyed on, percent of young adults preyed on and percent of adults preyed on were evaluated with a one-way ANCOVA with 'canopy height' as a fixed factor with 3 levels (mowed, short, long) and including shoot density as a covariate (since it differed slightly between treatments, and may also affect sea urchin visibility and thus predation risk). Before analysis, data were tested for normality and homoscedasticity using the Shapiro-Wilk's and Bartlett's test respectively. The percentage of adults preyed upon was analysed with a nonparametric equivalent of ANCOVA (Quade, 1967), as this variable was neither normal nor homoscedastic. All other variables met the normality and ho-

Figure 4.1: Photograph showing the contrast between a heavily grazed area (foreground; canopy height around 20 cm) and a caged plot just after cage removal (background), with a canopy height more than 3.5 times longer than uncaged areas.

moscedasticity assumptions necessary for the ANOVA and ANCOVA. Whenever an ANOVA or ANCOVA was significant, a multiple range contrast test was applied (Tukey HSD) to determine treatment-specific differences.

For the continuous approach, data exploration revealed a non-linear relationship between sea urchin survival and canopy height. In order to describe this relationship we used a generalized additive model (GAM) (Hastie & Tibshirani, 1990) with a log link function (using the Poisson distribution) to evaluate how urchin survival time (in days) varied in relation to the explanatory variable canopy height. We used the LOESS smoother from the gam package in R (R Development Core Team, 2012; Hastie, 2011), which applies a weighted linear regression within a moving window of a specified size (we selected a span containing the 80% of data, as it was considered the optimal choice after residuals inspection; see Zuur et al., 2009).

4.3 Results

Experiment 1: Habitat structure modification

Canopy height was more than 3.5 times higher inside herbivore exclusion cages than outside (P-value < 0.01, Table 4.1). The average canopy height inside enclosures was 96 ± 4 cm, while outside, in the presence of herbivory,

Table 4.1: Summary of the different analyses performed. *P*-values correspond to those provided by an F-test.

Variable	Effects	d.f.	% variance	*P*-value
ANOVAS				
Canopy height	Treatment	2	97.01	**0.0000**
	Error	6	2.99	
Shoot density	Treatment	2	74.54	**0.0165**
	Error	6	25.46	
ANCOVAS				
Percentage of juveniles preyed	Shoots	1	-	n.s.
	Treatment	2	-	n.s.
	Shoots × Treatment	2	-	n.s.
	Error	3	100	
Percentage of young adults preyed	Shoots	1	-	n.s.
	Treatment	2	93.6	**0.0078**
	Shoots × Treatment	2	-	n.s.
	Error	3	6.4	
Percentage of adults preyed	Shoots	1	n.p.	n.s.
	Treatment	2	n.p.	**0.0061**
	Shoots × Treatment	2	n.p.	n.s.
	Error	3	n.p.	

d.f., degrees of freedom; n.p., nonparametric; n.s., non-significant.

canopy height was 24 ± 11 cm on average. Seagrass shoots outside the exclosures also showed clear signs of intense fish herbivory (see Fig. 4.1).

Experiment 2: Size-specific predation risk

The percentage of juveniles preyed upon was not significantly different between canopy treatments (Fig. 4.2a, Table 4.1). In contrast, a strong effect of the factor canopy height was detected both for young and adult sea urchins predation (Table 4.1). In both cases, predation in the lowest canopy treatment (i.e. mowed) was significantly higher than in the short and long leaves treatments (confirmed by Tukey HSD, see Fig. 4.2b,c). Specifically the percentage of predation on young and adult urchins was 4 to 5 times higher in mowed treatments than in long-leaved ones. The effect of the covariate shoot density was not significant for any of the size classes (*P*-values > 0.3 in all cases).

The continuous approach confirmed that juvenile survival was not influenced by canopy height: both linear and additive models failed at describ-

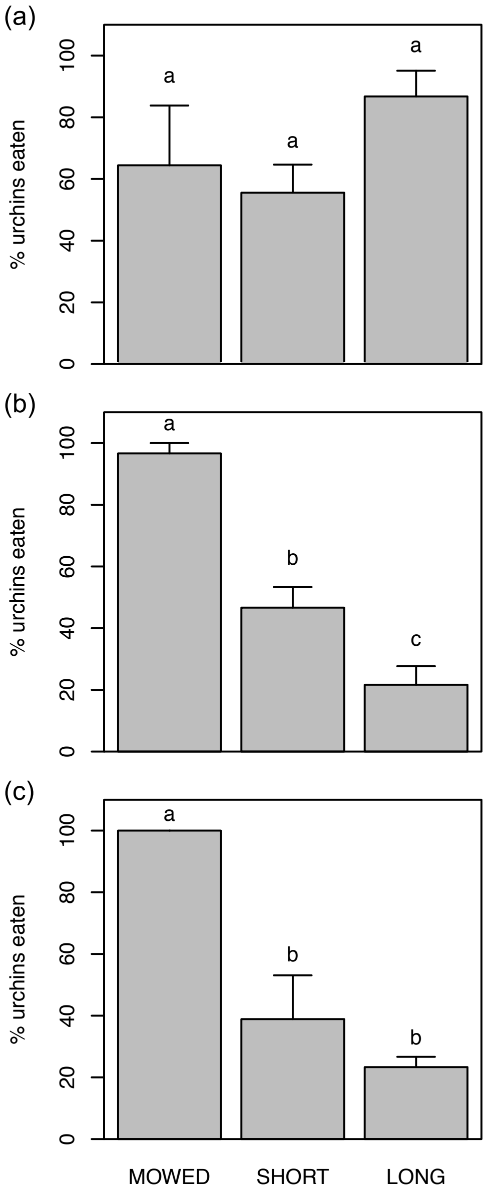


Figure 4.2: Percentage of (a) juveniles, (b) young adults or (c) adults preyed in each of the canopy height treatments (mean ± SE, $n = 3$). Bars labelled with the same lower case letter do not differ significantly according to Tukey HSD post-hoc test.

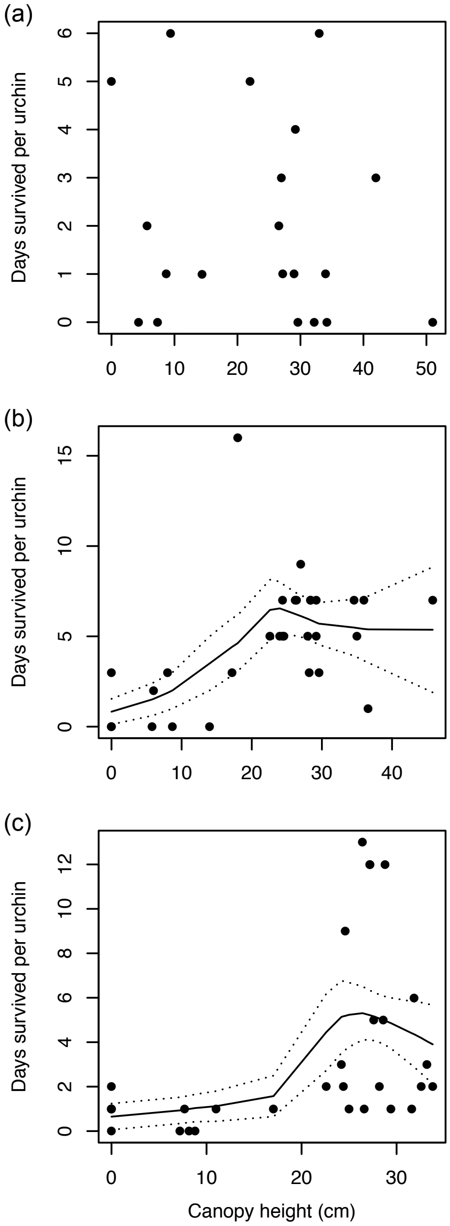


Figure 4.3: Scatter plots showing the relationship between (a) juveniles, (b) young adults or (c) adults survival time (in days) and their surrounding canopy height (n = 30). Solid lines in (b) and (c) correspond to the generalized additive model fitted values and dotted lines correspond to confidence intervals.

ing this relationship (Fig. 4.3a). In contrast, the survival of young adults and adults showed a non-linear relationship with canopy height that was successfully described by the generalized additive model (young adults: χ^2= 14.582, P-value = 0.0003; adults: χ^2= 17.806, P-value = 5.10^{-5}). For both, young and adult sea urchins, low survival times were observed in short canopy heights. Survival times increased with increasing canopy heights (gradually for young and abruptly for adults) until a plateau was reached for canopies above *c.* 25 cm (Fig. 4.3b,c). Adult survival time appears to decrease again after the plateau, although confidence intervals become wider and edge effects may occur at the margins of data sets (Zuur et al., 2009).

4.4 Discussion

Our results show that even in the relatively simple assemblage of the *P. oceanica* meadow, complex interactions exist that structure the community through at least two distinct indirect pathways. Intensive grazing by the herbivorous fish (*S. salpa*) modifies an important phenotypic trait (canopy height) of the foundational species and trophic resource (*P. oceanica*), and in doing so reduces available refugia for the sea urchin (*P. lividus*) against its dominant predators (Fig. 4.4). Uniquely, we show that predation pressure on a key herbivore can be modified both by the environmental context within which it finds itself, as well as by the actions of another herbivore that modifies the plant traits that create this environmental context. These act as two discrete pathways that interact in potentially non-linear ways, mediating top-down control in these ecosystems. These interactions do not affect smaller size classes of sea urchins, since they are still able to find sufficient refuge in grazed seagrass meadows. Taken together, our findings suggest that the prevailing tenet of top-down control that has dominated ecological theory after Hairston, Smith & Slobodkin (1960), may function in complex and often much more nuanced ways.

Clearly distinguishing interaction pathways is fundamental in modelling ecological systems (Werner & Peacor, 2003) since each pathway may imply very different consequences for overall system dynamics depending on the specific mechanism of action (e.g. interaction modification or interaction chain, trait- or environment-mediated). While the direct trophic pathways in our study are relatively simple (predation and herbivory), the mechanisms involved in the indirect interactions are complex: a species causes a phenotypic, trait-mediating change on a second species, which, in turn profoundly influences the environmental context of the predator-prey interaction occurring between two other species. Unusually, the indirect interactions we document are initiated by the principal herbivore in the system, and as such,

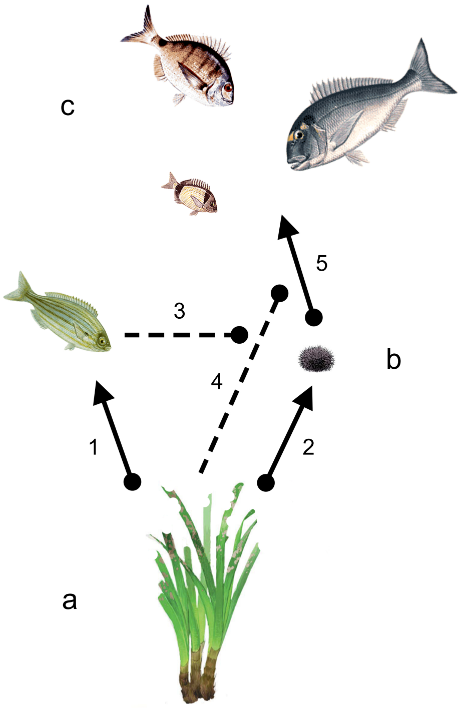


Figure 4.4: Interaction web including (a) the producer *Posidonia oceanica*, (b) the herbivores *Sarpa salpa* and *Paracentrotus lividus* and (c) a guild of predators: *Sparus aurata*, *Diplodus sargus* and *Diplodus vulgaris*. Each interaction is numbered: (1) and (2) represent herbivory (direct trophic), (3) corresponds to the interaction modification mediated by a trait change in the plant that modifies the environment-mediated interaction modification (4) of the predator-prey interaction between sea urchins and their predators (5).

is a unique reminder that species other than predators may play a greater-than-acknowledged role in shaping and modifying the system. Indeed, this type of indirect interaction is probably much more common than is recognized, particularly when initiators act as ecosystem engineers. For instance, ground squirrels, by constructing burrows and galleries, may reduce predation risk on other mammals (Waterman & Roth, 2007). In a context much more resonant with ours, Martin et al. (1989) indicated that complex higher order effects could arise in a marine system when blue crabs and a fish were stocked together through the effects of crabs on the abundance of an alga, which provides refuge for the prey of the fish. As with our study, this involves two interaction modifications, one trait- and the other environment-mediated. The role of ecosystem engineers is central to these examples, each influencing predation risk of other species in the system by modifying habitat structure.

This study supports a growing literature that, in recent years, have begun to re-evaluate the importance of habitat-modifying herbivores, in initiating powerful indirect effects (Gomez & Gonzalez-Megias, 2002; Lill & Marquis, 2003; Ohgushi, 2005; Bailey & Whitham, 2006; Pringle et al., 2007; Pringle, 2008). On the one hand, herbivores have long been known to play a significant role in reducing habitat complexity (e.g. Martin et al., 1989). At the same time, modifications in plant morphological traits can cause considerable functional changes in canopy characteristics, with cascading implications for the rest of the system (Huntzinger et al., 2008), including strong effects on predator-prey interactions (Crowder & Cooper, 1982; Swisher et al., 1998; Mattila et al., 2008; Farina et al., 2009). It is therefore natural to assume that any effects of consumers on plant density or structure could influence their vulnerability to predators (Werner & Peacor, 2003) even though few earlier studies have made these links explicit. In this study, we show that a herbivore fish can affect the predation risk of other herbivores (urchins) by modifying a plant trait that affects the environmental context in which the predator-prey interactions between urchins and their predators takes place. While we can not be certain of how important these interactions are in non-experimental situations, the effects of fish herbivory could potentially be as dramatic as a classical trophic cascade; long-term observations at our study site indicate that, without the structural complexity required for shelter, sea urchin populations at this site are headed for a potential collapse under predator pressure (Romero et al., 2012).

Interestingly, our study shows that interaction modifications may be subject to strong non-linear responses as well, with young and adult sea urchin survival plateauing beyond seagrass canopy heights of around 25 cm (see Fig. 4.3b,c). The functional form of these 'higher order interactions' (requiring higher-order, non-linear terms to model them in population equations, see Wootton, 2002) may take a variety of forms likely highly dependent on context-specific natural history. For instance, Wootton (1992) described a quadratic relationship in the way barnacles modify interactions between limpets and bird predators, reducing predation pressure at lower densities but increasing it as barnacle densities increased. In the meadows we studied, heavily grazed seagrass patches expose urchins to high predation risk; where grazing is less intense, patches have a higher canopy with more prey refugia. Beyond a certain canopy height (*c.* 25 cm in the present study), the increased length does not contribute further to survival since most young and adult sea urchins are probably already well sheltered from predation. This threshold value may be difficult to generalize, because it may depend on a suite of other structural attributes of the meadow (i.e. shoot density, presence of mat refuges; Heck & Orth, 2006; Farina et al., 2009). It is theoretically possible that high levels of sea urchin grazing could itself influence urchin predation risk, further complicating this interaction. However, the incidence of sea urchin herbivory is, in general, more limited compared to the pressure exerted by herbivorous fishes in *P. oceanica* meadows (Prado et al., 2007). More likely (although unexplored in our study) are behaviourally modified trophic interactions caused by changing structure, and indeed, *P. lividus* has been observed to modify its behaviour in the presence of predators (Hereu, 2005). While these so-called 'landscapes of fear' have typically been described as being driven by predator presence (see Schmitz et al., 2004, for a review), our study suggests they could just as well be mediated by a structure-modifying herbivore. If present, these behavioural modifications could additionally contribute to the observed non-linearity in functional responses.

Recent decades have seen an increasing emphasis on the role of top predators as controlling agents of ecosystems, and habitat management has focused almost exclusively on conserving these higher trophic functions, typically by managing the numbers of top predators inside protected areas or by enforcing hunting/fishing restrictions (Pinnegar et al., 2000; Sala & Sugihara, 2005). As our study shows however, if we only pay attention to the most conspicuous interactions, i.e. interaction chains (linkages of direct trophic pathways) we may encounter unexpected outcomes in the long term, such as an undesirable reduction or even local extinction of certain species. This is especially true when the predators (in our case predatory fishes) and the initiators of indirect interactions (in this case an herbivore fish) are equally affected by conservation measures, since they can interact with a positive feedback. In addition, when one of the species involved is an ecosystem engineer, increases in its numbers can have broad system-level ramifications (Jones et al., 1994). The dramatic decline and near extinction of sea urchin populations over the last decades in seagrass meadows in Medes Islands MPA where we conducted our field work (Romero et al., 2012), is most likely a result of the kind of complex interactions we describe in this study, and should serve as a powerful example of the perils of managing complex ecosystems against a single metric of success.

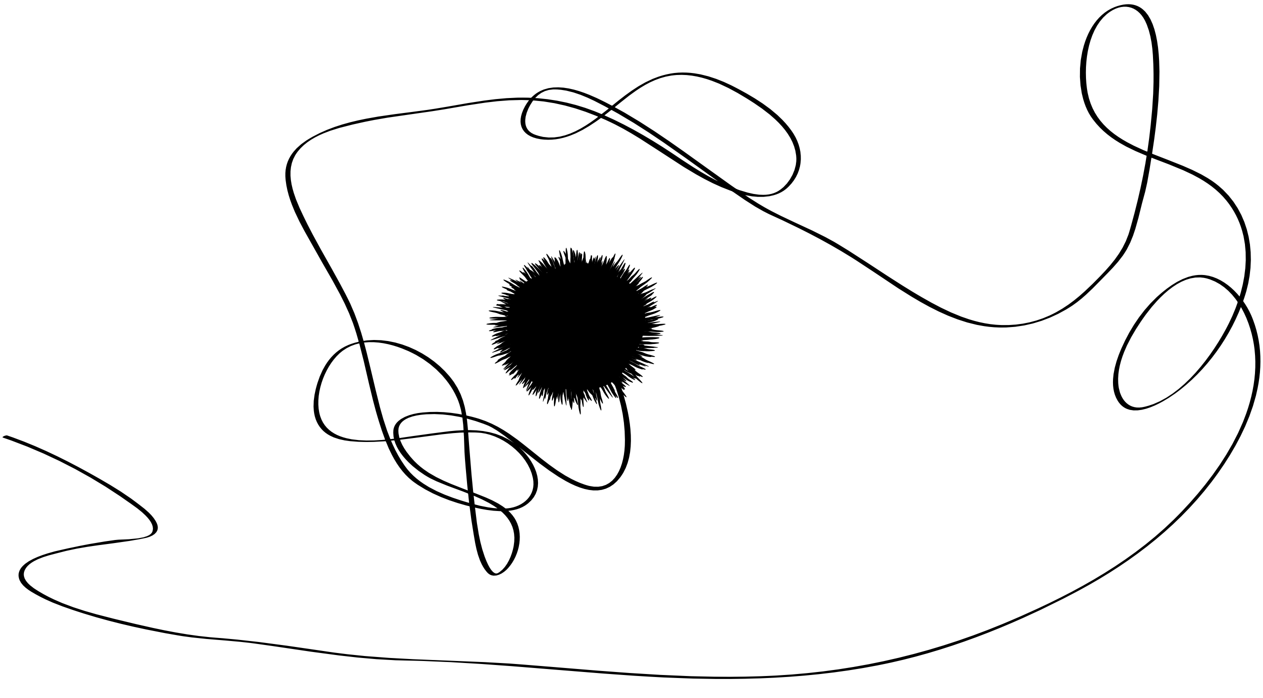
In conclusion, our study shows that intense grazing by a fish herbivore acting as an ecosystem engineer can have important implications for the entire community. These fish, by mediating an environment modification (through a change in the foundation species of the system), indirectly increase size-dependent predation risk on a potentially competing herbivore. Herbivores have to be recognized as potentially strong interactors capable not merely of initiating interaction cascades (as shown by Pringle et al., 2007) but also mediating behavioural cascades as a consequence of their ability to modify the habitat while acting as ecosystem engineers. At the same time, ecosystem-engineering species have to be recognized not just for the potential direct effects that they cause on the system, but also for the broad system-level ramifications of their actions, such as increases in predation to other species using the habitat. Bearing in mind that predation risk may not merely imply density effects to these organisms but also behavioural ones, the potential of this interaction to cause large-scale community-wide consequences is significant. Understanding how these complex interactions play themselves out in natural ecosystems may be vital in designing holistic and sustainable management plans for these ecosystems.

Acknowledgements

We are very grateful to Guillem Roca, Jordi Boada and Scott Bennett for field assistance. We also would like to thank Àlex Lorente and Medes MPA staff for interesting discussions and the processing of permits. Nachiket Kelkar and two anonymous reviewers greatly improved the manuscript with insightful comments. This research has been funded by the Spanish Ministry of Science and Innovation (projects CTM2010-22273-C02-01 and 02). The Spanish Ministry of Education supported JP (scolarship AP2008-01601). Fig. 4.4 was composed from pictures extracted and modified with permission from `www.gencat.cat`, Departament d'Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural (updated on 2007-10-31), Departament de Medi Ambient (updated on 2011-05-20), Generalitat de Catalunya.

5

Sea urchin movement responses to predator cues and non-homogeneous light



Resum

En general, s'espera que els animals modifiquin el seu comportament en funció dels estímuls que els envolten. Així com els patrons de moviment s'han estudiat sobretot des del punt de vista de la cerca d'aliment, el comportament de les espècies presa es pot veure molt influït pel risc de depredació. A més, és possible que existeixin alguns patrons de moviment que siguin millors per escapar dels depredadors que d'altres, i aquests moviments induïts per depredadors poden implicar alteracions en la distribució de les poblacions de preses. Els objectius d'aquest estudi van ser determinar en condicions controlades de laboratori, les respostes comportamentals (moviment) de garotes de l'espècie *Paracentrotus lividus*, una espècie clau en les comunitats de macròfits del Mediterrani, sotmeses a (i) aigua de mar control amb llum homogènia (experiment nul), (ii) un estímul químic difós d'un depredador amb llum homogènia (experiment amb depredadors), i (iii) a un estímul lluminós direccional amb aigua de mar control (experiment d'ombres). Vam quantificar el moviment dels eriçons mitjançant l'anàlisi de les trajectòries individuals amb funcions estructurals d'ordre q, cosa que ens va permetre d'identificar les propietats difusives de cada grup experimental. Així mateix, vam analitzar les velocitats mitjanes, la tortuositat de les trajectòries, i la uniformitat de la distribució inicial i final dels angles amb què es van orientar els diferents individus, gràcies a tests d'estadística circular. Els nostres resultats mostren com els *P. lividus* són capaços de detectar la presència de rastres químics de depredadors, i que almenys en absència de refugis, responen escapant de les senyals químiques passant de patrons de moviment superdifusius en ambients sense estímuls (experiment nul), a moviments pràcticament balístics amb major velocitat i menor tortuositat quan detecten els senyals químics del depredador. Aquests resultats documenten l'existència, en aquesta espècie, d'una resposta amb potencial valor adaptatiu. Per altra banda, i malgrat que aquesta espècie se sap que és capaç de detectar canvis de lluminositat, no vam detectar diferències en els patrons de moviment o d'orientació en funció de les diferències de llum. Els nostres resultats subratllen que el risc de depredació pot ser tan o més important en influir el moviment animal com la necessitat de cerca d'aliment, i que per tant, aquests aspectes s'haurien d'incorporar en l'anàlisi de les trajectòries al camp.

Abstract [1]

Animals are expected to switch their behaviour according to different stimuli. While movement strategies have been mostly studied within the context of foraging decisions, the behaviour of prey species is often induced also by predation risk. As it is for searching food, some movement patterns may be better to escape than others and such predator-induced movements may lead to significant alterations in prey population distribution. Our aims were to assess under controlled laboratory conditions the movement behavioural responses of the sea urchin *Paracentrotus lividus*, a key species in the Mediterranean subtidal macrophyte communities, subjected to (i) control water with homogeneous light (null experiment), (ii) a diffuse chemical stimulus from a predator with homogeneous light (predators experiment), and (iii) a directional light stimulus with control water (shadows experiment). We quantified movement based on q^{th} order structure functions analysis of individual trajectories, which allows us to identify the diffusive properties of each experimental group. In addition, we assessed their mean speeds and path tortuosity, and performed circular statistics analyses of the orientation of sea urchin initial and final bearings. Our results show that *P. lividus* can detect the presence of predator cues, and that at least in the absence of refuges, they flee from predator chemical stimuli by switching from superdiffusive motion in featureless environments (null experiment) into nearly ballistic movement patterns, with increased velocity and path straightness when predator cues are detected. This finding documents the existence, in this species, of a behavioural response with potential adaptive value. On the other hand, and although this species is known to be photosensitive, we did not detect differences in their movement patterns or orientation according to light differences. These results highlight that predation risk may be as important in determining animal movement patterns as feeding strategies, and should be taken into account when analysing trajectories in the field.

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[1] Pagès, J.F., Bartumeus, F., Romero, J., Alcoverro, T. **Manuscript in preparation.**

5.1 Introduction

Animals are expected to switch their behaviour as an optimal solution for changes in the scenarios they live (Bartumeus et al., 2010; Humphries et al., 2010). One of the most common expressions of behaviour modification is through changes in movement patterns. Yet a long-standing challenge is to understand the signals triggering such changes (Seuront & Stanley, in press).

Prey organisms exhibit a variety of adaptations for defending themselves from predators. These adaptations may be morphological (e.g. spines and armour), physiological (e.g. toxins), life-historical (e.g. delayed hatching) or behavioural (e.g. hiding, fleeing) (Kats & Dill, 1998). A first step for the behavioural ones is the detection of the risk that the presence or absence of certain cues implies. For many benthic marine organisms, visual (or phototactic) cues may be useful. They may not allow an organism to detect a predator over large distances (i.e. beyond their visual limits), or the past presence of a predator (Kats & Dill, 1998), but they may be useful to find a refuge (usually darker spots, such as holes, crevices, etc.). Conversely, chemical cues may be more reliable to assess the presence (present or past) of predators while providing advanced warning of danger (Nishizaki & Ackerman, 2005). Defensive adaptations that are mediated via predator chemical cues occur in terrestrial, freshwater and marine habitats (Kats & Dill, 1998). Once the cue has been detected, a behavioural reaction should be triggered. In the case of predator detection, avoidance and/or escape (i.e. fleeing) and refuge seeking are amongst the most common responses and involve changes in the trajectories or movement patterns of prey species. Since predator-avoidance, or shelter seeking behaviours, however, incur in a cost in the form of lower access/use of resources, it would be a selective advantage to assess the need to escape or shelter in an accurate manner to optimally balance potential risks (predation) with potential gains (food intake) (Nishizaki & Ackerman, 2005). However, while the study of escaping strategies has evolved a great deal in recent years, most studies have focused on the angles and time reaction of the response (see Domenici et al., 2011, for a review), but not on accurately studying escaping movement patterns. Exceptions are studies with planktonic species, such as dinoflagellates (Harvey & Menden-Deuer, 2012) and copepods (e.g. Hwang et al., 1994; Titelman, 2001; Bradley et al., 2013).

Echinoderms are a group of marine invertebrates with simple neuronal systems (e.g. Ruppert & Barnes, 1994), playing a very important role in marine benthic ecosystems. Indeed, some fields in ecological theory have evolved from seminal works involving key echinoderms (e.g. asteroids as keystone predators, Paine (1966); sea urchins as keystone herbivores leading to trophic cascades, Estes & Palmisano (1974)). They display several adaptations for sensing their environment and for detecting potential predators. Some species are known to display behavioural responses to light (Blevins & Johnsen, 2004; Yerramilli & Johnsen, 2010). Several species are also known to display chemosensory abilities to detect predators (Scheibling & Hamm, 1991; Vadas Sr & Elner, 2003; Manzur & Navarrete, 2011), or to detect cues from damaged conspecifics (Parker & Shulman, 1986; Hagen et al., 2002). However, the responses to these stimuli in terms of movement are not generally assessed, although it is known that some sea urchin species decrease their mobility and increase the time allocated to sheltering when living in marine protected areas, i.e. with high predator biomass, compared to unprotected areas, i.e. with low predator biomass (Hereu, 2005).

As a first insight into the ecological relevance of movement behaviour in such an important group of organisms, we attempt here an assessment, under controlled conditions, of the movement behavioural responses of sea urchins subjected to (i) control water with homogeneous light (null experiment), (ii) diffuse chemical stimuli from a predator with homogeneous light (predators experiment), and (iii) directional light stimuli with control water (shadows experiment). We expected that sea urchins would respond by switching their movement patterns in the presence of predator cues and that they would choose to move from the light to the shadow in the heterogeneous light experiment in the search for a refuge. We performed q^{th} order structure functions analysis of individual trajectories in order to identify the average diffusive properties of each experimental group. In addition, we assessed their mean speeds and path tortuosity and performed circular statistics analyses of the orientation of sea urchin initial and final bearings. We used as a model species *Paracentrotus lividus* (Lam.), the edible sea urchin, widely recognised as a key species in Mediterranean subtidal macrophyte communities (Sala et al., 1998; Prado et al., 2007; Hereu et al., 2008).

5.2 Methods

Sea urchin collection and care

For each round of trials around 30 adult *Paracentrotus lividus* sea urchins (all around 3-4 cm test without spines diameter) were collected near Blanes (41° 40′ N 2° 48′ E; 41° 44′ N 2° 57′ E). They were kept in aquariums with the same light cycle and similar temperature as those of the field and with a continuous flow of seawater (mean salinity 35.8 ± 0.2 psu, mean temperature 23.1 ± 0.5°C). Because preliminary tests showed that even moderately unhealthy or starved sea urchins displayed very different movement patterns from those fully healthy, they were tested as soon as possible after collection (after 1 day of acclimation and within a week) and they were given plenty of food during the acclimation (a mix of seagrass leaves and macroalgae).

Experimental arena

The experimental arena consisted of a metallic circular tank (3 m diameter) lined with plastic. A diffuse fluorescent light source was placed above the arena resulting in downwelling irradiance at the arena floor of 8 µmol photons m^{-2} s^{-1} (measured with a HOBO, Amplified Quantum Sensor, model SQ-200, Onset Computer Corporation, USA). A Nikon D80 (Nikon, Japan) digital SLR camera with a 17 mm lens was mounted 3 m above the arena. We set it in time-lapse mode with a 30 seconds interval between each image, since preliminary testing had shown that this time interval allowed sea urchins to move approximately one body length between photographs.

Experimental procedure

The arena was filled (water column = 20 cm) either with filtered seawater of the same temperature and salinity as that of the holding aquariums (i.e. control seawater: null and shadow experiments,) or with control seawater plus 6 *Hexaplex trunculus* (L.) (i.e. water conditioned with a predatory gastropod: predator experiment) that stayed there overnight and were returned to their holding aquariums just before the beginning of sea urchin movement experiments. Control seawater or predator-conditioned seawater was changed (i.e. the arena was refilled) on each day of trials, and the arena cleaned after each trial. Each sea urchin was tested once for the null (homogeneous light with control seawater) and predator experiments (homogeneous light with predator-conditioned seawater) and three times in a row for the shadow experiments (non-homogeneous light with control seawater; once with the shadow at 90°, at 180° and at 270° relative to magnetic east). The three different shadow positions allowed us to control for any spurious orientation to other features of the arena or room. The urchin was first placed in the centre of the arena (with half of the test in the light and half in the shadows, for the shadow experiments), the lights were turned off for 10 seconds, then on and the camera started to take photographs every 30 seconds. We considered the trial had ended when a sea urchin had approached less than 10 cm from the vertical walls of the edge of the arena. After the trial, the lights above the arena were again turned off, the arena was scrubbed to reduce the potential for trail following and the sea urchin was either returned to the aquariums and never used again (for null and predator experiments), or for the shadow experiment, placed again in the centre of the arena for the additional two trials (with the shadow randomly moved to another bearing). A final number of 29 sea urchins were used for the null experiment, 21 for the predator experiment and 16 for the shadow experiment.

Image and trajectory analysis

A total of 15 236 images were taken. These were transferred to a computer and the x and y coordinates of each urchin were obtained by means of a Matlab script (kindly provided by L. Salvador) using the image processing toolbox. These coordinates were then transferred to R (R Development Core Team, 2012) and analysed with the package adehabitatLT (Calenge et al., 2009), which computes the increments in the x and y axis for each step of the trajectory (time interval = 30 seconds). These increments were used to calculate the initial (after the first 5 time-steps) and final angles (at the end of the trajectory) of each sea urchin with the arctangent. For the shadow experiment, the mean absolute bearing vector for a given sea urchin (the circular mean of the three trials) was calculated following Batschelet (1981) and Yerramilli & Johnsen (2010). We also calculated the average bearing vector corrected for the position of the shadow (referred hereafter as the shadow-corrected bearing) following Yerramilli & Johnsen (2010). Finally the average absolute and shadow-corrected angles were calculated with the arctangent of the y and x components of the vectors (Batschelet, 1981). This procedure was done for the initial and final angles.

We also analysed each individual trajectory to assess the movement behaviour of sea urchins in each condition. We used a general numerical approach based on the analysis of the q^{th} order long-range correlations in sea urchin displacements (see Seuront & Stanley, in press). Specifically, the module of increments of two-dimensional displacements is $\| \Delta X_\tau \| \equiv \sqrt{(x_{t+\tau} - x_t)^2 + (y_{t+\tau} - y_t)^2}$, where τ is the temporal increment, and (x_t, y_t) and $(x_{t+\tau}, y_{t+\tau})$ are respectively the positions of a sea urchin at time t and $t + \tau$. The moments of order q ($q > 0$) of the module of two-dimensional displacements depend on the temporal increment τ as

$$\langle \| \Delta X_\tau \|^q \rangle \sim \tau^{\zeta(q)}$$

The exponents $\zeta(q)$ were estimated as the slope of the linear trend of $\| \Delta X_\tau \|^q$ vs. τ in log-log plots (see appendix in Seuront & Stanley, in press). The moment function $\zeta(q)$ characterises the statistics of the random walk $\| \Delta X_\tau \|$ of *P. lividus* regardless of the scale and intensity (Seuront, 2009), and the related diffusive properties. Low and high orders of moment q characterise respectively smaller and more frequent displacements, and larger and less frequent displacements. The mean ($q = 1$) and the variance ($q = 2$) are not sufficient to quantify the behaviour of probability density functions. A complete description requires an infinite number of moments (of q's), hence the use of the whole function $\zeta(q)$ instead of a single exponent (Seuront & Stanley, in press). Each individual-level function $\zeta(q)$ was plotted along with the results for the Brownian motion (dashed line in plots) and ballistic motion (dotted line in plots). With this analysis we could assess the nature of the diffusive properties of sea urchin trajectories, and discern whether these were ballistic, superdiffusive, Brownian or subdiffusive.

Finally, we calculated for each sea urchin (each individual was a replicate) the mean sea urchin speed and a measure of path tortuosity, the straightness index. The straightness index (I_s) is a dimensionless number that ranges from 1 (maximum straightness) to 0 (maximum tortuosity). It is the ratio of the Euclidian distance between the initial and final point of the trajectory, and the sum of Euclidian distances between pairs of points separated by a given time. Since different windows of time result in different I_s (Benhamou, 2004), we calculated this index for a range of window widths. Comparisons between experiments were consistent regardless of window width and, thus, we only present here the I_s for a window of 1 step (30 seconds).

Data analysis

We assessed the randomness of the distribution of the absolute initial and final angles obtained from each experiment (null, predator, shadow) with the Rayleigh test. Additionally, for the shadow experiment we also ran the Rayleigh test for the initial and final distribution of the shadow-corrected angles. Assumptions were tested and fulfilled in all cases (unimodality and von-Misses distribution).

The significance of the differences between the empirical values of the function $\zeta(q)$ was analysed with an ANOVA, considering as a dependent variable the 'slope of the exponents of the q^{th} order moments ($\zeta(q)$)' as a function of the fixed factor 'experiment' (3 levels: null, predator, shadow). Each individual sea urchin was considered a replicate. Normality and homoscedasticity were assessed with the visual inspection of plots of residuals vs. fitted values, and fulfilled.

Finally, mean sea urchin speed and the straightness index were analysed with an ANOVA to assess whether there existed differences in these variables between experiments (fixed factor, 3 levels: null, predator, shadow). Normality and homoscedasticity were assessed (visual inspection of residuals) and fulfilled for mean sea urchin speeds, but we arcsine-transformed the straightness index since it departed from normality (as in Domenici et al., 2003).

Table 5.1: Summary of the different Rayleigh tests performed to assess whether the distribution of initial and final angles was uniform for each experiment.

Response variable	n	Test statistic	P-value
Null initial angles	29	0.16	0.46
Null final angles	29	0.21	0.29
Predator initial angles	21	0.23	0.32
Predator final angles	21	0.19	0.48
Shadow-corrected initial angles	16	0.18	0.62
Shadow-corrected final angles	16	0.20	0.52

n: number of replicates

5.3 Results

As expected, *Paracentrotus lividus* sea urchins displayed a uniform distribution of both the initial and final angles for the experiments without stimuli (null) and the experiment with a diffuse chemical stimulus (predator experiment) (Table 5.1, Fig. 5.1). However, although we expected a response to a directional light stimulus in the shadow experiment, both final and initial absolute and shadow-corrected angles followed a uniform distribution (Table 5.1, Fig. 5.1). Neither directedness nor asymmetries in the distribution of angles were detected.

The scaling exponents of the q^{th} order moments ($\zeta(q)$) allowed us to distinguish between Brownian (Fig. 5.2a) and ballistic (Fig. 5.2c) sea urchin movement, depending on whether the empirical $\zeta(q)$ were closer to the limiting Brownian (dashed, lower line, Fig. 5.2b) or ballistic type of motion (dotted, upper line, Fig. 5.2d) respectively. Regarding the diffusive properties of the motion, lines falling between the theoretical ballistic and Brownian outputs are superdiffusive, and those below the dashed line of Brownian motion are subdiffusive. For the null and shadow experiments, there was a wide variability of individual behaviours, ranging from subdiffusive to superdiffusive and nearly ballistic (Fig. 5.3a,c). However, in general, sea urchins experiencing predator chemicals consistently switched these patterns into a more ballistic behaviour with less inter-individual variability (Fig. 5.3c). These differences were significant (Table 5.2) with the nature of sea urchins' trajectories in the null and shadow experiments being on average superdiffusive, compared to a nearly ballistic behaviour for sea urchins experiencing background predator chemical cues (Fig. 5.4a).

In line with the q^{th} order structure functions analysis of individual trajectories, sea urchins experiencing predator chemicals displayed on average the highest mean speeds (more than 10 cm min^{-1}, Table 5.2, Fig. 5.4b) and the least tortuous paths (highest straightness indexes, Table 5.2, Fig. 5.4c) compared to the null and shadow experiments.

Table 5.2: Summary of the ANOVAs performed to test whether the dependent variables ‘sea urchin type of trajectories (slope of the function $\zeta(q)$)’, ‘mean sea urchin speed’ and ‘straightness of sea urchin trajectories’ were different between experiments. *P*-values correspond to those provided by an F-test.

Response variable	Effects	d.f.	% variance	*P*-value
Slope of the function $\zeta(q)$	Experiment	2	82.69	**0.01 ***
	Residuals	63	17.31	
Mean speed	Experiment	2	88.13	**0.001 ****
	Residuals	63	11.87	
Straightness index (I_s)	Experiment	2	84.13	**0.007 ****
	Residuals	63	15.87	

d.f. degrees of freedom. Significance codes: *P*-value < 0.001***, < 0.01**, ≤ 0.05*

5.4 Discussion

Our results show that *Paracentrotus lividus* can detect the presence of predator cues, and that at least in the absence of refuges, they flee from this stimulus by switching their overall superdiffusive movement behaviour in a featureless environment (null experiment) into a nearly ballistic movement pattern, with increased velocity and path straightness. This finding documents the existence, in this species, of a behavioural response with potential adaptive value. In contrast, and although this species is known to be photosensitive, we did not detect differences in their movement patterns or orientation according to light differences. Organisms that rely on predator chemical cue detection may often have evolved chemically-mediated behavioural defences because the chemosensory detecting abilities were already in place due to previous selection for chemical detection of food or mates (Kats & Dill, 1998). Indeed, for macroinvertebrates with limited visual abilities, chemical cues may be their most important source for risk assessment and we show these imply changes in species movement behaviour. Given our model species is an ecologically important herbivore, it is reasonable to think that the observed predator-induced switches in its behaviour may cascade down to macrophyte communities.

The absence of a response to heterogeneous light stimuli in this study was a surprise. Neither the trajectories nor the initial or final angles indicated a response to light differences. In contrast, Domenici et al. (2003) showed

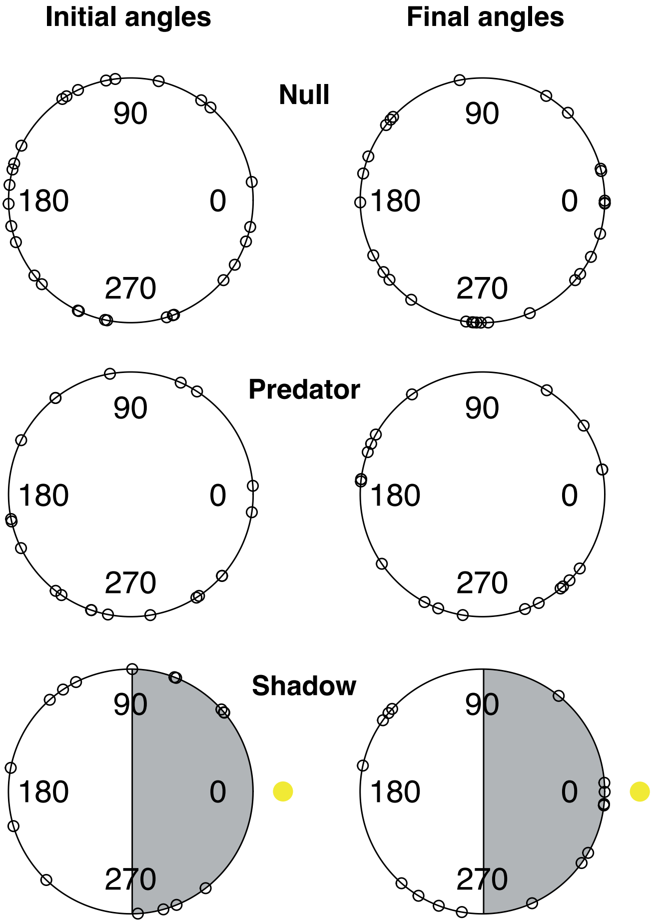


Figure 5.1: Sea urchin final and initial distribution of angles in the null ($n = 29$), predator ($n = 21$) and shadow ($n = 16$) experiments. For the shadow experiment we only show the circular mean of the 3 trials per sea urchin with the shadow-corrected angles (relative to the magnetic east). Note the uniform distribution of the angles in all of the experiments.

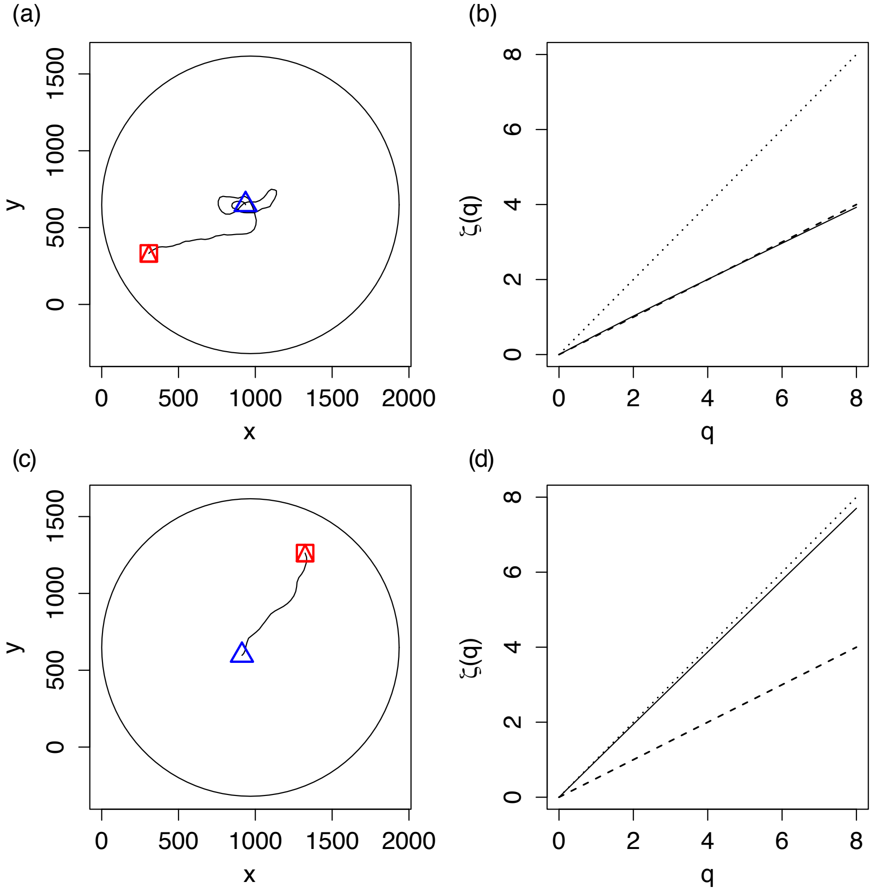


Figure 5.2: Examples of two extreme sea urchin trajectories analysed with q^{th} order structure functions. (a) Example of one of the tortuous trajectories obtained in our experiments, (b) which was identified as Brownian motion. The example in (c) is straighter, (d) and was identified as ballistic movement. In panels (b) and (d) the dotted and dashed lines are the theoretical outputs of a ballistic and a Brownian trajectory respectively, and the solid lines are the empirically obtained lines from the individual sea urchin trajectories in (a) and (c) respectively.

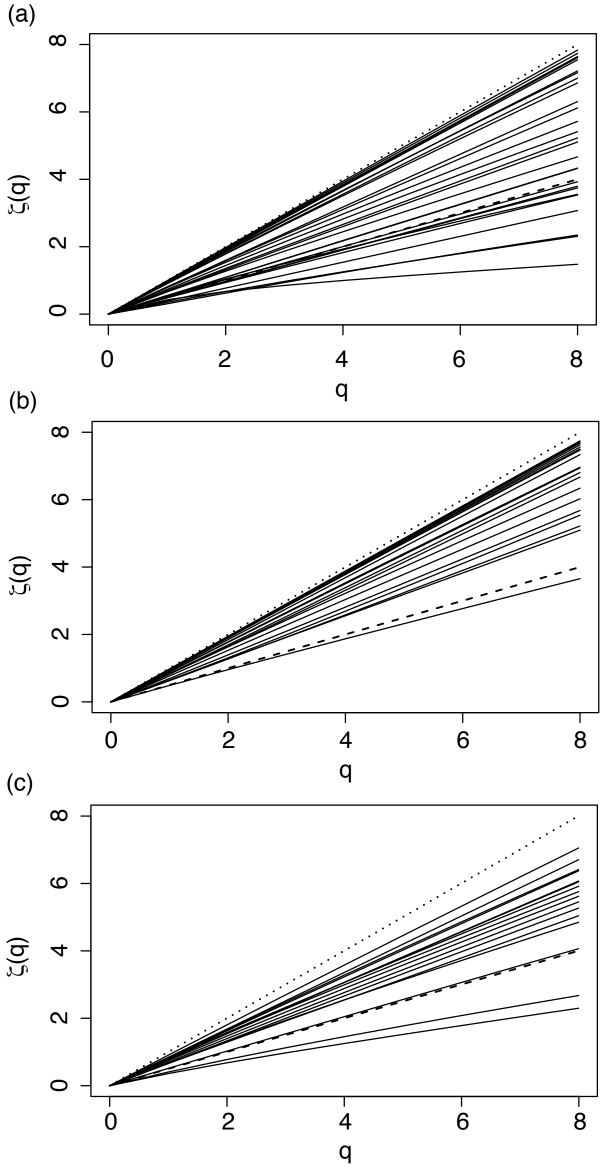


Figure 5.3: q^{th} order structure functions analysis of the individual sea urchin trajectories for (a) the null ($n = 29$), (b) predator ($n = 21$) and (c) shadow ($n = 16$) experiments. Note the wide inter-individual behaviour variability for the null and shadow experiments (a, c), while sea urchins subjected to predator chemicals (b) displayed, in general, more ballistic trajectories.

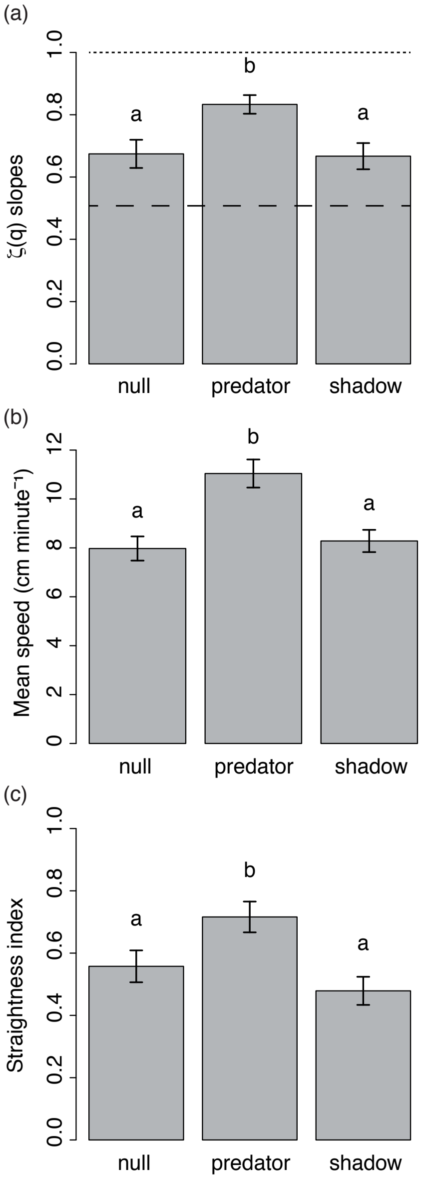


Figure 5.4: (a) Sea urchin trajectories from the predator experiments ($n = 21$) were significantly more ballistic compared to the trajectories from the null ($n = 29$) and shadow experiments ($n = 16$). The dashed and dotted lines represent the theoretical slope of a purely Brownian and ballistic motion respectively. This was also confirmed by (b) the higher sea urchin mean speed and (c) higher straightness index (less tortuosity) in the predator experiment compared to the null and shadow experiments. Different lower case letters indicate statistically significant differences according to a Tukey HSD test (see also Table 5.2).

that *P. lividus* sea urchins do actually respond to light stimuli with a negative phototaxis and works on other sea urchin species have found that they may orient towards or away from dark objects as small as occupying just 10 degrees of their visual field (Yerramilli & Johnsen, 2010). It may be adaptive to move to dark objects or shadow areas since holes and crevices usually used for shelter by sea urchins (specially from roving predators) are darker than their surroundings (Blevins & Johnsen, 2004). However, it is also known that sea urchins' response to light stimuli may be influenced by the light cycle the urchin has been exposed to before the experiments, the intensity of the light stimulus (Domenici et al., 2003), and the light quality (Adams, 2001). In our case, the light cycle in the lab mimicked that of natural conditions (individuals were not dark-adapted), and intensity of the light stimulus in our experiment was low. This contrasts with the above-mentioned experiments with intense lights and dark-adapted individuals of the same species by Domenici et al. (2003), which did respond to light with a negative phototaxis. The lack of orientation in our experiment could also be caused by an insufficient light contrast between the shadow and light zones, or as a consequence of the narrow spectrum of light wavelengths available with the fluorescent bulbs; lacking the UV range, which has been shown to produce shade seeking behaviour in other species (Adams, 2001).

Sea urchin trajectories without predator cues and with homogeneous light (i.e. null experiment) were in general superdiffusive, but with a great deal of variability (ranging from Brownian motion to almost ballistic). Superdiffusive movement patterns are a mathematically optimal search strategy for heterogeneous (patchy) and sparsely distributed resources (Bartumeus et al., 2005; Bartumeus & Levin, 2008). As opposed to a Brownian and/or superdiffusive search, ballistic movements may be generally used for escaping rather than for searching (James et al., 2008; Plank & James, 2008), maximizing the distance from potential chemical cue sources and minimizing thus the probabilities of an encounter with a predator. Similar escaping responses have been reported for plankton species (e.g. dinoflagellates and copepods, Harvey & Menden-Deuer, 2012; Bradley et al., 2013), with increased straightness in their trajectories when predators were detected, and increased speed or overall activity for snails, anemones and periwinkles. Increased locomotion speed as an escaping response has also been reported for bivalves, crustaceans, echinoderms, amphibians, reptiles, and mammals (Kats & Dill, 1998).

The behavioural switch of sea urchins exhibiting predator-induced escape/avoidance responses may result in a shift in their population distributions and predation pressure, which may even cascade down to the species they feed on (e.g. Ripple & Beschta, 2007). These behaviourally-mediated trophic cascades have been widely reported when prey-species modulate their behaviour as a consequence of predator presence, the so-called non-lethal effects (or indirect) of predators on prey (Schmitz et al., 1997). Indeed, *P. lividus* have been reported to increase their time allocated to sheltering in marine protected areas with increased predator biomass, and this may have effects on macroalgal communities (Hereu, 2005). Our results add to other works that have also found responses to predator chemical cues with different sea urchin species (Parker & Shulman, 1986; Scheibling & Hamm, 1991; Hagen et al., 2002; Vadas Sr & Elner, 2003; Manzur & Navarrete, 2011). It seems that *P. lividus* can react to the mere presence of predator chemical cues, while other species only react to cues from actual predator attacks on other conspecifics (e.g. Hagen et al., 2002). Given that the predator used in our experiment (the gastropod *Hexaplex trunculus*, the most important benthic predator in the area, Boada, 2012) was a slow benthic predator, the escaping strategy displayed by *P. lividus* may be adaptive, since they may be able to outrun the predator. This kind of straight-line motion responses have been observed in other urchins escaping from sea stars, for example, and may be a survival-enhancing response (Jensen, 1966). We would not expect the same kind of response to roving visual predators' cues, such as fishes, since it is difficult to conceive such type of responses to highly mobile visual predators as having any real adaptive value (Scheibling & Hamm, 1991). Fish predators usually prey upon sea urchins, and in this case, sea urchins would not be able to escape with fast movements.

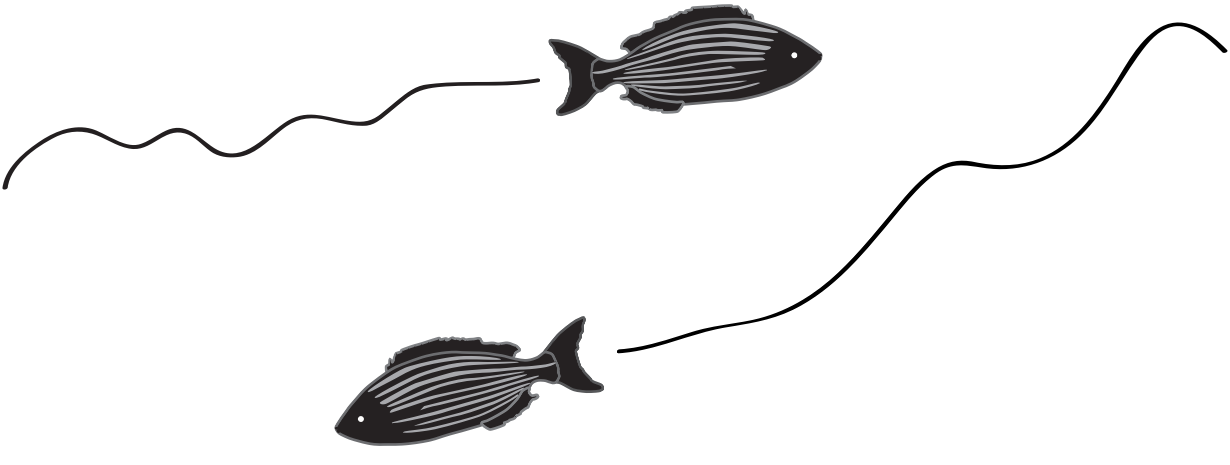
In conclusion, these results highlight that predation risk may be as important in determining animal movement patterns as feeding strategies, and should be taken into account when analysing trajectories in the field. As is for searching food, some movement patterns may be evolutionarily more optimal to escape or to search for shelter; and this may lead to changes in the population distributions of prey.

Acknowledgements

We would like to thank Liliana Salvador for her suggestions and valuable help with the image analysis, Laurent Seuront for his guidance on qth order structure functions analysis and Rohan Arthur for interesting discussions on previous versions of the manuscript. We are also grateful to Alessandro Gera, Jordi Boada, Simone Farina, Guillem Roca, Fiona Tomas for their help in sea urchin collection; and Àngel Luque, Paola Mura and Manuel Maldonado for technical assistance. The Spanish Ministry of Science and Innovation funded this research (projects CTM2010-22273-C02-01 and 02). The Spanish Ministry of Education supported JP (scholarship AP2008-01601).

6

Evaluating a key herbivorous fish as a mobile link: a Brownian bridge approach



Resum

Els organismes mòbils connectors poden actuar de vectors de matèria i transport d'energia entre ecosistemes, gràcies al seu moviment entre hàbitats. A més, si aquests organismes mòbils són espècies claus, els seus patrons de moviment poden tenir conseqüències importants pel funcionament dels ecosistemes que connecten. El peix herbívor mediterrani, *Sarpa salpa*, ha estat identificat com a clau en ecosistemes de plantes marines i de macroalgues. El nostre objectiu en el present estudi, va ser avaluar el potencial d'aquesta espècie de ser considerada connectora, mitjançant (1) l'anàlisi de la seva capacitat de connexió entre hàbitats, la importància d'aquestes connexions, i el seu ús dels hàbitats; i determinant (2) la consistència a nivell diari dels patrons observats al llarg d'aproximadament un any de dades. Vam utilitzar el marc dels models de ponts Brownians (Brownian bridge movement models, BBMM) per analitzar els patrons de moviment de 18 peixos marcats amb telemetria acústica passiva (duració mitjana del seguiment 103 ± 22 dies) i un anàlisi de temps-freqüència per analitzar els seus patrons temporals. Els nostres resultats mostren que els peixos de l'espècie *S. salpa* són capaços de fer excursions entre diferents hàbitats i fins i tot entre hàbitats distants (de l'ordre de km) amb àrees de campeig grans (mitjana 251 ± 95 ha). Tot i la seva gran mobilitat, *S. salpa* utilitza més intensament les praderes les plantes marines que els hàbitats rocosos. A més, els nostres resultats confirmen l'existència de patrons diaris per aquesta espècie, majoritàriament observats a la pradera de posidònia, amb els peixos movent-se de les zones més someres durant el dia a zones més profundes durant la nit. Aquests patrons van ser visibles la major part de l'any. En conjunt, els nostres resultats suggereixen que el peix *S. salpa* pot actuar com a organisme connector enllaçant àrees someres i profundes de les praderes a nivell diari i connectant diferents hàbitats distants, donats els seus moviments de llarga distància.

Abstract [1] [2]

By moving between habitats, mobile link organisms serve as vectors of material and energy transport between ecosystems. Additionally, if these mobile species are key organisms, their movement patterns can have profound consequences on the functioning of the ecosystems they link. The Mediterranean herbivorous fish, *Sarpa salpa*, has been defined as a key organism in seagrass and rocky macroalgal habitats. Our objective in this study was to evaluate the potential of this species to be considered a mobile link by (1) assessing its capacity to connect different habitats, the strength of these connections, and the habitat use; and by (2) determining whether the patterns observed were consistent on a diel basis and over an annual period. We used the recently developed Brownian bridge movement models (BBMM) framework to analyse the movement patterns of 18 fish tracked with passive acoustic telemetry (mean tracking duration 103 ± 22 days) and a time-frequency analysis to assess their temporal patterns. Our results showed that *S. salpa* performed trips between different and distant habitats (on the order of km) with large home ranges (overall mean 251 ± 95 ha). Despite its high mobility, *S. salpa* used more intensively seagrass rather than rocky habitats. In addition, our results confirm the existence of diel patterns for this species, mostly observed in the seagrass habitat, with fishes moving from shallow areas during the day to deeper areas at night-time. These patterns were visible for most of the year. Taken together, these results suggest that *S. salpa* may act as a mobile link by connecting shallow and deep areas of the meadow at a daily basis and linking different and distant habitats given their long-distance movements.

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[1] Pagès, J.F., Bartumeus, F., Hereu, B., López-Sanz, À., Romero, J., Alcoverro, T. (in revision in Marine Ecology-Progress Series).

[2] See supplementary materials in Appendix A.

6.1 Introduction

Mobile links are organisms able to move between habitats and ecosystems that support essential functions by connecting areas and contributing to ecosystem resilience (Gilbert, 1980; Nyström & Folke, 2001). Connections may be achieved by organisms passively drifting from one habitat to another (e.g. larvae in seawater, anemochorous seeds) or by their active movement. Active mobile links are animals that provide a multitude of different functions such as pollination, seed dispersal and translocation of nutrients (Ogden & Ehrlich, 1977; Meyer et al., 1983; García et al., 2013), which can have substantial effects on ecosystem functioning and structure (Lundberg & Moberg, 2003). Additionally, if these mobile species are key organisms, as is the case of some herbivores, their movement patterns can have profound consequences on the functioning of the ecosystems they link. Indeed, herbivores play a central position in the organization of communities and ecosystems (Burkepile & Hay, 2006; Gruner et al., 2008) and often they do not distribute their impacts uniformly among the habitats they travel across (e.g. McCook, 1997; Knapp et al., 1999). Foraging theory predicts habitat selection on the basis of resource quality and abundance (Charnov, 1976), but other factors such as predation risk (Brown & Kotler, 2004; Hoey & Bellwood, 2011), animal state (Schuck-Paim et al., 2004) or landscape spatial configuration (Haynes & Cronin, 2003; Fortin et al., 2005; Hoey & Bellwood, 2011) also influence animal foraging decisions and movement patterns. Therefore, to fully assess whether an organism effectively can function as an active mobile link between habitats or ecosystems, two key issues should be addressed: the spatial arrangement of habitats and the movement patterns of the animal.

Marine landscapes (i.e. seascapes, Pittman et al., 2011) are assumed to have a higher level of connectivity than terrestrial ones (Tanner, 2006), which reinforces the possibility of generalist mobile fish herbivores to serve as mobile links. In seascapes, where GPS positioning is not possible, acoustic telemetry has become increasingly used to track animals in space and time. Descriptive analyses (frequency distribution of detections) and or space utilisation methods (minimum convex polygons and kernel utilisation distributions) have been widely applied, providing key information on animal space use. However, the temporal component between successive locations, which is crucial to assess the connection between habitats, is often disregarded (Jacoby et al., 2012). Brownian bridge movement models (BBMM, Horne et al., 2007; Kranstauber et al., 2012) consider both the spatial and the temporal component of movement. BBMMs explicitly address the problem of connections (i.e. bridges) between successive locations, and thus, are useful to determine whether or not highly mobile species act as links between habitats.

In the Western Mediterranean the herbivorous fish *Sarpa salpa* (L.) exerts a profound impact in different coastal habitats that include the consumption of a great proportion of seagrass annual primary production (Prado et al., 2007), drastic reductions on seagrass canopy structure that can foster predation on seagrass-dwelling organisms (Pagès et al., 2012), or its influence on the vertical distribution of canopy-forming algae (Vergés et al., 2009), among others (e.g. Sala & Boudouresque, 1997). *S. salpa* fishes are diurnal browsers and generalist herbivores, allocating most of their daytime to foraging (*c.* 65% of their time) in both seagrass (Ferrari, 2006; Jadot et al., 2006; Abecasis et al., 2012) and rocky habitats (Tomas et al., 2011). Nevertheless, it remains unclear whether individuals are systematically capable of connecting different habitats or if, on the contrary, individuals found in rocky habitats belong to different populations from those in seagrass beds (as seen by Fox & Bellwood, 2011, with rabbitfishes in coral reefs). Given that seagrass beds and rocky habitats are usually found forming a mosaic, it seems reasonable to assume individual commuting among habitats. If these trips were frequent and enough time was spent in each habitat to imply a translocation of materials and energy, the ecological implications would be sound.

Our study aims were (1) to determine whether the herbivorous fish *S. salpa* commutes between different habitats in a seascape mosaic, characterise the strength and variability of these connections and the habitat use in each of these systems; and (2) to determine if the patterns observed are consistent on a diel basis and over an annual period. To address objective (1) we analysed the movement data recorded by passive acoustic telemetry with the BBMM framework, and we used a time-frequency analysis (Continuous Wavelet Transform, CWT) to evaluate the temporal patterns for this species along the tracking period (objective 2). If *S. salpa* uses and commutes between different habitats, and these patterns are sustained on time, we will be able to discuss the potentiality of this species to be considered an active mobile link.

6.2 Materials and methods

Study area and receiver set up

This work was conducted between October 2008 and October 2009 in Medes Islands Marine Protected Area and the adjacent unprotected stretch of coast, located on the north-western Mediterranean. The study area is a mosaic of habitats composed of sandy bottoms, *P. oceanica* seagrass meadows and macroalgal communities in rocky habitats (Fig. 6.1a, Hereu et al., 2010, 2011). Rocky areas (with macroalgal communities) occupy a larger area compared to seagrass communities (for each part of seagrass habitats there are nine parts of rocky habitats, see Fig. 6.1a). A fixed array of 26 single-channel omnidirectional hydrophones (VR2 receivers, VEMCO, Nova Scotia, Canada) was deployed around the Medes Islands archipelago and along the coast. Receivers' detection range was established prior to fish tagging, placing tags at different distances from receivers (for 30-60 minutes). Distances of more than 250 m resulted in a sharp drop of detection rates (below 10% of the expected number of detections), and this was considered the receivers' detection range. The average distance between receivers was 210 m. Receivers were retrieved, data downloaded, cleaned of biofouling, and redeployed 5 times during the study (in November 2008, January 2009, May 2009, August 2009 and October 2009).

Acoustic tagging procedure

S. salpa individuals were fished on the 16th and 17th October 2008. Twenty fishes were captured at four different sites (see Fig. 6.1a, five fishes per site) during daytime using seine fishing net by circling schools of *S. salpa* fish. Since there is no evidence of sexual dimorphism on this species, individuals were not assigned a sex. Each fish was measured to the nearest 0.5 cm (Total Length) and tagged following the protocol in Jadot et al. (2006). After recovery, they were returned to their respective sites. We used VEMCO acoustic transmitters (V9P-2L, 9 mm diameter × 47 mm length) with 120 s average repeat rate, a depth accuracy of ± 2.5 m and an estimated battery life of 522 days. Previous studies have shown that surgical tag implantation has a very limited impact on the behaviour and physical status of this species (Jadot, 2003). It should be noted that four of the most frequently detected five fishes (called residents, see below) were captured in the meadow zone (see Fig. 6.1a, Table A.1).

Spatial patterns

For each fish, we calculated the total period between its releasing date and its last day of detection (total period of detection or tracking period, TP), as well as the number of days detected (DD), following March et al. (2010). These descriptors were used to calculate the Residence Index (RI) per fish, defined as the quotient between DD and TP for that individual (March et al., 2010). Fishes with a RI > 0.6 (i.e. fishes that were detected within the array of receivers for more than the 60% of days during their tracking period, and tracked more than 5 days) were considered 'resident' as opposed to the 'non-resident' ones (RI < 0.6). Utilisation distributions and home ranges were assessed for both resident and non-resident fishes. For non-residents, these estimations should be viewed as minimum areas of utilisation, since their estimates may be biased due to their low number of detections within the array. Further analyses were run only for residents, which accounted for the vast majority of detections (see Results).

We used the recently developed Brownian bridge movement model (BBMM) approach (Horne et al., 2007; Kranstauber et al., 2012) to estimate individual fish utilisation distributions (UD). Utilisation distribution estimation provides an objective way to define an animal's normal activities (Powell, 2000). UDs are probability density functions that provide the animal's probability of use for each cell (i.e. pixel) of a given grid (raster map). We only calculated UDs for those individuals with more than 50 data points (locations) and more than 5 days detected (see Table A.1, i.e. 5 resident and 5 non-resident fishes). UD estimation through BBMM has several advantages over the classical location-based kernel density estimator (KUD). While KUD method only assesses the spatial arrangement of locations, BBMM considers the time dependence between them. This makes BBMM a particularly useful method to assess the capability of an animal to behave as a mobile link, given that it is especially successful at detecting the connectivity between highly used areas. Moreover, it assumes the animal is moving following a conditional random walk movement model between pairs of locations (i.e. a random walk conditioned by a known starting and ending location); and finally, it allows to take location error into account (see Calenge, 2011, for a thorough comparison between KUD and BBMM methods) (biotelemetry error, i.e. 250 m in our case; see appendix A for a complete explanation of BBMM implementation to our data set; see an example of a data set in Table A.2). BBMM calculations were performed in R (R Development Core Team, 2012) using the package BBMM (Nelson et al., 2011).

Home ranges

Individual fish UDs obtained from the BBMM were used to calculate individual home range areas. The smallest area accounting for the 95% of the total probability of use is usually defined as the animal home range (Powell, 2000). Thus, for each individual UD we calculated the home range area as the 95% volume isopleth of the UD and the core areas of usage were also calculated as the 50% volume isopleth of the UD. These calculations were performed in ARCGIS10 (ESRI, Redlands, CA, USA) and GME (Beyer, 2011).

Space use

On the other hand, the individual UDs obtained from the BBMM were also used to assess population-level space use. We summed the cell values for all resident fish UDs ($n = 5$) and the cell values of non-residents UDs ($n = 5$) respectively and then re-scaled their cumulative cell values to sum to 1 (since

UDs are probability density functions, Powell, 2000). In this way we obtained the population-level UD for residents and non-residents respectively. This is equivalent to projecting each individual UD onto a grid, and allows for the spatial assessment of the overall most used areas of that population (see e.g. Horne et al., 2007; Sawyer et al., 2009).

Occasional excursions from each habitat

For resident fishes, we assessed the importance of occasional movements by calculating the probabilities of a fish making an excursion of a given duration departing from a given habitat (meadow or no-meadow areas). First, receivers were grouped according to the presence or absence of *P. oceanica* in their range of detection. We labelled the receivers in the seagrass habitat as 'meadow' (the 4 receivers with seagrass within their detection range, see Fig. 6.1a) and 'no-meadow' (the rest of the receivers). We define excursion time as any time interval between two consecutive locations on the same receiver. We represented the excursion times in each habitat in a log-log scale. This is an adequate way to visualize fat tail distributions, that is, distributions where extreme values show non-negligible probabilities (Pueyo, 2006; Sims et al., 2007).

Receiver-based descriptors

In order to determine whether receivers are located in travelling zones or in intensively used areas within the habitat, we computed, for the resident fishes, the percentage of consecutive revisits to the same receiver as the ratio between consecutive revisits and the sum of consecutive with non-consecutive revisits. Non-consecutive revisits are those that reach a particular receiver after having been detected previously in another receiver. Low ratios of consecutive visits suggest the receivers are located in a travelling zone, whereas high ratios suggest the receivers are in intensively used areas. We complemented this information with the mean excursion duration from each receiver (time interval between consecutive detections on that receiver) and the number of detections in each receiver (see results).

BBMM on passive acoustic telemetry data sets: UD estimation biases

Despite the acknowledged suitability of BBMM to provide insight into the movements of terrestrial tracked animals using GPS data (Horne et al., 2007; Sawyer et al., 2009), this is the first time the method is applied to a marine data set. The application of BBMM to passive acoustic telemetry data sets may show two specific problems that one needs to be aware of. First, when individuals consecutively revisit the same receiver, the model assumes the existence of a pure diffusive movement (not bridged) around that receiver, which is proportional to the time spent between the two consecutive locations. This leads to a circular-shaped utilisation distribution around that receiver. If the time lag between two consecutive locations at the same receiver is very large, then the local UD (around the receiver) could be overestimated because it might well be the case that the animal departed the area out of the network receivers and returned to the same area later on. Thus, the BBMM method is very suitable for species that move throughout the receivers' network area, while it is less appropriate for species that display permanent site-fidelity with low mobility, or that display movements much broader than the receivers network area of detection. Another potential limitation is the presence of acoustic shadows, that is, areas within the receiver detection range where the transmitter cannot be located (e.g. in crevices, holes, behind big boulders, etc.). As an example, if an animal went from receiver A to receiver C, without being detected at the intermediate receiver B, then a non-realistic bridge would be modelled between receiver A and C, with receiver B not playing any role in the bridge. The limitations commented above should be borne in mind when trying to interpret UDs and home ranges calculated with a BBMM from a passive acoustic data set.

Temporal patterns

To study fish behaviour on the depth axis, we assessed day and night depth distribution for resident fish in meadow and no-meadow habitats. Data were split into periods of day and night, according to the sunset-sunrise time calendar obtained from the U.S. Naval Observatory (Astronomical Applications Department, accessed 1st June 2011 `http://aa.usno.navy.mil`). We calculated the mean depth per day and night for the whole data set for each fish. Then, the dependent variable fish mean depth was analysed with a 2-way ANOVA to test the effects of the fixed factors habitat (2 levels: meadow, no-meadow) and phase of the day (2 levels: day, night). Normality and homoscedasticity were tested and fulfilled.

We also tested whether there were differences in the frequency of detections according to the fixed factors phase of the day (2 levels: day and night), habitat (2 levels: meadow, no-meadow) and season (just 2 levels: autumn, winter, because we did not have enough fish individuals [replicates] for the rest of seasons). Detection frequencies were fit to a linear model and the variance structure of heteroscedastic variables (season and habitat) was included as weights within the linear model. The best weighted model was selected using Akaike's Information Criterion (AIC) (Zuur et al., 2009). Normality was tested and fulfilled. Data were analysed with the package nlme in the statis-

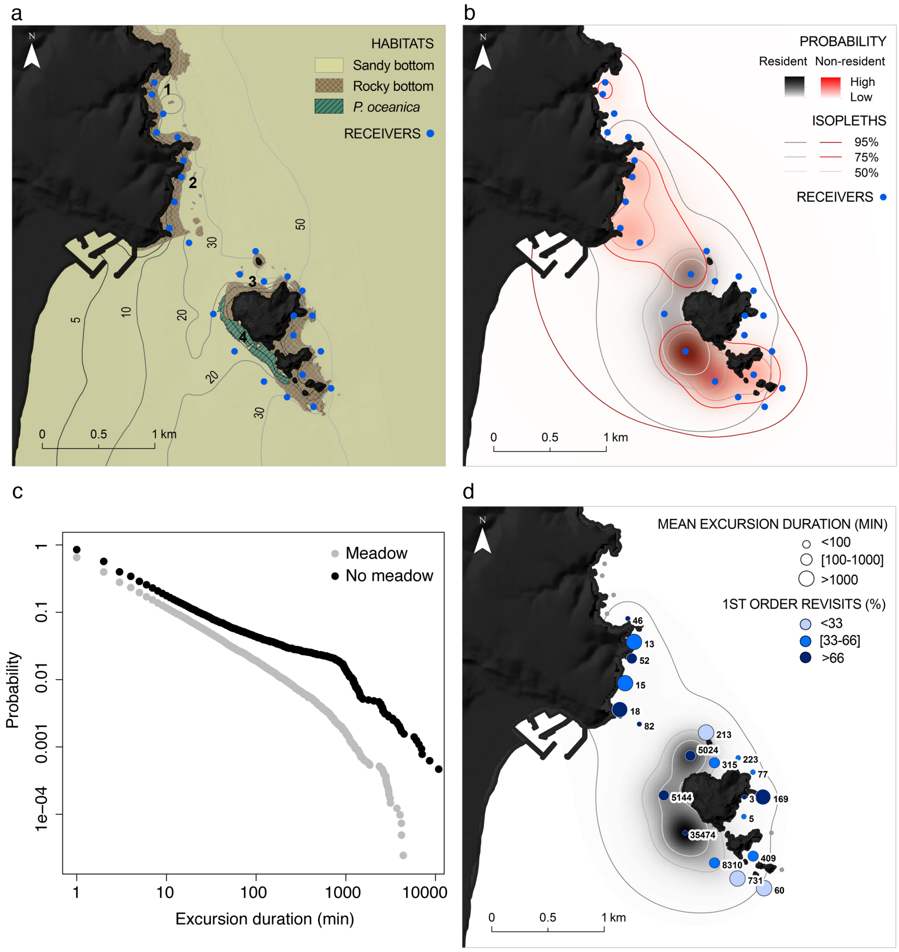

Figure 6.1: Spatial patterns. (a) Study site's map of habitats with isobaths. Numbers (1-4) represent the fishing-releasing sites (see methods). (b) BBMM space use estimation for resident and non-resident populations. Note a higher intensity of use on the area with seagrass (specially for residents). (c) Log–log plot of the probability of making excursions of time x in 'Meadow' and 'No-meadow' habitats. Note the higher probability of conducting very long excursions in 'No-meadow' habitats compared to 'Meadow' ones. (d) Residents' mean excursion duration and percentage of consecutive revisits for each receiver. The shaded area corresponds to the result of the space use estimation through BBMM for residents (same legend as Fig. 6.1b).

tical software R (Bates et al., 2011; Pinheiro et al., 2011; R Development Core Team, 2012).

The temporal patterns of hourly detections were examined by visually inspecting the chronograms for each resident fish. A time-frequency analysis (the Continuous Wavelet Transform - CWT) was then used with the pooled data set of all residents, in order to identify periodic patterns in *S. salpa* hourly detections (as used in e.g. March et al., 2010; Alós et al., 2012). Time-frequency methods are more powerful than frequency ones because they allow us to track periodicity across time (Subbey et al., 2008). Most traditional mathematical methods examine periodicities in the frequency domain, and therefore implicitly assume that the underlying processes are stationary in time. In contrast, wavelet transforms expand time series into time frequency space and can therefore find localized intermittent periodicities (Grinsted et al., 2004). We computed (Matlab) a 2-dimensional wavelet spectrum (i.e. Morlet wavelet) and a point-wise test (95% significance level) on previously normalized data (i.e. log-transformation) (Grinsted et al., 2004).

6.3 Results

Spatial patterns

Five resident fish accounted for the 96% of detections, while non-resident fishes accounted for the remaining 4% (Fig. A.1, Table A.1). Home range areas for individual *S. salpa* varied from 40.64 ha to 967.04 ha (Table A.1, Fig. A.2). The mean home-range area for residents was 254 ± 83 ha, and 241 ± 161 ha for non-residents (averaging the individual home range areas of the 5 residents, and the 5 non-residents respectively). Residents' space use (i.e. the spatial projection of the sum of all resident individual UDs) evidenced that the seagrass meadow was intensively used, as shown by their core area that was centred on the meadow. Residents also used rocky habitats from the islands and even from the coast 1.5 km apart from their core area, an evidence of large scale commuting (Fig. 6.1b,d). Non-residents population space use (i.e. the projection of non-residents' individual UDs) covered nearly all coastal zones of the study area (Fig. 6.1b). Non-resident population showed different cores of activity (50% isopleth), two on the coast and one on the islands, partially located on the seagrass habitat. Both residents and non-residents populations overlapped their core areas on the *P. oceanica* habitat, in the south-western coast of the islands (Fig. 6.1a,b).

The probability distribution of a resident fish to perform an excursion of a particular duration showed a fat-tailed decay, in particular with a power law like scaling (i.e. a straight-lined decay in Fig. 6.1c). This held for meadow and no-meadow receivers, showing that regardless of the habitat the vast majority of excursions departing from a receiver were very short in duration, but from time to time very long excursions also occurred. The probability of performing very long excursions was not negligible and depended on the habitat the receiver was located in, excursions departing from no-meadow receivers being larger than those departing from meadows receivers. For example, the probability of making excursions of 1000 minutes (*c.* 17 hours) was low, but it was around two orders of magnitude higher in the no-meadow receivers compared to those in the meadow (Fig. 6.1c). These results suggest a larger site fidelity to meadow compared to no-meadow areas. More generally, meadow receivers showed a higher number of detections, high consecutive revisits ratio (Fig. 6.1d), and low mean excursion duration. This should not come as a surprise given that the set of receivers located in the meadow showed the highest space use probability (Fig. 6.1d). The set of receivers located in no-meadow areas, specially those at the edges of the receiver's array, showed a lower consecutive revisits ratio, a high variability on excursion durations, and a much lower probability of space use (Fig. 6.1d).

Temporal patterns

S. salpa depth preference differed significantly between habitats and phase of the day (Fig. 6.2, Table 6.1). In seagrass habitat, the majority of detections during daytime were in shallow depths (mean diurnal depth = 5.2 ± 0.2 m), whereas, at night, detections were significantly deeper (mean nocturnal depth = 8.5 ± 0.9 m, inset Fig. 6.2a, Fig. A.3). In contrast, this cycle was not significant in rocky habitats, where fish remained most of the time at similar depths (P-value > 0.05, inset Fig. 6.2b, Fig. A.3). It is worthy to note that *S. salpa* depth use in the area of the meadow (Fig. 6.2a) matches seagrass habitat depth distribution (Fig. 6.1a).

We found a significant effect of habitat type and day phase on the frequency of detections (p-values < 0.05, Table 6.1), but no direct effects of seasonality (Table 6.1). Receivers in meadow areas presented a higher amount of detections than receivers in no-meadow areas. In the former most detections were nocturnal, whereas in the latter most detections were received during the day (see Fig. A.4a). In autumn there was a significantly higher frequency of detections at night compared to daytime, but these differences were not significant in winter (see the significant Season × Phase interaction in Table 6.1; see also Fig. A.4b).

Inspecting the chronograms from individual resident fishes (Fig. A.5), a diel pattern became evident when considering hourly detection rates. The similarities observed at the individual level (Fig. A.6, with some variability), allowed us to aggregate the data for all residents. The diel cycle persisted, with the highest rate of detections per hour at night, while at sunrise and late afternoon there was the minimum number of detections and, during daytime, the detection rate remained low (Fig. 6.3a, see also individual level data in Fig. A.6). Wavelet spectrograms of the time series evidenced the existence of a diel cycle on the residents' hourly detection rate (period = 24 hours, see dashed lines in Fig. 6.3b; see individual-level wavelet spectrograms, Fig. A.7). This pattern was significant (with some non-significant patches) for most of the time series until most fishes stopped transmitting. For periods around 128-256 hours (5-10 days) and especially around 512 hours (21 days) there were also significant patches (Fig. 6.3b).

Table 6.1: Analyses of variance performed. *P*-values correspond to those provided by an F-test.

Response variable	Effects	d.f.	F	*P*-value
Fish depth	Phase	1	12.66	**0.003** **
	Habitat	1	5.01	**0.039** *
	Phase × Habitat	1	2.08	0.168
	Residuals	16		
Frequency of detections	Habitat	1	96.88	**<0.0001** ***
	Season	1	1.01	0.326
	Phase	1	55.51	**<0.0001** ***
	Habitat × Season	1	0.73	0.400
	Habitat × Phase	1	112.91	**<0.0001** ***
	Season × Phase	1	9.13	**0.006** **
	Habitat × Season × Phase	1	2.35	0.138

d.f. degrees of freedom. Significance codes: *P*-value < 0.001***, < 0.01**, $\leq$ 0.05*

6.4 Discussion

The large home ranges of *S. salpa*, the connection observed between areas with the BBMM models, the trips observed between distant habitats and the consistency of these patterns in time suggest that *S. salpa* might act as a mobile link. The application of BBMM on passive acoustic telemetry data has allowed us to detect which of the highly frequented areas are more likely to be connected. This would not have been possible with the classical KUD approach (compare the UD obtained with the BBMM in Fig. 6.1d with the UDs obtained with the KUD in Fig. A.8). Despite its high mobility, *S. salpa* used more intensively seagrass rather than rocky habitats, especially resident fishes (i.e. those spending more than 60% of time within the area of detection of the receivers network). In addition, our results confirm the existence of diel patterns for this species, mostly observed in the seagrass habitat, with fishes moving from shallow areas during the day to deeper areas at night-time. These patterns were visible for most of the year and also highlight the potential link between shallow and deep areas of seagrass meadows.

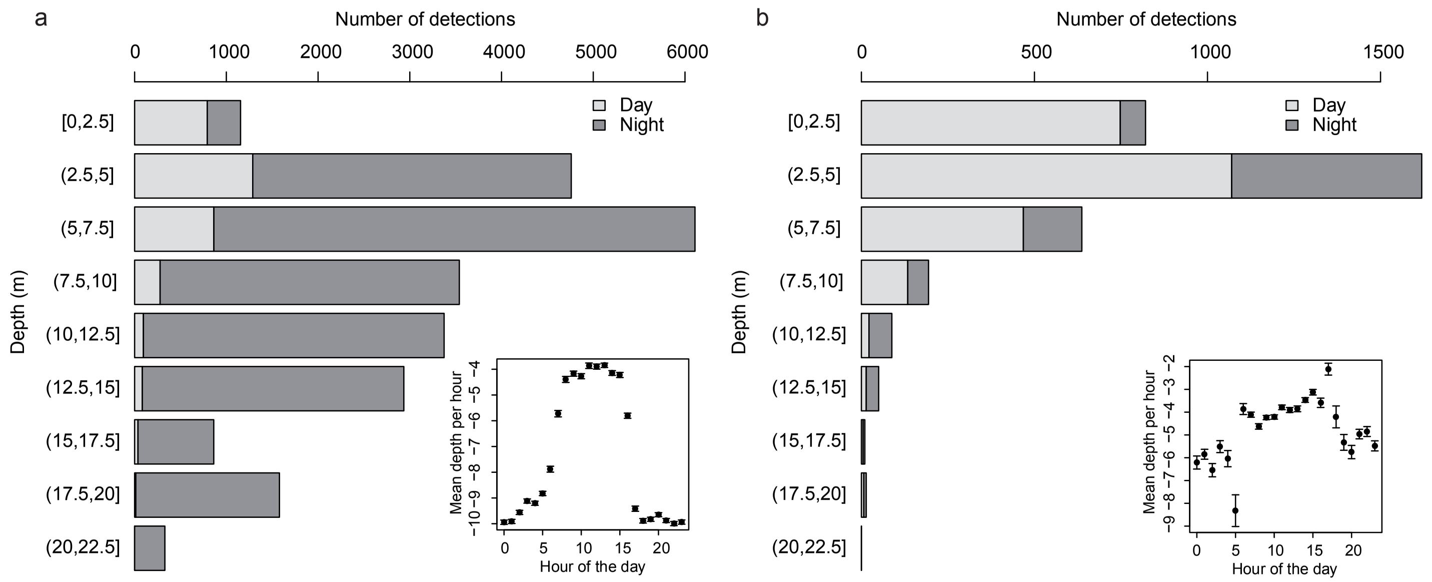

Figure 6.2: Depth patterns. Number of diurnal and nocturnal detections classified by depth in (a) seagrass and (b) rocky systems. The insets show the mean depth along the 24 hours of the day. Note that a 24-hour depth cycle is evident in the seagrass (inset (a)) whereas this is not the case in rocky systems (inset (b)).

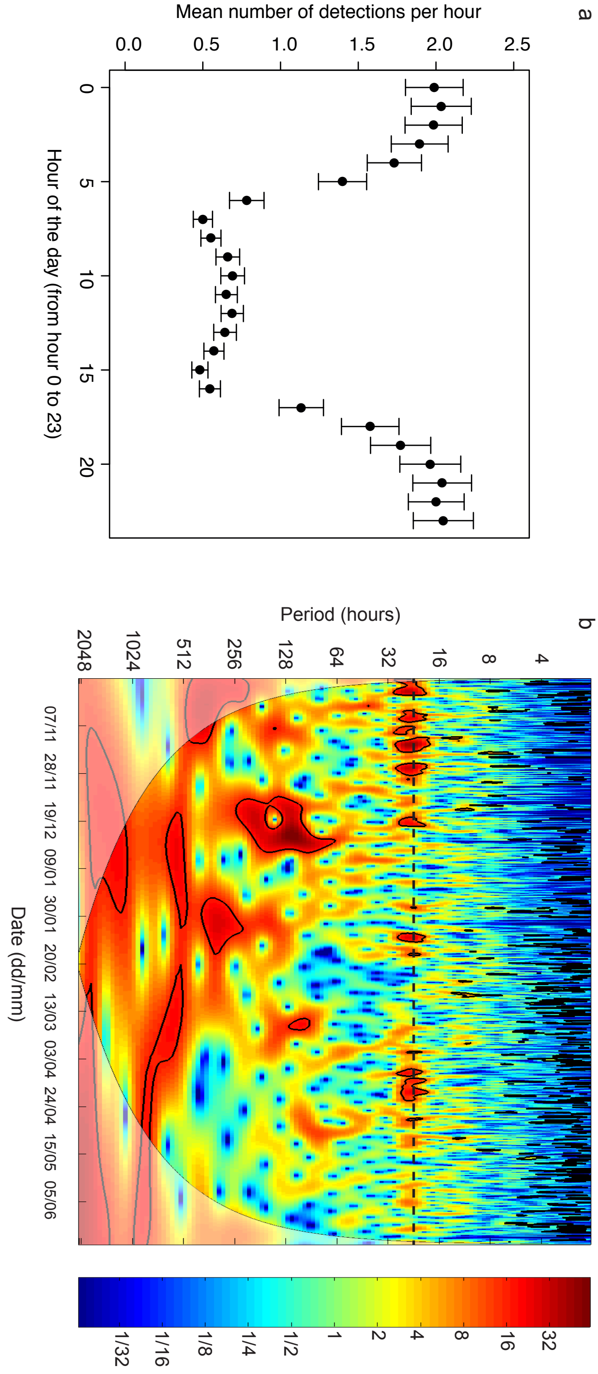

Figure 6.3: Temporal patterns of the frequency of hourly detections pooling all residents. (a) The mean number of detections per hour (pooling all residents) evidences a diel cycle, with higher detection rate at night compared to daytime. (b) Wavelet spectrum for the number of hourly detections of resident fishes pooled together. Significant cycles were detected for a 24 h period (horizontal dashed line) and for periods around 512 hours (21 days). The thick contour designates the 95% confidence level. The cone of influence where edge effects might distort the picture is shown as a lighter shade. The scale bar represents the intensity of the time-frequency space over time.

Demersal fishes have been generally found to display restricted home ranges and high site fidelity (e.g. Chapman & Kramer, 2000; Topping et al., 2005; March et al., 2010; Alós et al., 2012). These small home range sizes do not prevent fishes to connect habitats that are close enough one to each other. For example, habitat connection has been thoroughly demonstrated for *Haemulidae* fishes in back-reef habitats (Meyer et al., 1983; Verweij & Nagelkerken, 2007). However, we found that *S. salpa* displayed large home range areas (overall mean of individual home ranges = 251 ± 95 ha) that encompassed different kinds of habitats and ecosystems, with high variability among individuals. This was true for resident and for non-resident fishes (Table A.1). Inter-individual variability in home range size has been generally found, both for *S. salpa* (Jadot et al., 2002), as well as for other species (e.g. Marshell et al., 2011). In addition, we found that *S. salpa* fishes conducted long trips (on the order of some km) between distant habitats. Indeed, they even often crossed the sand channel that separates Medes Islands from the coast (see the bridge between the islands and the coast in Fig. 6.1b,d, see also Table A.1), although several studies have shown that species usually avoid crossing habitat edges, especially among those that are highly contrasting (known as hard edges), such as seagrass-sand edges (Chapman & Kramer, 2000; Haynes & Cronin, 2003, 2006).

Despite its large mobility, resident *S. salpa* fishes showed a clear and long-term (i.e. one year) preference for the seagrass meadow evidenced by the high utilisation of this habitat, where they spent more than 88% of time on average. They allocated a low proportion of time to rocky compared to seagrass systems, but the connection between both types of habitats was non-negligible. In contrast, non-resident fish (75% of the tracked individuals) were characterised by frequent excursions out of the receiver array and by a very short tracking period that resulted in a much lower number of detections. Hence, it is difficult to fully assert whether this group could have a major role in connecting the habitats within the network of receivers to other distant habitats or whether they were simply residents in seagrass habitats out of the network of receivers only sporadically visiting the area of study. Because of that, non-resident estimates of space use and home ranges should be viewed as minimum areas of utilisation, since these could be biased due to their low number of detections within the array.

Temporal trends within each habitat were also observed. *S. salpa* was more often detected in the seagrass at night than during the day; this cycle was consistent despite the fact that *S. salpa* is a diurnal feeder that increases its activity during daytime (Verlaque, 1990; Ferrari, 2006). There is some controversy on how cycles on the rate of detections may arise. It has been suggested that detection frequency and movement rate may be negatively correlated (Topping et al., 2005), or even that cycles may arise as a result of the environmental noise (Payne et al., 2010), but a growing number of studies have related changes in habitat use with diel cycles (March et al., 2010; Alós et al., 2011, 2012). In our case, the generating mechanism is very likely to be related to the loss of acoustic transmission inside the canopy of seagrass meadows, already described by other authors (which can decrease the number of detections by up to 80%, March et al., 2010). The aforesaid technical restriction could, in fact, be used as a proxy for *S. salpa* activity in the meadow. For this species it is well established that diurnal time is allocated to foraging in the seagrass (Verlaque, 1990; Ferrari, 2006), thus, the low detection rates observed during the day may mean the animal is feeding in the meadow, in close contact with the canopy, which is known to produce high acoustic losses. Conversely, at night the higher number of detections might suggest the animal is outside the canopy. This day-night cycle on the number of detections per hour was sustained for at least 6 months, as shown by the CWT analysis, and no effects of seasonality were evident despite both seagrass and macroalgal biomass and production have a seasonal pattern in the study area (Alcoverro et al., 1995; Hereu et al., 2008). Diel cycles had already been identified for this species on the short-term (i.e. one month, Jadot et al., 2006), but it was unclear whether these were maintained for the whole year, since it had been suggested that *S. salpa* fishes conducted a migration from shallow waters to deeper ones (i.e. below 30 m) in autumn-winter in order to spawn (Verlaque, 1990). Our results challenge this migration hypothesis, in spite of the low number of fishes studied.

Additionally to the cycle on hourly detection rates, a diel cycle on depth use was also observed in the seagrass habitat, with mean depths moving from 4-5 m at daytime to 9-10 m at night (see inset Fig. 6.2a). These results match with the results discussed in the previous paragraph and with the higher herbivory rates generally observed on shallow areas compared to deeper ones (Vergés et al., 2012). Indeed, in the studied seagrass meadow it may be optimal to restrict feeding activity to the shallow waters, where seagrass is 2.7 times denser and with 3 times more cover compared to the deeper part of the meadow (Romero et al., 2012). High detection rate in deeper grounds at night give us a clue on the behaviour of this species that has been described to rest at night at the seagrass-sand edge (Ferrari, 2006; Jadot et al., 2006) (see that the seagrass-sand edge is at *c.* 10m in Fig. 6.1a). Thus, *S. salpa* fishes could be exporting organic matter from their feeding grounds (shallower parts of the meadow) to their resting sites (seagrass-sand edge), as has been observed for other mobile fishes (Meyer et al., 1983; Verweij & Nagelkerken, 2007). Conversely these diel patterns on depth preference were not observed in rocky habitats.

The integration of the spatial and temporal habitat use with both fish mobility and the proportion of area occupied by each habitat in the seascape mosaic identifies the fish *S. salpa* as a potential mobile link. While previous studies pointed out that *S. salpa* acted as a key herbivore in seagrass and rocky macroalgal habitats independently (e.g. Prado et al., 2007; Vergés et al., 2009), our study connects the use of both habitats by the same individuals or schools. On the one hand, mobile links can potentially transfer energy, matter and other functions (Nyström & Folke, 2001; Lundberg & Moberg, 2003). Energy and matter transfer might be provided by *S. salpa*, since fishes foraging in seagrasses have been observed to defecate pellets with algal traces from nearby rocky reefs and vice versa (Tomas et al., 2010). The long gut transit times (*c.* 5 gut lengths per body length, Havelange et al., 1997) observed in *S. salpa* could facilitate this transfer. However, since the studied fishes spent most of the time on seagrass habitat, the main transfer of energy would be between shallow and deep areas of the meadow at a daily basis (see previous paragraph). On the other hand, *S. salpa* is also a voracious herbivore, substantially shaping seagrass and macroalgal habitats. Even though the proportion of seagrass habitats in the studied area was clearly lower than macroalgal-dominated rocky areas (Fig. 6.1a), the fishes stayed more time on seagrass habitat, and thus, seagrasses would be more susceptible to be grazed by *S. salpa* than macroalgal communities from rocky areas. In this work we did not directly assess the relationship between *S. salpa* movement patterns and their functional consequences in the ecosystem. However, works in the same geographic area suggest that the movement patterns we have found resonate with grazing intensity spatial patterns. In Medes Islands area, *S. salpa* has been observed to intensively defoliate seagrass plants in summer (Tomas et al., 2005b; Prado et al., 2007) compared to a more limited fish grazing effect in macroalgal communities (Hereu et al., 2008). Thus to understand the seascape-dependent distribution of fish herbivory impacts it becomes important not merely to know the consumption rates, diets and preferences of these species within the system, but also herbivore movements across time and space, along with the spatial configuration of the seascape mosaic.

Acknowledgements

We are very grateful to David Díaz, Cristina Linares and Mikel Zabala for their work in setting up and maintaining the array of receivers, to Eneko Aspillaga, Miquel Sacanell, Guillem Roca, Laura Navarro and Alessandro Gera for field assistance and to Medes MPA staff for providing permits and cartography. Aitana Oltra aided with the analyses in GIS, Marc Macias and Aslak Grinsted helped with CWT time series analysis, and John Palmer and Antoni Fernández-Guerra helped with the implementation of BBMM. We would also like to thank Liliana Salvador, Rohan Arthur and four anonymous reviewers for their insightful comments. Fig. 6.1 uses a topographic base map 1:50 000 property of Institut Cartogràfic de Catalunya (accessible from `www.icc.cat`). This research has been funded by the Spanish Ministry of Science and Innovation (projects CTM2010-22273-C02-01 and 02). The Spanish Ministry of Education supported JP (scholarship AP2008-01601). We are indebted with Àlex Lorente, responsible for the Medes Islands marine reserve that sadly deceased in a diving accident. He was always willing to make the reserve a pleasant and easy place to work.

Appendix [3]

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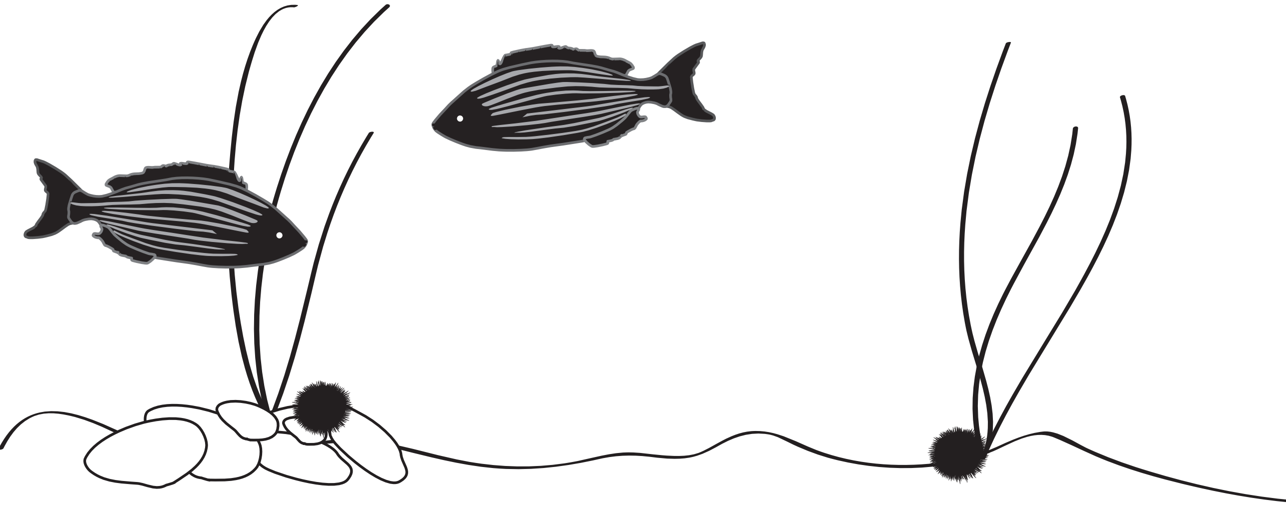
[3] See supplementary materials in Appendix A.

7

Seascape attributes influence seagrass-herbivore interactions



Resum

Els atributs de paisatge poden influenciar l'estructura de les poblacions, la composició de les comunitats i els processos ecològics. Malgrat la seva importància, però, els efectes del paisatge en les funcions ecosistèmiques han estat generalment aproximades a través de l'estudi de l'abundància i la riquesa d'espècies del sistema. L'herbivorisme és un procés ecològic que pot veure's afectat per diversos atributs del paisatge. El nostre objectiu va ser l'anàlisi dels efectes de tres atributs (la composició de la matriu, la distància a les roques més properes i l'efecte dels marges) sobre els nivells reals d'herbivorisme, en un sistema planta-herbívors relativament senzill. Els paisatges escollits (en 3 llocs relativament similars) estan dominats per la planta marina *Posidonia oceanica*, el principal productor primari dels ecosistemes bentònics Mediterranis, que és capaç de créixer en fons rocosos i en fons de sorra (diferents matrius). Els seus dos herbívors principals són el peix *Sarpa salpa* i la garota *Paracentrotus lividus*. Ambdues espècies presenten diferències de moviment, comportament i risc de depredació. La nostra hipòtesi era que la interacció entre el comportament alimentari d'aquestes espècies i la configuració del paisatge influenciaria els impactes en la planta. Per això, vam mesurar les taxes d'herbivorisme, l'abundància d'herbívors, producció primària i qualitat de la planta (C:N) en taques de la planta marina envoltades de roca o sorra (atribut de matriu), en taques a prop o lluny de zones rocoses (atribut de distància) i en els marges i el centre de praderes limitant per un costat amb roca i per l'altre amb sorra (atribut de marges). Els nostres resultats mostren que la matriu i els marges de la pradera van afectar significativament els nivells reals d'herbivorisme, essent la causa d'això el comportament alimentari de les dues espècies d'herbívors claus del sistema. En canvi, la qualitat de la planta no va explicar els patrons observats, ja que entre els diferents atributs no va variar la raó C:N. Les taxes d'herbivorisme van ser més altes en les taques en matriu de roca que en les de matriu de sorra; i l'herbivorisme al centre de les praderes va ser més alt que als marges. En canvi, la distància entre taques de posidònia i les zones de roca no va afectar els nivells d'herbivorisme, almenys en l'escala del present estudi. L'heterogeneïtat espacial observada en l'herbivorisme pot tenir implicacions importants en altres processos ecològics. Els nostres resultats reforcen la idea que cal un estudi més holístic, no només de l'abundància-distribució de les espècies sinó també dels processos ecològics com l'herbivorisme, ja que zones amb abundàncies similars d'herbívors poden tenir nivells d'herbivorisme dispars.

Abstract [1]

Landscape attributes can strongly influence population structure, community composition and ecosystem processes. However, despite their importance, the effects of landscape structure on ecosystem functions have been mostly drawn from data on species richness and abundance. Herbivory is a key ecological process that may be affected by several landscape attributes. Our aim was to assess the effects of three attributes (i.e. matrix composition, distance to the nearest rocky reef and edges effects) on the actual levels of herbivory in a relatively simple plant-herbivore system. The chosen seascapes (at 3 relatively similar and representative sites) were dominated by the seagrass *Posidonia oceanica*, the dominant benthic producer in the Mediterranean, which can grow over sand or rocky bottoms (matrix). The two principal seagrass herbivores are the fish *Sarpa salpa* and the sea urchin *Paracentrotus lividus*. Both display differences in movement, behaviour and predation risk. We hypothesised that the interaction of the animal feeding behaviour with the seascape would influence their impacts on the seagrass. We measured herbivory rates, herbivore abundance, primary production and plant quality (C:N) in seagrass patches embedded in rock or sand (matrix attribute), in patches near or far from a rocky reef (distance attribute) and at the edges and interior of meadows limiting with rocky habitats from one side and sand areas to the other (edges attribute). Our results show that matrix and meadow edges significantly affected the actual levels of herbivory, being the cause of these effects the feeding behaviour of the two key herbivores of the system. Food quality did not explain the detected herbivory patterns, as similar C:N values were observed between the different seascape attributes. Herbivory rates were higher in seagrass patches embedded in a rocky matrix compared to those on a sand matrix; and herbivory at the centre of seagrass meadows was higher than at the edges. In contrast, patch distance to rocky reefs did not affect herbivory, at least at the scale tested. The observed spatial heterogeneity may have sound consequences on other ecological processes. Our results enforce the idea that the study of not only species abundance or distribution, but also of ecosystem processes, such as herbivory, may be crucial in improving our knowledge of landscape ecology, since areas with similar abundances of herbivores may show contrasting herbivory levels.

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[1] Pagès, J.F., Gera, A., Romero, J., Alcoverro, T. (in preparation).

7.1 Introduction

Landscape attributes can strongly influence population structure, community composition and ecosystem processes (Pickett & Cadenasso, 1995). Traditionally, most landscape studies have dealt with the influence of landscape attributes on species distribution, abundance or richness (Dieköetter et al., 2007). In contrast, fewer studies have focused on the effects of these attributes on ecosystem processes, functions or indirect interactions (but see Andren & Angelstam, 1988; Cronin, 2003; Dieköetter et al., 2007; Macreadie et al., 2012). Moreover, despite their importance, functional effects have been drawn mostly from data on species richness and abundance (Valladares et al., 2006).

One of the processes usually claimed to be highly affected by landscape structure is herbivory (e.g. Dieköetter et al., 2007; Haynes & Crist, 2009), which is acknowledged to be a key ecological process (Burkepile, 2013) known to regulate rates of primary production and nutrient cycling (Abbas et al., 2012; Gera et al., in press), to influence species interactions (Martin et al., 1989; Pringle et al., 2007; Pagès et al., 2012) or community composition, diversity and biomass (Hobbs, 1996; Knapp et al., 1999) among others. Again, however, the understanding of the influence of landscape attributes on herbivores' activity has mostly been drawn from indirect evidences, such as herbivore abundance or distribution (e.g. Dieköetter et al., 2007) or visual assessments of damaged tissues (e.g. Thies et al., 2003; Simonetti et al., 2007). There is large available evidence that herbivores do not distribute randomly across the mosaic of habitats, and often concentrate or dilute in space as a function of the landscape configuration, generating spatial heterogeneity (Pickett & Cadenasso, 1995; Vergés et al., 2011). This is in part the result of species-specific perception abilities (Thies et al., 2003), and of the fact that herbivores can interact with landscapes at several levels (Dunning et al., 1992), according to their degree of mobility (Ricketts, 2001).

Mobile generalist herbivores may make foraging choices based on specific properties of the patch, i.e. as a function of the amount of patch resources (i.e. patch size, MacArthur & Pianka, 1966), as a function of food quality (i.e. high-quality, less-defended patches are expected to be preferred; Haynes & Cronin, 2004), taking predation risk into account (the so-called landscape of fear; e.g. Brown & Kotler, 2004) or influenced by social behaviour (e.g. McNaughton, 1984; Black et al., 1992). In addition, the context in which the patch is embedded (i.e. the landscape) may be influential. In a landscape composed of patches of focal habitat embedded in a matrix habitat, generalist mobile herbivores have been shown to often choose patches within a matrix with other resources that may complement or supplement their diet (i.e. complementation or supplementation hypotheses, Dunning et al., 1992; Haynes et al., 2007).

In contrast, landscape effects on low-mobility herbivores, are of a different nature.

Low-mobility herbivores are more prone to be affected by the presence of edges, which may be a barrier for their movement (Ricketts, 2001). In these cases, patch-specific patterns may dominate, and recruitment-mortality processes within the patch may become the main driver of herbivore abundance and eventually of herbivory pressure. Indeed, herbivores may either aggregate in areas close to habitat edges (Cantrell & Cosner, 1999; Haynes & Cronin, 2003) or avoid them, as predation is known to be more intense in the edges of habitats than in the centre (Andren & Angelstam, 1988; Gorman et al., 2009), both mechanisms generating potential edge-related heterogeneities. However, if edges are more permeable (i.e. soft edges, e.g. between two types of vegetated areas) low-mobility herbivores may be able to move between both areas and their choices and foraging behaviour may be influenced by similar factors as for mobile herbivores (see previous paragraph). Again, matrix composition has been shown to be a crucial aspect in determining how edges will be perceived (Cronin, 2003; Haynes & Cronin, 2003). If the matrix habitat is very contrasting with the patch habitat, edges may be perceived as hard, thus inhibiting migration; conversely, less contrasting matrix types, with similar structure to patch habitat, may favour softer patch edges (i.e. low contrast), with higher permeability (Stamps et al., 1987). These aspects, will influence the movement ecology of low mobility herbivores and their abundance-distribution patterns thus affecting the processes within focal habitat patches (Haynes & Cronin, 2003, 2006).

Underwater landscapes in the coastal zone (seascapes), as many other linear ones (such as those along rivers, or tops of mountain chains), naturally consist of relatively small patches of habitat isolated one another by matrices of different nature and with a tendency of being miniaturized (Goodsell et al., 2007). This type of structure makes them ideal candidates to study ecosystem processes at a scale that is relevant for the seascape (Nally & Quinn, 1998). However, it has also to be taken into account that marine seascapes have specific features that make them unique. Seascapes are generally more connected than terrestrial systems, and this may mean that some seascape barriers could be less important, particularly during the larval phases (Tanner, 2006). However, hard edges also exist in the sea, particularly for the adult phase of animals with restricted movement patterns (e.g. echinoderms, Hereu, 2005).

Seagrass meadows are common nearshore vegetated ecosystems, frequently interspersed with rock or sandy habitats and with a propensity to form differently sized patches, specially in shallow areas (i.e. 0-10 m). Thus, the understanding of their ecological functions at a seascape level seems relevant. Indeed, it is known that seagrass patch size influences within-patch species richness and abundance (e.g. MacReadie et al., 2009), that patches embedded in different matrices display contrasting species abundances (e.g. Tanner, 2006), that edges can modify within-patch species abundance and distribution (Smith et al., 2010), and that seagrass patches display shorter canopies near coral reefs than far from them (Valentine et al., 2007). More recently, ecosystem processes, such as primary production and nutrient cycling have also been observed to change as a result of seagrass patch size (Gera et al., in press), and specifically, herbivory increases with the reduction of the meadow size (Prado et al., 2008). However, studies dealing with the effects of seascape attributes on seagrass ecosystem processes are very scarce, and those assessing the effects of seascape attributes other than patch size, on seagrass functioning, to the best of our knowledge, are very limited.

In this study we take advantage of a relatively simple plant-herbivores system that consists on one plant species (the Mediterranean endemic seagrass *Posidonia oceanica*) and two dominant herbivorous species, a fish and an echinoderm. Both are generalists, strong interactors (Pagès et al., 2012) and display contrasting movement patterns (high and low mobility). We expect that different seascape attributes will differently affect each of these herbivores, and thus their herbivory rates, according to their mobility. We want to test if behind the multiple herbivore-mediated processes interacting with the seascape, there is any generalised attribute that can determine the spatial patterns of herbivory in seagrass-dominated seascapes in the Mediterranean, and try to elucidate some of the mechanisms behind them. Specifically, we assessed the actual levels of herbivory of each herbivore in (i) seagrass patches embedded in rock or sand matrices (hereafter matrix attribute), (ii) seagrass patches embedded in a sand matrix and either near or far from rocky reefs (hereafter distance attribute) and (iii) at the centre and edges of seagrass meadows bordering from one side with a rock matrix (rock edge) and from the other with a sand matrix (sand edge; hereafter edges attribute) (see Fig. 7.1). Additionally, plant quality was assessed in each of these patches.

7.2 Materials and methods

Study system

Posidonia oceanica (L.) Delile is a habitat-forming seagrass whose meadows, considered among the most productive communities in the Mediterranean (Cebrian et al., 1996), provide shelter, food or substrate to a great number and variety of species (Mazzella et al., 1989; Francour, 1997). This seagrass tends to form patchy meadows, specially in shallow areas, and it can be found growing over rocky substrates (i.e. embedded within a rock matrix)

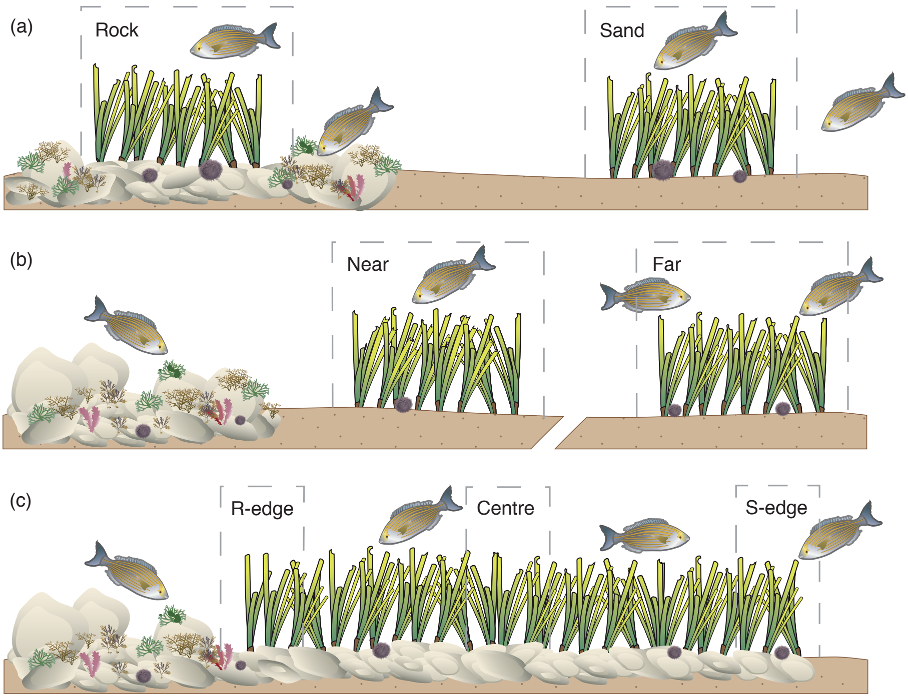

Figure 7.1: Experimental design. (a) Matrix experiment consisted of measuring ecological features from seagrass patches embedded in a rock matrix (n = 4) and patches in a sand matrix (n = 4), in 3 sites. (b) Distance experiment involved measuring ecological parameters from seagrass patches embedded in a sand matrix and either near (*c.* 5 m, n = 4) or far (*c.* 20 m, n = 4) from a rocky reef, in 3 sites. (c) In the edges experiment we measured ecological features in 5 zones at the centre of a meadow (*c.* 200 m^2) and 5 zones at the rock and sand edges, also in 3 sites.

or in sand areas (i.e. embedded within a sand matrix) (e.g. Montefalcone et al., 2010). The macroherbivore guild is limited, with just two key species responsible for the bulk herbivory: the sparid fish *Sarpa salpa* (L.) and the sea urchin *Paracentrotus lividus* (Lam.) (Tomas et al., 2005b). Both are considered generalists and can produce great impacts in different macrophyte communities, consuming on average more than 40% of seagrass leaf production (Prado et al., 2007). Maximum activity of both herbivorous species is concentrated in summer and at the upper infralittoral zone (Prado et al., 2007).

The sparid fish *S. salpa* is considered a roving herbivore that displays home ranges on the order of hectares (Jadot et al., 2006, Pagès et al. unpublished manuscript). It is a generalist capable of connecting distant habitats (on the order of kilometres, Pagès et al. unpublished manuscript). Adults tend to prefer seagrass leaves (but they also feed frequently on macroalgae) and juveniles' diet is usually more based on macroalgae (Verlaque, 1990). It is a schooling herbivore (hundreds of individuals) and we can assume that nowadays adults are subject to a very limited predation risk, if any. In contrast, *P. lividus* sea urchins display restricted movement patterns (average distance from initial position after 3 months = 1.5 m, Hereu, 2005), and generally do not cross sandy areas (Dance, 1987). *P. lividus* diet is also varied, and involves different species of macroalgae, and seagrass leaves as well. In addition, both the adults and the juveniles of this species are highly preyed by a wide variety of fishes (Sala, 1997). Considering that *S. salpa* and *P. lividus* are the only important herbivores in the Western Mediterranean seagrass meadows, these differences in movement, behaviour and predation risk may determine their ability to forage in different seascape configurations and may influence their impacts on the ecosystem.

Field design

To assess the importance of different seascape attributes (matrix, distance to neighbouring habitats and matrix dependent edge effects) in determining herbivory rates we selected three shallow (5-8 m depth) *P. oceanica* seagrass meadows with a similar seascape configuration. The sites, separated by few kilometres, are situated along the northern part of the Catalan coast (NW Mediterranean). The experimental deployment, for each site, was as follows. For the matrix attribute we selected eight seagrass patches of similar sizes (mean size = 5.1 ± 0.9 m^2) embedded in two different matrices: 4 patches in 'rock' and 4 patches in 'sand' (Fig. 7.1a). For the distance attribute, we again selected eight seagrass patches of similar sizes (mean size = 4.1 ± 0.5 m^2) all embedded in a sand matrix and either 'near' (4 patches, mean distance from a rocky reef = 5.6 ± 0.7 m) or 'far' from a rocky reef (4 patches, mean distance from a rocky reef = 23.1 ± 2 m) (Fig. 7.1b). For the edge attribute, we selected 15 zones (approx. 5 m2) within a continuous meadow at 3 positions: 5 at the centre of the meadow, 5 at the edge bordering with a rock matrix ('rock edge') and 5 at the edge limiting with a sand matrix ('sand edge') (Fig. 7.1c). At each one of the selected patches (or zones) we measured total and herbivore-specific (fish or sea urchin) herbivory rates. To assess the impact of these herbivory rates and for comparative purposes, we also measured primary production. Herbivore abundance was also estimated, to test if the rates of herbivory were related to site-specific or attribute-specific herbivore abundance. Additionally, to test if plant quality was responsible for any of the observed patterns we analysed plant tissues nutrient content (carbon:nitrogen ratio).

Response variable assessments

Primary production (as inferred from its surrogate, leaf growth) and direct herbivory rates were estimated in July 2011, when herbivory is at its seasonal maximum (Prado et al., 2007), on the same *P. oceanica* shoots. Primary production was estimated using a modified Zieman's method (Zieman, 1974; Pérez & Romero, 1994) and herbivory was assessed with a tethering technique similar to the one used in Prado et al. (2007). SCUBA divers marked 5 shoots per patch for matrix and distance experiments (5 shoots per patch, 4 patches, 2 conditions, 3 sites, resulting in a total of 120 marked shoots for each experiment [matrix and distance]) and 3 shoots per zone for edges experiment (3 shoots per zone, 5 zones, 3 positions, 3 sites, resulting in a total of 135 marked shoots). In each shoot we marked the base of the leaves (piercing the leaf with a needle) to measure leaf elongation. We also counted the initial number of leaves, the initial leaf length and the state of the apical part of each leaf (broken, eaten by fish, eaten by sea urchin or intact). 15 days later all marked shoots were collected and were transported to the lab for sorting. For each shoot, we counted the number of leaves, and, for each leaf, we measured its length and examined the state of the apical part. For each leaf, the new leaf tissue produced (between the pierced mark and the ligula) was also measured (i.e. leaf elongation). Primary production (cm shoot^{-1} day^{-1}) of pierced shoots was determined by dividing the cm of new tissue produced by the number of days elapsed since marking. Shoot herbivory rates (cm shoot^{-1} day^{-1}) were estimated for each of the collected shoots by adding leaf elongation (cm of new tissues produced) to the initial length and subtracting this total from the final leaf length, finally divided by the number of days elapsed since marking (Prado et al., 2007). Only leaves that had clear herbivore bite marks were assigned to herbivory and the rest were discarded to avoid herbivory overestimates. Both herbivores leave bite marks of distinctly identifiable shapes (e.g. Tomas et al., 2005b), we were therefore able to separately estimate seagrass removal rates for sea urchins and for fish (herbivore-specific herbivory rates). In statistical analyses, the mean of these 3-5 marked shoots was taken as the primary production and herbivory rate of each experimental unit (i.e. patch [matrix, distance experiments] or zone of the meadow [edges experiments]). Production-herbivory balances were obtained by subtracting herbivory (cm shoot^{-1} day^{-1}) from production (as leaf elongation, cm shoot^{-1} day^{-1}) to assess whether shoot length (and, consequently, canopy height) was overall increasing (if production outpaced herbivory) or decreasing (if herbivory was greater than production) for the period considered (July, i.e. early summer).

Sea urchin density for each condition was determined by counting adult sea urchin abundance (test size $\geq$ 3 cm) in quadrats randomly placed in each patch for matrix and distance experiments (3 quadrats per patch, 4 patches, 2 conditions, 3 sites, resulting in a total of 72 quadrats for each experiment) or zone for the edges experiment (2 quadrats per zone, 5 zones, 3 positions, 3 sites, resulting in a total of 90 quadrats). In statistical analyses, the mean of these 3-2 quadrats was taken as the sea urchin density of each experimental unit (i.e. patch [matrix, distance experiments] or zone of the meadow [edges experiments]). We did not assess fish herbivore abundance in each condition since *S. salpa* are very mobile and display a home range greater than our experimental scale (i.e. on the order of hectares Jadot et al., 2006, Pagès et al. unpublished manuscript). We therefore can assume that within each site, every patch or zone is equally susceptible of being visited by *S. salpa* fishes. As a result, potential differences in fish herbivory between matrices, distances to the rocky reef or zones will be the result of behavioural choices made by these fishes.

Leaf nitrogen (% N) and carbon (% C) were analysed in order to obtain C:N ratio, which has been used as an indicator of food (plant) quality (e.g. Haynes & Cronin, 2004). To obtain adequate leaf biomass for these analyses we pooled 3-5 shoots together resulting in one sample per experimental unit (i.e. per patch [matrix and distance experiments, 4 patches, 2 conditions, 3 sites, 24 samples in total] or per zone [edges experiment, 5 zones per position, 3 positions, 3 sites, 45 samples in total]). Seagrass leaves were dried at 70ºC for 48 hours, ground to a fine powder and then encapsulated. Leaf nitrogen and carbon concentration were measured using an elemental analyser EA1108 (Carlo Erba Instruments).

Statistical analyses

We used linear mixed effects models to determine how seagrass response variables (i.e. total herbivory rates, herbivore-specific herbivory rates, sea urchin density, primary production, production-herbivory balance and plant quality [C:N ratio]) varied according to the different seascape attributes studied (i.e. matrix composition, distance to the nearest rocky reef, edge effects). For the matrix attribute, 'matrix' was considered a fixed factor with 2 levels (rock and sand); for the distance attribute, 'distance' was considered a fixed factor with 2 levels (near and far); and for the edges attribute, 'position' was the fixed factor with 3 levels (rock edge, centre, sand edge). In addition, 'site' was included as a random factor to account for the variance shared between those measurements taken from the same site (3 levels, the 3 sites [except for the variables related to herbivory in the edges experiment, which only had 2 suitable sites, since the third hardly presented herbivory at all, possibly due to a problem with the shoot marking technique]). In those attributes that involved patches (matrix and distance attributes) patch size (m^2) was also included into the models as a covariate to control for this possible source of variation. Finally, to assess the response variable herbivore-specific herbivory rate, 'animal' was also included into the model as a fixed factor with 2 levels (fish and sea urchin).

We conducted multiple comparisons using Tukey's HSD on those dependent variables that showed a significant effect in our linear mixed effects analyses. This enabled us to test pairwise differences between variables. Normality and homogeneity were checked graphically by inspecting residuals and fitted values. Whenever a variable was clearly heteroscedastic its variance structure was included as weights within the linear mixed effects model and the best weighted model was selected using Akaike's Information Criterion (AIC) (Zuur et al., 2009). All data were analysed with the packages nlme and lme4 in the statistical software R (Bates et al., 2011; Pinheiro et al., 2011; R Development Core Team, 2012).

7.3 Results

Matrix composition had a significant effect on total herbivory rates(Table 7.1). Indeed, those meadows embedded in a rock matrix suffered three-times more herbivory than those surrounded by a sand habitat (Fig. 7.2a), and this was independent of the site (Table 7.1). There were no significant differences between herbivore-specific rates in any of the matrix types, although fish herbivory (57 ± 15%) seemed to prevail over sea urchin herbivory rates in both of them (Fig. 7.2b). We did not find any shift on the proportion of herbivory caused by each herbivore species according to matrix composition (matrix × animal effect not significant, Fig. 7.2b, Table 7.1). Sea urchin density was not significantly different across matrices, despite a tendency of increased sea urchin densities in patches embedded in rock matrix compared to the ones in sand (Fig. 7.2c, Table 7.1). Seagrass primary production was not affected by the intervening matrix composition either (Table 7.1) and was very similar between patches embedded in both matrix types (mean = 1.7 ± 0.3 cm shoot^{-1} day^{-1}, Fig. 7.2d). Accordingly, the production-herbivory balance in shoots from patches within the rock matrix was negative, with a daily mean of leaf length loss of 0.82 ± 0.3 cm; in contrast, shoots from sand patches presented a neutral balance between herbivory and production (Fig. 7.2e, Table 7.1). No differences in plant quality were found between seagrass patches on sand or rock matrices (Fig. 7.2f).

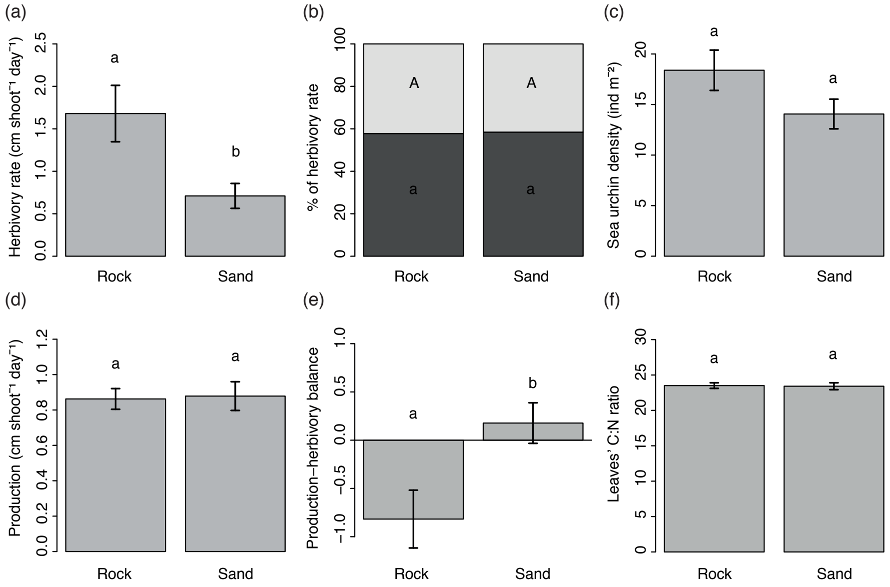

Figure 7.2: Matrix experiment. (a) Total herbivory rates, (b) percentage of herbivory rate accounted by each herbivore (dark grey bars correspond to fish herbivory [*S. salpa*] and light grey ones to urchin herbivory [*P. lividus*]), (c) sea urchin density, (d) seagrass primary production, (e) balance between production and herbivory (cm shoot^{-1} day^{-1}) and (f) plant quality (leaves' C:N ratio) in *P. oceanica* patches embedded in a rock or in a sand matrix. Bars labelled with the same letter do not differ significantly according to a Tukey HSD post hoc test.

Table 7.1: Model results for the matrix experiment. The significance of random factors was assessed comparing the mixed effects with the linear model using the Akaike's Information Criterion (AIC); thus, we cannot display the F-values of these tests.

Response variable	Effects	d.f.	F	*P*-value
Herbivory	Site (random)	2	-	0.812
	Matrix	1	23.2	**0.000** ***
	Size	1	595.7	**0.000** ***
	Matrix × size	1	15.1	**0.001** **
	Residual	18		
Herbivore-specific herbivory	Site (random)	2	-	0.648
	Matrix	1	4.1	**0.050** *
	Animal	1	0.4	0.520
	Size	1	1.6	0.214
	Matrix × animal	1	0.4	0.516
	Matrix × size	1	0.9	0.342
	Animal × size	1	0.8	0.379
	Matrix × animal × size	1	0.6	0.441
	Residual	36		
Sea urchin density	Site (random)	2	-	0.999
	Matrix	1	1.8	0.195
	Size	1	0.9	0.352
	Matrix × size	1	0.0	0.996
	Residual	18		
Primary production	Site (random)	2	-	**0.01** **
	Matrix	1	0.6	0.466
	Size	1	1.8	0.194
	Matrix × size	1	1.1	0.314
	Residual	18		
Production-herbivory balance	Site (random)	2	-	1
	Matrix	1	13.2	**0.002** **
	Size	1	443.4	**0.000** ***
	Matrix × size	1	5.5	**0.030** *
	Residual	18		
Plant quality (C:N)	Site (random)	2	-	**0.028** *
	Matrix	1	0.0	0.920
	Size	1	0.5	0.487
	Matrix × size	1	6.0	**0.026** *
	Residual	16		

d.f. degrees of freedom. Significance codes: *P*-value < 0.001***, < 0.01**, ≤ 0.05*

Patch distance from rocky reefs did not influence total herbivory rates, with very similar values between patches near and far from the rocky reefs (Fig. 7.3a, Table 7.2). However, fish herbivory was significantly higher than urchin herbivory (Table 7.2) only in patches far from the rocky reefs according to pairwise comparisons (i.e. differences between grazers not significant in patches 'near'). Specifically, while each herbivore accounted for half of the total herbivory rates in 'near' patches, in 'far' patches fish herbivores made up three-quarters of the total herbivory with sea urchins grazing the remaining quarter (Fig. 7.3b). Distance to the rocky reef did not have an effect on sea urchin densities, despite a tendency of lower densities in distant patches compared to those near the rocky reef (Fig. 7.3c, Table 7.2). Similarly, we found no effects of distance on primary production, production-herbivory balances or plant quality (Fig. 7.3d,e,f, Table 7.2). The random factor 'site' did not show significant effects on any of the response variables studied (Table 7.2).

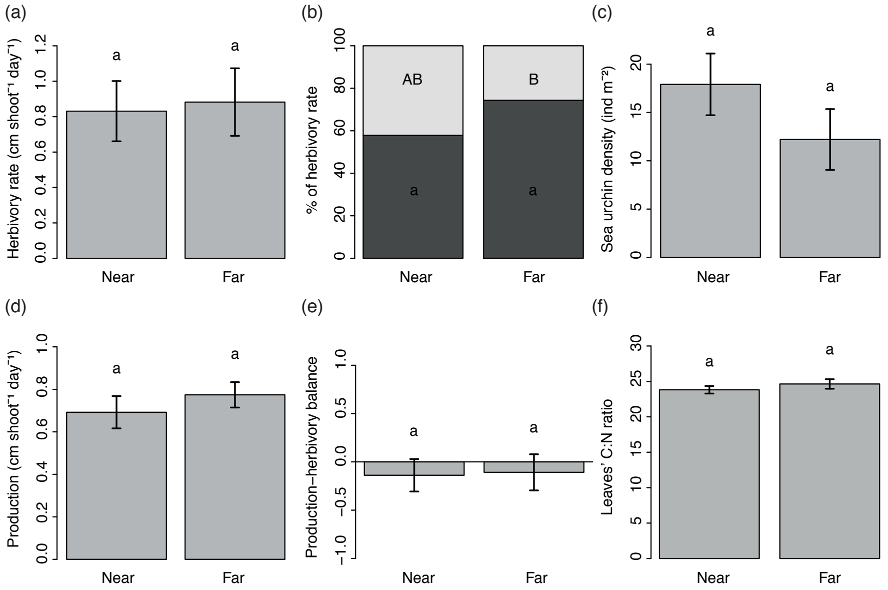

Figure 7.3: Distance experiment. (a) Total herbivory rates, (b) percentage of herbivory rate accounted by each herbivore (dark grey bars correspond to fish herbivory [*S. salpa*] and light grey ones to urchin herbivory [*P. lividus*]), (c) sea urchin density, (d) seagrass primary production, (e) balance between production and herbivory (cm shoot^{-1} day^{-1}) and (f) plant quality (leaves' C:N ratio) in *P. oceanica* patches placed either near or far from a rocky reef. Bars labelled with the same letter do not differ significantly according to a Tukey HSD post hoc test.

Table 7.2: Model results for the distance experiment. The significance of random factors was assessed comparing mixed effects with linear models using the Akaike's Information Criterion (AIC); thus, we cannot display the F-values of these tests.

Response variable	Effects	d.f.	F	*P*-value
Herbivory	Site (random)	2	-	0.532
	Distance	1	0.0	0.947
	Size	1	0.1	0.708
	Distance × size	1	0.3	0.562
	Residual	19		
Herbivore-specific herbivory	Site (random)	2	-	0.222
	Distance	1	0.0	0.933
	Animal	1	5.5	**0.025** *
	Size	1	0.1	0.757
	Distance × animal	1	1.0	0.321
	Distance × size	1	0.5	0.474
	Animal × size	1	0.0	0.894
	Distance × animal × size	1	0.0	0.968
	Residual	40		
Sea urchin density	Site (random)	2	-	0.173
	Distance	1	0.0	0.905
	Size	1	6.9	**0.017** *
	Distance × size	1	4.7	**0.047** *
	Residual	18		
Primary production	Site (random)	2	-	1
	Distance	1	0.0	0.845
	Size	1	5.7	**0.027** *
	Distance × size	1	0.0	0.948
	Residual	18		
Production-herbivory balance	Site (random)	2	-	0.113
	Distance	1	0.0	0.900
	Size	1	0.0	0.860
	Distance × size	1	0.4	0.549
	Residual	18		
Plant quality (C:N)	Site (random)	2	-	0.992
	Distance	1	0.1	0.762
	Size	1	10.5	**0.004** **
	Distance × size	1	0.2	0.672
	Residual	19		

d.f. degrees of freedom. Significance codes: P-value < 0.001***, < 0.01**, $\leq$ 0.05*

Position within the meadow had a clear influence on herbivory (Fig. 7.4a, Table 7.3). Both edges presented lower levels of herbivory compared to the centre of the meadow, but differences were only significant between the rock edge and the centre of the meadow according to Tukey's HSD pairwise comparison. Specifically, herbivory rates were 3.6 times higher at the centre of the meadow compared to the rock edge (Fig. 7.4a). These differences are attributable to an increased pressure exerted by fish grazers at the centre of the meadow (as shown by the significant grazer effect; Fig. 7.4b, Table 7.3), which accounted for the 80% of the total herbivore rate at this zone. Sea urchin density was not significantly different among positions in the meadow, despite a non-significant trend to lower sea urchin density from the rock towards the sand edge (Fig. 7.4c, Table 7.3). Primary production and plant quality did not differ according to meadow position (Fig. 7.4d,f, Table 7.3). Accordingly, significant differences on production-herbivory balances were evident (Table 7.3), with a highly negative balance at the centre of the meadow (shoots shortening) compared to the edges, especially to the rock edge, whose shoots displayed a slightly positive balance (Fig. 7.4e). The random factor 'site' did not show significant effects on any of the response variables studied (Table 7.3).

For the experiments that involved the use of discrete patches as experimental units, the covariate patch size presented significant relationships with primary production (Tables 7.1 and 7.2) and plant quality (Table 7.2), as has been previously found in studies with the same seagrass species (Gera et al., in press).

7.4 Discussion

Our results demonstrate that seascape attributes can modulate herbivory in seagrass ecosystems. Specifically, both matrix composition and edges effects influenced herbivore consumption, while we did not find any significant distance effect. Herbivory rates were increased in seagrass patches embedded in a rocky matrix compared to those on a sand matrix; and herbivory inside seagrass meadows was higher than at the edges. Moreover, edge effects appeared to be matrix dependent. In contrast, patch distance to rocky reefs did not play any role at determining plant-herbivore interactions or ecological processes in *P. oceanica* seagrass meadows, at least at the scale tested. Previous studies on terrestrial systems had found that matrix composition affected herbivore abundances (Haynes et al., 2007; Haynes & Crist, 2009; Öckinger et al., 2012), pollinator visitation (Dieköetter et al., 2007), herbivore movements (Ricketts, 2001; Haynes & Cronin, 2003), and plant damage (Thies et al., 2003). Here we show that matrix and patch edges significantly affected the actual levels of

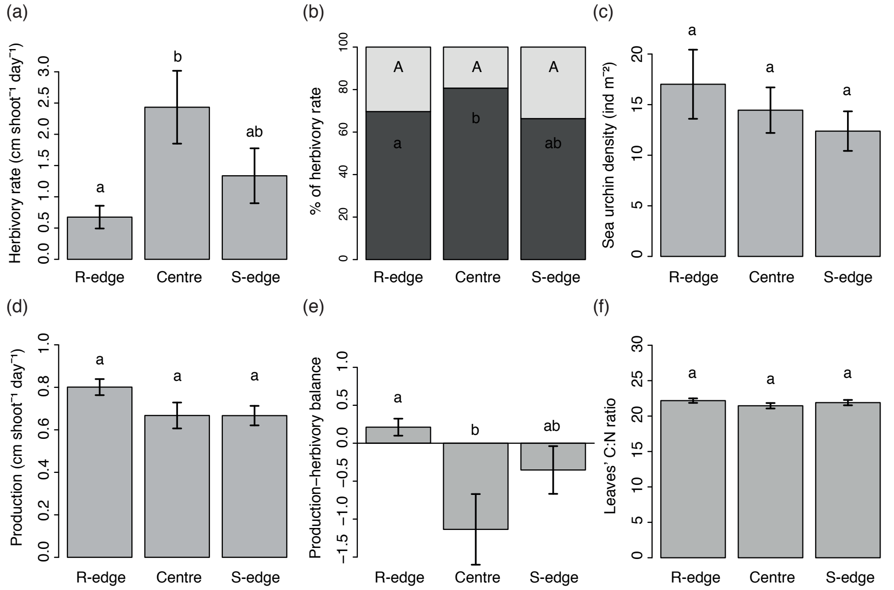

Figure 7.4: Edges experiment. (a) Total herbivory rates, (b) percentage of herbivory rate accounted by each herbivore (dark grey bars correspond to fish herbivory [*S. salpa*] and light grey ones to urchin herbivory [*P. lividus*]), (c) sea urchin density, (d) seagrass primary production, (e) balance between production and herbivory (cm shoot^{-1} day^{-1}) and (f) plant quality (leaves' C:N ratio) in areas placed at the rock edge, centre or sand edge of *P. oceanica* meadows. Bars labelled with the same letter do not differ significantly according to a Tukey HSD post hoc test.

herbivory being the cause of this effect the feeding behaviour of the two key herbivores of the system, and not the differences in food quality as has been widely reported (Haynes & Cronin, 2004).

Herbivory was maximal at the centre of seagrass patches while edges were less grazed (specially the rocky edge). This grazing peak at the centre of meadows was likely related to fish herbivores' behaviour, since fish herbivory was particularly higher at meadow interiors, attaining the 80% of the total herbivory rates measured at the meadow centre (Fig. 7.4b). Similar patterns have been attributed to higher predation risk at the edges, which has been shown, in turn, to imply not only abundance, but also behavioural effects on other marine species, leading to lower impacts on their resources (Macreadie et al., 2012). This does not seem to be the case here, given the present rarity of *S. salpa* predators. Most likely, the grazing peak at the centre of meadows is related to group feeding behaviour in this species. For fishes foraging in large schools it may be optimal to start foraging from the centre of meadows, as has been observed for goose flocks (Black et al., 1992). Because flocks land

Table 7.3: Model results for the edges experiment. The significance of random factors was assessed comparing the mixed effects with the linear model using the Akaike's Information Criterion (AIC); thus, we cannot display the F-values of these tests.

Response variable	Effects	d.f.	F	*P*-value
Herbivory	Site (random)	1	-	1
	Position	2	6.8	**0.004 ****
	Residual	25		
Herbivore-specific herbivory	Site (random)	1	-	1
	Position	2	3.6	**0.036 ***
	Animal	1	5.3	**0.026 ***
	Position × animal	1	1.8	0.183
	Residual	50		
Sea urchin density	Site (random)	2	-	1
	Position	2	0.8	0.467
	Residual	24		
Primary production	Site (random)	2	-	1
	Position	2	2.7	0.08
	Residual	40		
Production-herbivory balance	Site (random)	2	-	0.107
	Position	2	4.9	**0.012 ***
	Residual	40		
Plant quality (C:N)	Site (random)	2	-	1
	Position	2	1	0.380
	Residual	40		

d.f. degrees of freedom. Significance codes: *P*-value < 0.001***, < 0.01**, ≤ 0.05*

in the middle of fields and forage outwards, the centre of fields are exploited more heavily than the edges (Black & Owen, 1989; Krebs & Davies, 1993). Sea urchin herbivory, in contrast, appeared to play a minor role in determining the observed herbivory patterns. Sea urchin abundance at the rock-seagrass edge was slightly (although non-significantly) higher than at the centre and at the seagrass-sand edge, most possibly due to a migration of recruits from the rocky matrix (Prado et al., 2012). These differences in abundance were not reflected on the total herbivory rate.

Matrix composition played a major role in influencing herbivory rates of both generalist herbivores of the system, with herbivory rates in seagrass patches embedded in rocks being three times higher than those of patches embedded in sand. This is consistent with several studies that have observed that generalist species are more prone to be affected by the intervening matrix than specialists (Brotons et al., 2003; Steffan-Dewenter, 2003; Dieköetter et al., 2007). Eventually, the feeding specialization of the principal herbivores of the system will determine the manner and strength with which landscape attributes affect levels of herbivory (Haynes & Crist, 2009), since generalists may feed both on the focal habitat (in this case the seagrass) and in the intervening matrix (in this case, the sand or rocky matrix, but only rocky areas sustain macroalgal growth). A possible mechanism behind the patterns observed is the complementation or supplementation hypotheses (Dunning et al., 1992). These hypotheses highlight the requirement for many species to link together different habitat elements, including a wider variety of food resources, to complete their life cycles (Dunning et al., 1992; Haynes et al., 2007). Matrix composition has however also been found to frequently covary with other factors, in many plant-herbivore systems (Haynes & Cronin, 2004). Plant patch quality is the most frequent confounding factor with matrix composition, since the surrounding habitat may affect abiotic and biotic processes within the patch. Nutrient availability, water movement, light availability and competitive interactions could vary between matrices (Haynes & Cronin, 2004). However, seagrass quality did not covary with matrix in the present study, as shown by the similar carbon and nitrogen content of leaves from both matrices. In addition, rocky areas are preferred recruitment sites for sea urchins (Prado et al., 2012), which also find in mixed rocky-seagrass mosaics high availability of shelter and from which they have been observed to migrate to seagrass patches (Ceccherelli et al., 2009). In contrast, sea urchins cannot recruit, forage or shelter in sandy areas, and they generally do not cross seagrass-sand edges (Dance, 1987). Indeed, matrix type has been shown to affect edge-mediated behaviour and emigration rates of various species (Ricketts, 2001; Haynes & Cronin, 2003, 2006). This has been attributed to differential predation risk according to the matrix they are in. Thus, although we did not find significant differences in sea urchin abundance between patches embedded in rock or in sand, sea urchins sheltering or foraging within the rock matrix (ignored in our abundance estimates) may cross the rock-seagrass edge and feed on the seagrass, further increasing herbivory in these patches. Conversely, no sea urchin immigration occurs in patches surrounded by sand, since it involves crossing a hard edge (sand-seagrass), and moving across a risky matrix (Farina et al. unpublished manuscript). These aspects could further explain the contrasting herbivory rates found in seagrass patches embedded in rocky areas as opposed to the ones embedded in sand.

Patch distance from rocky reefs did not play a role at determining herbivory rates, despite several studies on coral reefs that have found that herbivory is usually higher close to reefs and decreases with distance (Valentine et al., 2007; Vergés et al., 2011). However, in this case, the selected distance between rocky reefs and the farthest patches was clearly insufficient to find any pattern given the known mobility of *S. salpa*, which can even connect habitats separated on the order of kilometres (Pagès et al. unpublished manuscript). It is interesting to note, however, the higher contribution of fishes to total herbivory rates at far patches compared to the patches near the rocky reef. Indeed, patches 'near' displayed slightly higher (non-significant, though) sea urchin abundance.

We have shown that in seagrass meadows, matrix and edges seascape attributes are capable of inducing spatial heterogeneity in an ecological process: herbivory. The high herbivory rates found in patches embedded in rock compared to sand, and at the interior of meadows compared to the edges may have sound consequences on other ecological processes, particularly at rates exceeding leaf growth. This negative balance does not imply a meadow decline, as it only occurs in early summer, when herbivory is at its maximum and leaf growth at sub-maximum, and is largely compensated over the whole yearly cycle (Prado et al., 2007). However, and despite this, herbivory outpacing production in these areas means that canopy height is decreasing day after day (at a rate of *c.* 1 cm per shoot per day), with possible consequences for predation risk of seagrass-dwelling species, including the sea urchins (Pagès et al., 2012). Moreover, seagrass shoots subjected to these imbalances between production and herbivory have been observed to decrease shoot nutrient stocks (Vergés et al., 2008), likely limiting their long-term primary production or even decrease reproduction (Planes et al., 2011). In spite of the huge herbivory that some seagrass areas suffer, we should bear in mind that herbivory in the Mediterranean is highly seasonal, with high rates during summer and low rates in winter (Prado et al., 2007). This aspect may be crucial for *P. oceanica* seagrass survival in the areas of the seascape where herbivory is more intense.

Our results enforce the idea that the study of not only species abundance or distribution, but also of ecosystem processes, such as herbivory, may be crucial in improving our knowledge of landscape ecology. In this study, by measuring direct herbivory rates, we show that distribution-abundance studies may not be sufficient for a complete understanding of ecosystem processes in different landscapes, since areas with very similar abundances of herbivores showed contrasting herbivory levels. Indeed, despite the impacts of herbivory in marine ecosystems are consistently higher than estimates from terrestrial vegetation (Cyr & Pace, 1993; Cebrian, 1999; Poore et al., 2012), there are few studies assessing the effects of landscape attributes on the actual levels of herbivory in these systems (but see Gera et al., in press). Moreover, the behavioural ecology and movement patterns of the key species of the system may also be fundamental in order to predict the spatial heterogeneity of ecological processes, which may ultimately influence plant production, nutrient cycling, plant reproductive success and trophic pathways of the system.

Acknowledgements

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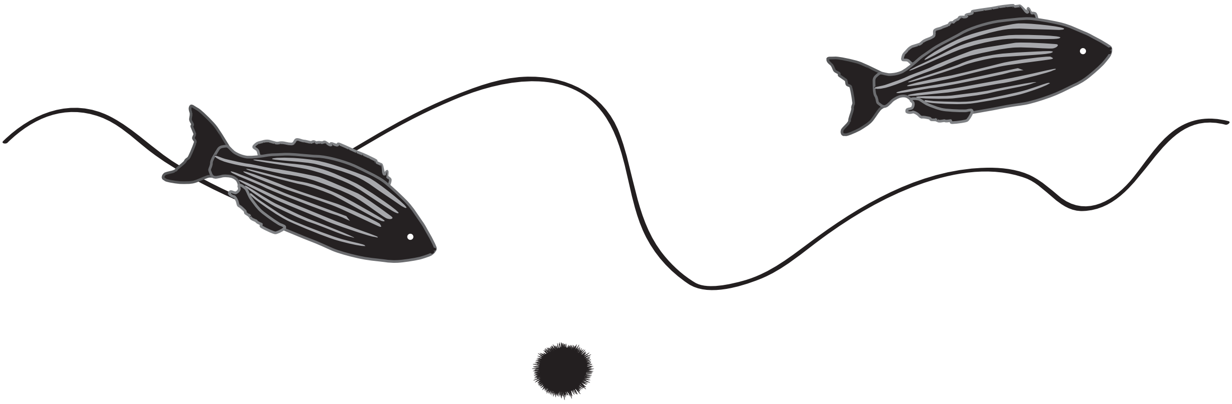
8

The Mediterranean benthic herbivores show diverse responses to extreme storm disturbances



Resum

Les tempestes extremes són un dels principals elements modeladors de l'estructura de les comunitats bentòniques marines. Amb tot, l'efecte d'aquestes tempestes sobre els processos ecològics ha estat molt menys estudiat. Específicament, l'herbivorisme és un dels mecanismes de control més importants de les comunitats de macròfits marins del Mediterrani, amb dues espècies d'herbívors claus: la garota *Paracentrotus lividus* i el peix *Sarpa salpa*. Per tant, els efectes de les tempestes extremes sobre aquests dos herbívors (a nivell de població o de comportament) poden ser crucials pel funcionament de l'ecosistema. Per intentar aprofundir en aquest tema, vam aprofitar dos estudis paral·lels que estàvem duent a terme abans, durant i després d'una tempesta catastròfica i imprevista. Vam obtenir les abundàncies de peixos i de garotes abans i després del temporal en àrees fixes (una sola àrea per les garotes i tres zones pels transectes visuals de peixos). Així mateix, vam estudiar la resposta a la pertorbació a nivell comportamental de salpes que havien estat marcades amb transmissors acústics. Donada la seva baixa mobilitat, les garotes van ser altament afectades per la tempesta (aproximadament 50 % de pèrdua d'individus) amb més pèrdua en aquelles taques més densament poblades. Això podria ser per la disponibilitat limitada de refugis a les taques. En canvi, l'abundància de salpes no es va veure afectada per la tempesta, ja que els peixos es van moure a zones més protegides (a més profunditat) gràcies a la gran mobilitat d'aquests peixos. Els nostres resultats subratllen que les tempestes catastròfiques afecten diferencialment les dues espècies de macroherbívors dominants de les zones de macroalgues i de praderes de plantes marines, donades les seves diferències de mobilitat i de cerca de refugi. Aquest estudi posa de manifest que davant de pertorbacions de gran magnitud, la presència de diferents respostes en el sí del grup d'herbívors, pot ser crític pel manteniment de l'herbivorisme al sistema.

Abstract [1]

Catastrophic storms have been observed to be one of the major elements in shaping the standing structure of marine benthic ecosystems. Yet, little is known about the effect of catastrophic storms on ecosystem processes. Specifically, herbivory is the main control mechanism of macrophyte communities in the Mediterranean, with two main key herbivores: the sea urchin *Paracentrotus lividus* and the fish *Sarpa salpa*. Consequently, the effects of extreme storm events on these two herbivores (at the population level and on their behaviour) may be critical for the functioning of the ecosystem. With the aim of filling this gap, we took advantage of two parallel studies that were conducted before, during and after an unexpected catastrophic storm event. Specifically, fish and sea urchin abundance were assessed before and after the storm in monitored fixed areas (one site for sea urchin assessment and 3 sites for fish visual transects). Additionally, we investigated the behavioural response to the disturbance of *S. salpa* fishes that had been tagged with acoustic transmitters. Given their low mobility, sea urchins were severely affected by the storm (*c.* 50% losses) with higher losses in those patches with a higher density of sea urchins. This may be due to a limited availability of refuges within each patch. In contrast, fish abundance was not affected, as fish were able to move to protected areas (i.e. deeper) as a result of the high mobility of this species. Our results highlight that catastrophic storms differentially affect the two dominant macroherbivores of rocky macroalgal and seagrass systems due to differences in mobility and escaping strategies. This study emphasizes that under catastrophic disturbances, the presence of different responses among the key herbivores of the system may be critical for the maintenance of the herbivory function.

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[1] See original publication in Pagès et al. (2013).

8.1 Introduction

Most ecosystems are subject to disturbance regimes that operate across a range of temporal and spatial scales (Elmqvist et al., 2003). These disturbances, either by chronic (low energy, frequent) or catastrophic (high energy, infrequent) conditions are widely recognized as influencing the size, shape and abundance of many species in terrestrial and marine ecosystems (Walsh, 1983; Denny, 1994; Trussell, 1997; Siddon & Witman, 2003; Hereu et al., 2012c). Specifically, marine systems are particularly more prone to be regularly disturbed than many terrestrial settings due to the increased kinetic energy of the fluid medium in which they occur (Koch et al., 2006). Hydrodynamic forces generated by waves are among the most important mechanisms of disturbance in coastal systems (Dayton et al., 1992; Hughes, 1994; Marbà & Duarte, 1995). Indeed, extreme storm events expose most organisms to hydrodynamic forces that exceed their mechanical limits (Denny, 1994), and thus provide a mechanism for re-initiating ecological succession in disturbance-generated patches (Sousa, 2001).

Depending on the spatial and temporal extent of the damage caused by the storm, the functioning and processes of ecosystems may be also importantly disrupted (Elmqvist et al., 2003). However, little is known on the effects of large infrequent disturbances on these functional aspects. Herbivory is a crucial ecological process in marine systems where it is known to contribute to the structure and organization of communities (Cyr & Pace, 1993; Poore et al., 2012). In tropical environments, herbivory is responsible for maintaining coral reefs in a coral-dominated state (Bellwood et al., 2006; Hughes et al., 2007) and for exerting a great pressure on submersed vegetation, either on seagrasses or macroalgae (Heck & Valentine, 2006). In temperate environments, herbivory plays a central role as well, and it may induce shifts from macroalgal-dominated areas into coralline barrens, when herbivores are released from control by predators (Estes & Palmisano, 1974; Harrold & Reed, 1985). Moreover, substantial effects of temperate herbivores have also been observed on seagrasses, such as the creation of mowed patches where seagrass primary production and canopy structure are severely altered (Tomas et al., 2005b; Prado et al., 2007). Due to its central role in structuring marine communities (Poore et al., 2012), disturbances affecting herbivory may profoundly influence underwater landscapes and associated ecosystem functions (e.g. Hughes, 1994). A first step towards the understanding of how large infrequent storms may affect herbivory is to study the responses of key herbivores.

Animals are known to display contrasting responses to disturbances depending on their life-history traits (Sousa, 1980). Indeed, response diversity, the diversity of responses to environmental forcing among species that contribute to the same ecosystem function, appears to be particularly crucial when the system is subjected to disturbances (Elmqvist et al., 2003; Nyström, 2006). Compared to sessile organisms, the responses of mobile marine animals to disturbance have been less studied (but see for example Letourneur et al., 1993; Denny & Gaylord, 1996; Siddon & Witman, 2003), although extreme environmental conditions and physical forces can directly kill appreciable numbers of mobile marine animals (Sousa, 2001). Mobile animals can behaviourally avoid potentially lethal environmental stresses, an option not available to structural species. Highly mobile species can avoid the disturbance by actively moving to areas where hydrodynamic forces are less intense (Walsh, 1983; Letourneur et al., 1993). This avoidance strategy will be successful or will fail depending on the rapidity with which harsh conditions develop and their intensity, as well as the degree of mobility of the organisms in question (Sousa, 2001). When mobility is limited, the effects of storms may be dependent on the number of refuges available in the habitat, and the capacity of the species to seek refuge (e.g. Fulton et al., 2001). Whatever the individual response, each ecosystem will have a set of herbivores and the final effect of the disturbance on the herbivory process will be dependent on the responses of the key herbivores of the system, which in turn rely on their biological traits.

One classical example demonstrating the importance of different species displaying diverse responses in ecosystem resilience is that provided by Hughes (1994), reporting the well-known phase shift that occurred in the Caribbean coral reefs. In that case, overfishing sustained for decades reduced fish herbivores thus eroding response diversity in the functional group of grazers (Elmqvist et al., 2003; Nyström, 2006). However, their function (i.e. herbivory) was still maintained due to an increase in sea urchin grazing that preserved for a while a coral-dominated state. Nevertheless, when a species-specific pathogen plus a hurricane dramatically reduced the population of sea urchins, no other herbivore could compensate this loss and a shift to a macroalgal state took place. Beyond this example, the theoretical base supporting that having species that respond differently to disturbances can stabilize ecosystem process rates is strong (Elmqvist et al., 2003; Hooper et al., 2005; Nyström, 2006), and this theoretical work has outpaced experimental work (but see Winfree & Kremen, 2009), particularly in marine systems. Overall, there is a lack of studies assessing responses (particularly behavioural) to and recovery from a variety of disturbances (Hooper et al., 2005). This is especially true for mobile non-habitat forming key species, as they are more difficult to follow and generally do not form part of routine monitoring programs, which is how most disturbance effects are detected.

Herbivory is one of the main drivers of Mediterranean macrophyte communities. The two dominant herbivores, the low mobility sea urchin *Paracentrotus lividus* (Lam.) and the highly mobile fish *Sarpa salpa* (L.), have been identified as key organisms determining the organisation and functioning of macroalgal (Guidetti, 2006; Hereu, 2006) and seagrass communities (Tomas et al., 2005b; Pagès et al., 2012). Both herbivores are browsers, although sea urchins may also be considered grazers in macroalgal systems (where they may induce coralline barrens Guidetti, 2006). As a first step towards the understanding of the potential effects of extreme storms on the herbivory process of Mediterranean macrophyte systems, we took advantage of a severe disturbance that occurred in December 2008, consisting on a violent and unprecedented storm. Our aims were (i) to test the response to the storm in terms of abundance of these two herbivores and (ii) to assess which were their escaping strategies. We hypothesised that each species would differ in its strategy depending on its degree of mobility. To address these objectives we used two parallel studies we were conducting before, during and after the storm. Specifically we assessed the responses in terms of abundance of both species, by monitoring fixed areas before and after the storm, and behaviour in fishes tagged with acoustic transmitters during the same period.

8.2 Materials and methods

Ethics statement

The Ethics Committee of the University of Barcelona issued a favourable report on the fish tagging protocol. The Department of Environment of the Catalan Government gives the permissions for fishing, operating and releasing the animals in the Medes Islands Marine Reserve. The reserve guards and the Spanish Marine Police (GEAS) supervised all operations.

The storm and the system

The severe coastal storm that took place in the Catalan coast (NW Mediterranean) on 26-27th December 2008 was a low frequency event with a returning period of more than 100 years. It hit with maximum winds of up to 20 m/s, significant wave heights as large as 8 m, record maximum wave heights in excess of 14 m, and wave periods of up to 14 s (Sanchez-Vidal et al., 2012). Damage to shallow coastal communities by currents and sand scouring during the storm is well documented after scientific scuba diving inspections (Mateo & García-Rubies, 2012). Substantial reductions were observed on algal cover (Hereu et al., 2012b), populations of sea urchins (Hereu et al., 2012a),

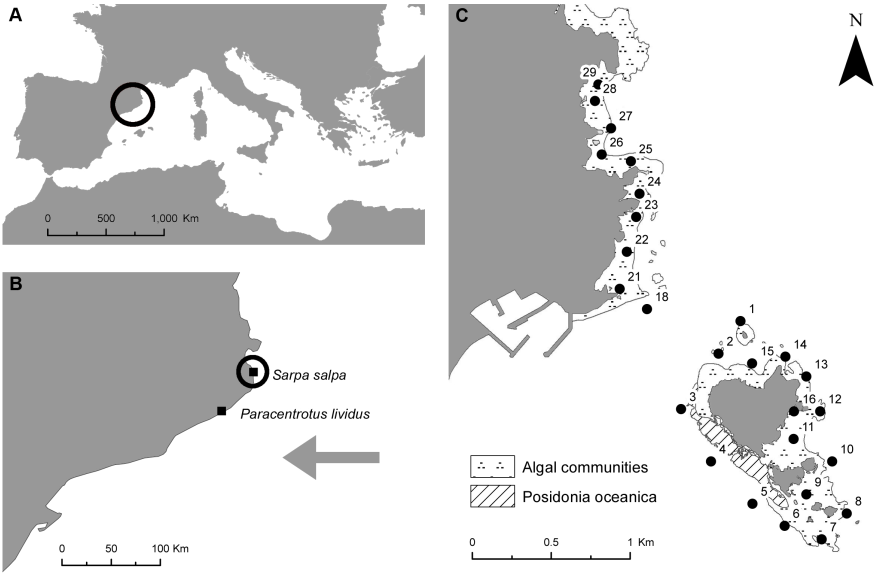


Figure 8.1: Location of the two monitoring programs conducted before and after the severe Easterly storm. Circled areas are zoomed in the next panel. The grey arrow in panel b) points out the direction of the storm (east). Panel c) shows the passive acoustic monitoring array deployed to track *S. salpa* individuals. Each receiver is numbered. This figure is composed of a topographic base map 1:50 000 property of the Institut Cartogràfic de Catalunya (accessible from `www.icc.cat`) and a bionomic map property of the Universitat de Barcelona (Hereu et al., 2010, 2011).

long-lived species of brown algae (Navarro et al., 2011) and populations of gorgonians (Coma et al., 2012) in rocky substrates. In sandy bottoms, the storm strongly buried (>10 cm of burial) at least 20% of *Posidonia oceanica* (L.) Delile seagrass beds at depths less than 10 m and damaged and destroyed an unknown amount by abrasion, unearthing and uprooting of plants, which is particularly significant given the suspected very low recovery rate of this community (Alcoverro et al., 2012). The effects of this storm in terms of buried seagrass were visible to as deep as 23 m in some *P. oceanica* meadows. Our two study areas (see below) were severely affected by the storm, as they were included in the area where the storm energy was the highest (Fig. 8.1).

Paracentrotus lividus assessment

Sea urchin population assessment was conducted in a shallow patchy *P. oceanica* meadow located on the Catalan Coast (N 41°41′ E 2°49′, Fig. 8.1), which had been monitored for 10 years and specifically 5 months prior to the storm event. The meadow is located at 8 m depth, in an open area exposed to east waves and currents, and therefore was importantly affected by the storm. The area boasts a large number of *P. oceanica* patches of different sizes and shapes. Each patch is separated from others by sand. In order to monitor these patches we marked 19 of them in summer 2008 with numbered iron bars.

Seagrass patch area before (2008) and after the storm (2009) was estimated by means of scaled photography. Photographs of each patch were taken from a zenithal point of view along with a known-length object (i.e. a 1.5 m iron bar). These pictures were then transferred to a computer where they were analysed in imageJ (v1.42q National Institutes of Health, USA). Each image was scaled using the known-length object and then the edge of each patch was traced in order to calculate the area. Additionally the percentage of buried, unburied and normal matte conditions was assessed visually for each seagrass patch few weeks after the storm. The same two divers, who had previously intercalibrated among themselves, made all estimations.

P. lividus total abundance (total number of individuals) per patch, density (number of individuals per square metre) and size distribution were obtained for the same 19 patches of different sizes (i.e. from <0.5 to 5 m^2) before and after the storm. This was done by exhaustive visual inspection and careful, repeated introduction of bare hands among the rhizomes to allow sensing of hidden individuals (Prado et al., 2009). For every urchin counted, its horizontal test diameter without spines (TD) was measured to the nearest mm with a calliper. The same protocol was used before (i.e. summer-autumn 2008) and after the storm (i.e. spring-summer 2009). Assuming that (i) our sampling method is able to effectively detect urchins >1 cm (test without spines); (ii) that adult *P. lividus* populations are very homogeneous and relatively stable over long periods of time (Dance, 1987; Hereu, 2004); and that (iii) migration is unlikely between seagrass patches in the study site owing to their being in a sand matrix and separated by some metres one another (Dance, 1987), we can compare populations in each patch before and after the storm with a high confidence that the urchins lost were gone as a consequence of the storm.

Sarpa salpa assessment

S. salpa abundance sampling was also carried out in the Catalan coast, in Medes Islands Marine Protected Area and its neighbouring unprotected coast (N 42°3′, E 3°13′; Fig. 8.1b,c) during the years 1999, 2002, 2005 (before the storm), 2009 (after the storm), 2011 and 2012. Abundance was assessed by scuba diving over 50×5 m (250 m^2) transects haphazardly placed in 3 zones within the study area between 5 and 10 m depth. All *S. salpa* fish in each transect were counted. A total of 136 transects were sampled between 1999 and 2012. Sampling was always conducted during summertime (from August to

September) in order to avoid seasonal differences among years.

An acoustic monitoring programme to estimate movement patterns of *S. salpa* fishes started 2 months prior to the storm and ended 10 months after. It was also carried out in Medes Islands Marine Protected Area and its adjacent unprotected stretch of coast (N 42°3′, E 3°13′; Fig.8.1b,c). There, a fixed array of receivers (VEMCO, VR2 receivers, Nova Scotia, Canada) was deployed around the islands and along the coast (Fig. 8.1c). Receivers' detection range was established at 250 m prior to fish tagging. The average distance between receivers was 210 m. Receivers were retrieved, data downloaded, cleaned of biofouling, and redeployed 5 times during the study (in November 2008, January 2009, May 2009, August 2009 and October 2009).

S. salpa individuals were fished and tagged on the 16^{th} and 17^{th} October 2008. Twenty fishes were captured at four different sites using seine-fishing nets. Following capture, fishes were transferred to an anaesthetic bath of 0.2 ml l^{-1} 2-phenoxyethanol (Jadot et al., 2006). When each fish was immobilized (showing no reaction to external stimuli) they were placed on a V-shaped support. Incision area was de-scaled and an incision approximately 2 cm long was made between the anal fin and the anus. An acoustic transmitter (VEMCO, V9P-2L, 9 mm diameter × 47 mm length, 120 s average repeat rate, 522 days of estimated battery life, ± 2.5 m depth accuracy) coated in antiseptic was inserted into the peritoneal cavity. The incision was closed using a sterile surgical stapler (3-4 staples). Fishes were placed in a monitoring bucket where their gills were flooded with fresh seawater until they regained equilibrium. Subsequently, they were kept in an underwater cage until complete recovery, and then they were released to their respective fishing-sites. The full procedure (from anaesthesia to initial recovery) took around 7 min. Previous studies have shown that surgical tag implantation has a very limited impact on the behaviour and physical status of this species (Jadot, 2003). From the 20 fishes tagged, 16 fishes were lost before the storm event, and only four were still being continuously tracked around that time (26-27^{th} December 2008). These are the only ones that are analysed here.

Data analysis

Two dependent variables were assessed from the sea urchins' data set. Sea urchin abundance per patch and number of sea urchins lost per patch. Regarding sea urchin abundance, a general linear model (GLM) with a negative binomial distribution (and a logarithmic link function) was used to test the significance of the explanatory variables. Negative binomial distributions are generally used to deal with count data with overdispersion (Zuur et al., 2009), as it was the case. We introduced into the model 'time' (2 levels: before and after the storm) and sea urchin 'size' (6 levels: 1-2] cm, 2-3] cm, 3-4] cm, 4-5] cm 5-6] cm and >6 cm test diameter) as fixed factors and 'patch area' and '% of unburied matte' (rhizome layer exposed) as fixed continuous variables. A preliminary exploration identified collinearity among the variables % of unburied matte (rhizome layer exposed), % of buried and % normal matte conditions. Thus, only % of unburied matte was entered into the model. On the other hand, the dependent variable number of sea urchins lost per patch was analysed with a GLM with a poisson distribution (and a logarithmic link). We wanted to test whether there were differences in the number of sea urchins lost according to the fixed explanatory factor sea urchin 'size' (factor with 6 levels, see above), and the continuous variables 'sea urchin density before the storm', '% of seagrass area lost as a consequence of the storm' and '% of unburied matte'. Since the number of sea urchins lost per patch depended on the abundance of sea urchins per patch, this variable was included as an offset (Zuur et al., 2009). In this way, we modelled the effect of explanatory variables on the ratio between the number of sea urchins lost per patch and the abundance of sea urchins per patch. In all cases, the best models were selected based on the Akaike's Information Criterion (AIC) (Zuur et al., 2009). Data were checked for normality by the visual inspection of plots of residuals and fitted values.

Table 8.1: Sea urchin data analysis. Generalized linear models (GLMs) showing the effect of explanatory variables to sea urchin abundance and number of sea urchins lost after the storm. The table shows the best-selected models with parameter estimates. The best selected models were a GLM with a negative binomial distribution (and a logarithmic link function) for sea urchin abundance; and a GLM with poisson distribution (and a logarithmic link function, Φ (dispersion) = 0.81) for sea urchins lost.

Dependent variable	Effect	Coefficient (SE)	*z*-value
Sea urchin abundance	Intercept	11.1 (3.3)	**3.4** ***
	Time	-1.4 (0.4)	**-3.5** ***
	Area	-5.1 (2.1)	**-2.5** *
	Size 1-2]	-0.1 (0.3)	-0.3
	Size 2-3]	0.1 (0.3)	0.2
	Size 3-4]	-0.2 (0.3)	-0.6
	Size 4-5]	0.5 (0.3)	1.5
	Size 5-6]	1.4 (0.3)	**4.4** ***
	Time × Area	0.7 (0.3)	**2.6** **
Sea urchins lost	Intercept	-1.8 (0.3)	**-6.5** ***
	Density 2008	0.04 (0.01)	**3.6** ***
	% of patch area lost	0.01 (0.00)	**2.7** **

Significance codes: 0 ***, 0.001 **, 0.01 *, 0.05 ·, 0.1 . SE: Standard Error.

All data were analysed with the packages MASS (Venables & Ripley, 2002) and stats in the statistical software R (R Development Core Team, 2012).

Regarding S. salpa, we also modelled their abundance (from the visual transects) as a function of the fixed factors 'year' (6 levels: 1999, 2002, 2005 [before the storm], 2009 [after the storm], 2011 and 2012) and 'zone' (3 levels, the 3 sampled zones). Given that the data set was again count data with overdispersion, we used a GLM with a negative binomial distribution (and a logarithmic link). We were also interested in knowing whether the movement behaviour of tagged fish was related to the storm event. To this end we correlated for each fish ($n = 4$) its daily mean depth and its total distance travelled per day with the daily maximum wave height obtained at the same site (kindly provided by Josep Pascual, from l'Estartit Observatory N 42°3', E 3°12'). Fish depth is one of the parameters that fish transmitters provide, but total distance travelled per fish was calculated from the fish detections among different receivers with the package adehabitaLT in R (Calenge, 2006). These distances should be viewed with caution and as a comparative measure between days and fishes. It should be borne in mind that the distances calculated do not derive from the actual fish trajectory but from the receivers that detect a given fish at a given time (e.g. if a fish is continuously moving on the periphery of the detection range between two receivers, it would actually move some tens of metres but since it would have been detected by different receivers, the estimated distance would be much higher). All time series were detrended, if necessary, by regressing each of them with time. If the regression was significant (i.e. a trend was found), the residuals were used in further analyses. Normality of the time series was checked before calculating regressions and if not fulfilled, time series were transformed. Finally, the cross-correlation coefficients (Pearson) between each fish time series and the daily maximum wave height were calculated at different time lags. All calculations were performed in R.

8.3 Results

Paracentrotus lividus assessment

The generalised linear model for sea urchin abundance revealed that the factor time, i.e. the storm, had a great effect on the abundance of sea urchins per patch (Fig. 8.2a, Table 8.1). Indeed, total sea urchin abundance (adding all patches) before the storm was 280 individuals, whereas after the storm total abundance had decreased to 145 individuals, resulting thus in a loss of 48% of sea urchins. The 5-6 cm size-class was significantly more abundant compared to the others (Fig. 8.2b, Table 8.1). However, sea urchin loss was similar across all size classes (Fig. 8.2b), as the interaction time × size was not significant, and was dropped from the best-selected model. Sea urchin abundance was also significantly dependent on patch area (Table 8.1). However, the relationship between patch area and sea urchin abundance was influenced by the factor time, as indicated by the significant time × area interaction. This may be related, on the one hand, to the fact that the storm affected the area of seagrass patches, making them shrink in size. And on the other, to the fact that before the storm smaller patches exhibited higher sea urchin abundance, i.e. were denser than bigger patches; while after the storm smaller patches displayed lower sea urchin abundance (Fig. 8.2c). These results agree with the significant effect of sea urchin density before the storm on the dependent variable number of sea urchins lost (Table 8.1, Fig. 8.2d). This means that the denser the sea urchin population in the patch, the more sea urchins were lost per patch as a consequence of the storm (Fig. 8.2d). The % of patch area lost because of the storm had also a significant influence on the number of sea urchins lost (Table 8.1). However, the effect of this parameter was limited (see the low coefficient in Table 8.1). Finally, sea urchin loss was independent from the % of unburied matte or sea urchin size, since these variables were dropped from the model during model selection.

Sarpa salpa assessment

In contrast to the sea urchin population, *S. salpa* abundance was not influenced by the storm, as shown by the non-significant year effect (Fig. 8.3, Table 8.2). In contrast, fish behaviour did respond to the severe storm of December 2008 (see Fig. 8.4a to note that this storm was the heaviest of the whole time series), as well as to other important storms along the tracking period (see Figs. 8.4, 8.5). Indeed, all fish individuals presented a depth distribution that was significantly and negatively correlated with the time series of maximum wave heights (Hmax) (Table 8.3, Fig. 8.4). This means that fishes moved to deeper areas on stormy days (Hmax and *S. salpa* daily mean depth time series were on phase, see Table 8.3). In addition, the distance travelled per day was also significantly correlated with Hmax (except for fish SS93), but positively in this case (Table 8.3, see Fig. 8.5). Thus, fishes made longer trips on stormy days (both time series were on phase). In fact, in some cases fishes moved from their core areas (mostly receiver 4, see Fig. 8.1c) to distant zones even outside our receiver array (see blank spaces in the time series of fish SS92 and SS93, Fig. 8.5d,e). Some fishes rapidly returned to their core areas few days after the storm (Fig. 8.5b,c), while others returned after some months (Fig. 8.5d), and one never returned (Fig. 8.5e).

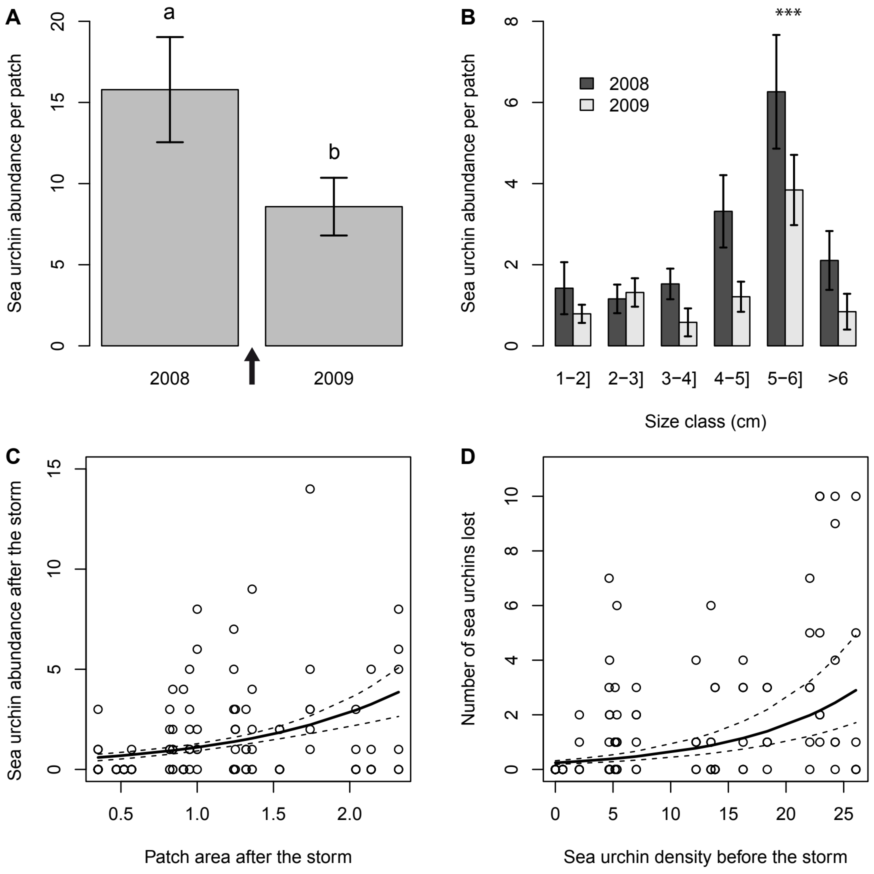


Figure 8.2: Effects of the storm on *P. lividus* population. a) Effect of the factor time (before the storm [2008] and after the storm [2009]) to the mean sea urchin abundance per patch. Different lower case letters indicate statistically significant differences (see Table 8.1). The arrow symbolizes the storm event. b) Effect of the factor size and time on mean sea urchin abundance per patch. Note that sea urchins of 5-6 cm were the most abundant; the asterisks show this was significant (Table 8.1). c) Effect of seagrass patch area after the storm on the abundance of sea urchins per patch after the storm. d) Effect of sea urchin density before the storm on the number of sea urchins lost per patch. Model fits are plotted as solid lines ± the standard error (see model coefficients in Table 8.1).

Table 8.2: *S. salpa* abundance analysis. Results of *S. salpa* abundance model selection with a generalized linear model (GLM). The selected family distribution for the GLM was a negative binomial (with a logarithmic link function) owing to the overdispersion present in the data set. We present the significance of dropping each variable one by one from the full model. The full model was $Abundance \sim Zone + Year + Zone \times Year$. Akaike's Information Criterion (AIC) was used to select the best model, evaluating the trade-off between model parsimony and goodness of fit. The lower the AIC the better the model.

Term dropped	d.f.	AIC	Likelihood ratio test	*P*-value
<None>	13	1034		
Zone × Year	9	1031	4.8	0.3
Year	4	1024	3.1	0.7
Zone	7	1027	0.2	0.9

Table 8.3: *S. salpa* time series analysis. Pearson correlation coefficients between the time series of individual fishes and of the daily maximum wave heights (Hmax). The first column indicates the time series that are being compared. The second column indicates the duration of the time series analysed. We then indicate the lag, in days, at which the correlation coefficient was maximal, and these coefficients. We finally specify the treatment applied to each fish time series, which were transformed and/or detrended if necessary. Hmax time series was always log-transformed and detrended, since it did not fulfil normality or stationarity.

Comparison	Ts. length	Lag	Coefficient	Fish ts. filtering
Hmax - SS77_depth	95 d	0 d	**-0.52** ***	Detrended
Hmax - SS91_depth	228 d	0 d	**-0.27** **	Log and detrended
Hmax - SS92_depth	79 d	0 d	**-0.58** ***	Log and detrended
Hmax - SS93_depth	61 d	0 d	**-0.33** **	Log and detrended
Hmax - SS77_distance	98 d	0 d	**0.39** ***	Sqrt
Hmax - SS91_distance	228 d	0 d	**0.19** **	Log
Hmax - SS92_distance	79 d	0 d	**0.40** ***	Sqrt and detrended
Hmax - SS93_distance	62 d	-	n.s.	Log and detrended

Sqrt., square root transformation; log., log-transformation. Significance codes: 0***, 0.001**, 0.01*, 0.05 ·, 0.1 .

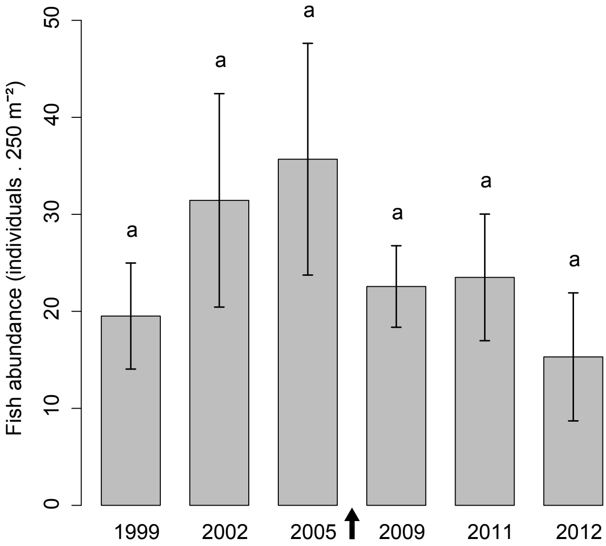


Figure 8.3: Effects of the storm on *S. salpa* population. Mean *S. salpa* abundance per transect (number of *S. salpa* individuals per 250 m^2) as a function of the factor year. The same lower case letters indicate that differences were not statistically significant (see Table 8.2). The arrow indicates the storm event (December 2008).

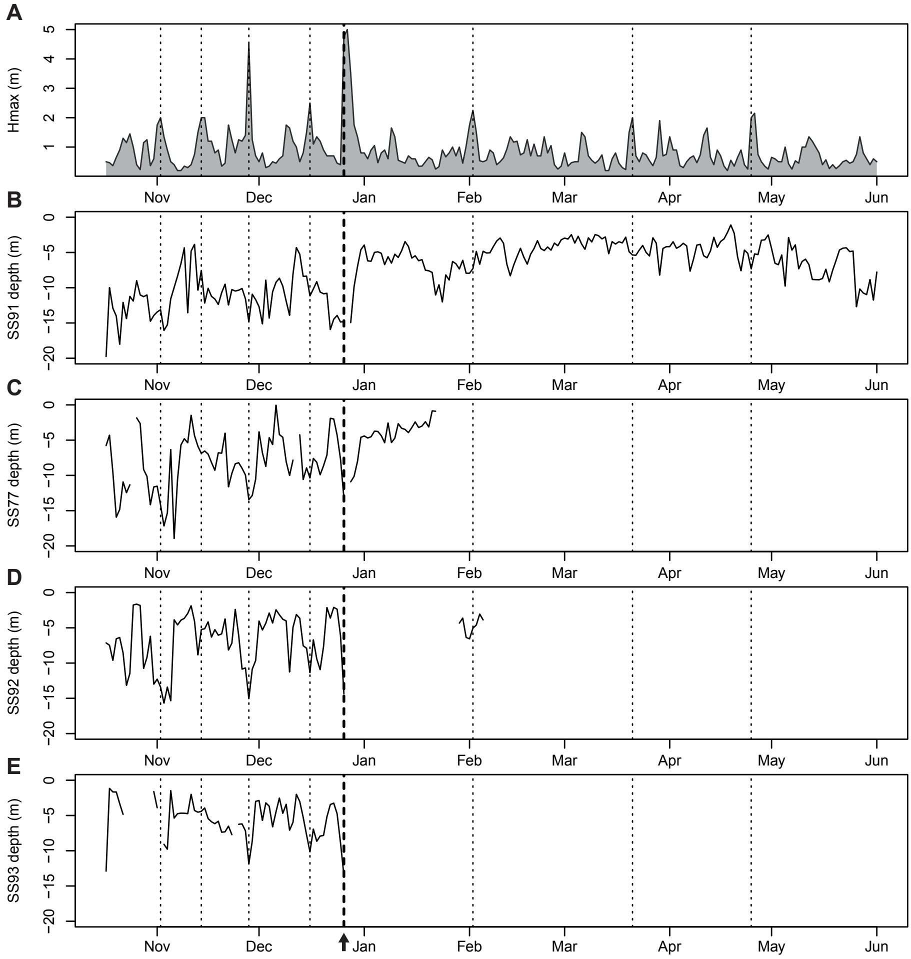


Figure 8.4: Time series of the daily maximum wave height (Hmax) and *S. salpa* daily mean depth. Each panel corresponds to an individual fish. Vertical dotted lines indicate the date of storms with Hmax > 2 m, and the thicker dashed line with an arrow indicates the date of the December 2008 catastrophic storm event. Note that fishes responded to most storms by moving to deeper areas. Note the disappearance of some fishes for several days following the studied storm.

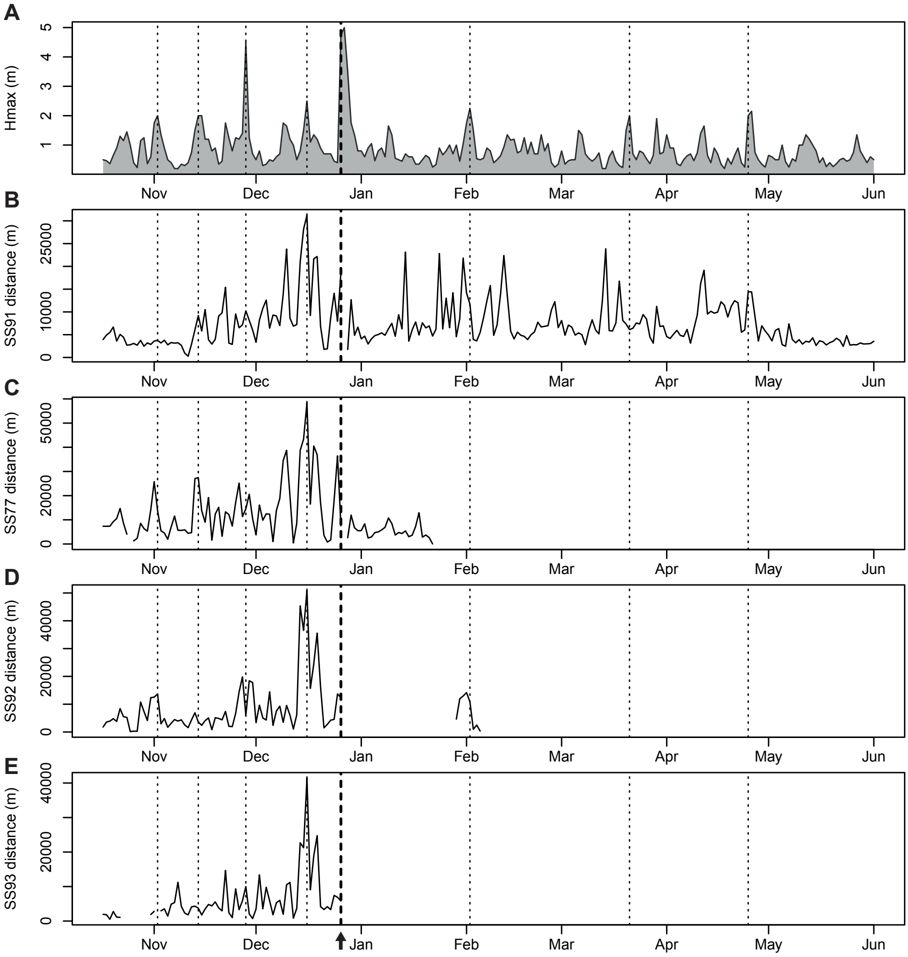


Figure 8.5: Time series of the daily maximum wave height (Hmax) and *S. salpa* travelled distanced per day. Each panel corresponds to an individual fish. Vertical dotted lines indicate the date of storms with Hmax > 2 m, and the thicker dashed line with an arrow indicates the date of the December 2008 catastrophic storm event. Note that in general the distances travelled per day were higher in stormy days.

8.4 Discussion

As expected from their very different movement capacities, both herbivores responded differently to the extreme storm event. In terms of abundance, the mobile species (the fish *S. salpa*) endured the disturbance with non-significant losses, while nearly half of the population of the least mobile species (the sea urchin *P. lividus*) was wiped out by the waves in seagrass meadows. The higher survival observed for the fish population could be the result of their active escaping strategy, consisting on sinking to deeper waters or on moving to other areas. In contrast, the sea urchin could only seek shelter within the seagrass habitat, which appears to give a moderate protection against currents and waves, at least in such extreme events. These findings suggest that, after the catastrophic storm, herbivory by fishes may remain more or less unaffected, while herbivory by sea urchins may substantially decrease without disappearing. This is particularly relevant in Mediterranean seagrass and rocky systems, given their low number of species within the macroherbivorous group.

P. lividus cannot move great distances (Dance, 1987; Hereu, 2005), and therefore, their only possible mechanism to withstand a storm is by using the habitat for shelter. Sea urchins have been observed to decrease their ability to forage even in low hydrodynamic regimes (much lower than their dislodgement forces) (Siddon & Witman, 2003) and to hide in crevices and decrease their movement rates when water turbulence increases (Dance, 1987; Denny & Gaylord, 1996). In spite of these behavioural adjustments (i.e. decreased movement rates, shelter-seeking behaviour), under extreme storm events sea urchin populations are generally importantly affected (Ebeling et al., 1985; Hughes, 1994; Hereu et al., 2012a). In this study, the seagrass-dwelling population of sea urchins was also greatly affected by the storm, with half of the population swept away from the studied seagrass patches. Our results suggest that shelter-seeking behaviour could have attenuated sea urchin losses on those patches with available refuges, since patches displaying a higher density of sea urchins before the storm (putatively with less refuge availability) lost more individuals during the event. *P. oceanica* is known to provide sea urchins with shelter from predation within the root-rhizome layer (Farina et al., 2009; Prado et al., 2009), and it is very likely that they are also using this complex structure to escape from increased water movement. We also expected a significant effect of size on the number of sea urchins lost. Bigger sea urchins are more prone to be dislodged, given that the force due to water's acceleration increases faster than the organism's structural strength as the organism grows (Denny et al., 1985). However, this was not the case in the present study, most probably due to the attenuating effect of the seagrass (Koch et al., 2006). In contrast, in a much less structured habitat (rocky bottom with boulders) the same storm caused sharper sea urchin abundance decreases (65% on average, Hereu et al., 2012c, compared to 48% in the seagrass), with a significant size effect. In that case, since algal canopies provide less protection than seagrass canopies (specially compared to the large *P. oceanica* seagrass), smaller sea urchins were still able to find shelter, but larger ones could not find suitable refuges and were nearly all lost (80-100% of individuals above 3 cm, Hereu et al., 2012a). Thus, our results suggest that being inside a seagrass canopy gives better chances of surviving an extreme storm than being in an algal-covered rocky habitat.

The escaping strategy used by *S. salpa* appeared to be more successful and was in clear contrast with that of sea urchins. Few *S. salpa* individuals were found stranded on the beaches after the storm and no sound effects on their population were apparent in the long-term data series of *S. salpa* abundance (Fig. 8.3). This is in accordance with the fact that at least three out of the four fishes tagged survived the storm, while we cannot attribute the disappearance of the fourth to mortality, since it could have relocated to areas out of our receiver array. These herbivorous fishes actively moved to deeper, more protected waters the day of the storm, which presumably reduced the probability of being swept ashore by large waves as well as mitigated the potential effects of mechanical damages from suspended sand and other debris (Walsh, 1983). Indeed, fishes responded by moving to deeper areas in most of the storms observed during the studied period, as shown by the negative correlation found between maximum wave height and *S. salpa* daily mean depth (Fig. 8.4, Table 8.3). In addition, stormy days were days of long distance movements (positive correlation between wave height and distance moved, Table 8.3, Fig. 8.5), since fishes presumably moved from their core areas (seagrass meadow area, see Fig. 8.1c, Pagès et al. unpublished manuscript) to more protected zones. This has been reported after hurricanes for coral reef fish species (Kaufman, 1983; Lassig, 1983; Letourneur et al., 1993), and sometimes has been attributed to the effect of currents.

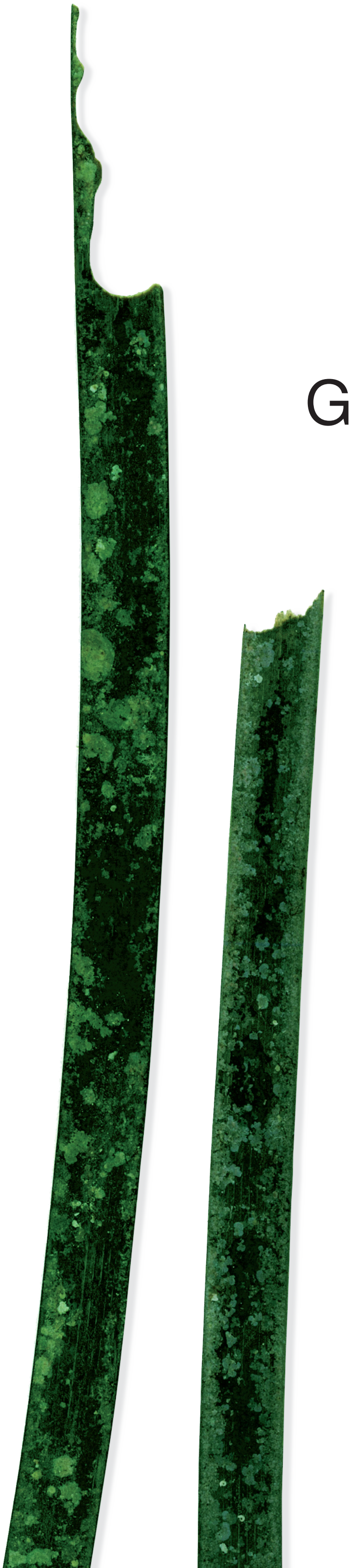
The contrasting responses of both key herbivores clearly points out that mobility patterns can be fundamental to understand species-specific responses to catastrophic storm events. As seen, each of these herbivores operates at a different scale. Sea urchins escaped taking advantage of the structure offered by the seagrass habitat, and at the most making movements on the metre scale (i.e. moving deeper into the root-rhizome layer of the seagrass, moving towards nearby crevices, etc.) due to their small home range (Palacin et al., 1997; Hereu, 2005). On the other hand, *S. salpa* escaped moving hundreds of metres or even some kilometres (Figs. 8.4, 8.5) given its large home range (Jadot et al., 2006; Abecasis et al., 2012, Pagès et al.

unpublished manuscript). It may not be surprising that two herbivorous species so profoundly different in many traits (an echinoderm and a fish) show differential responses when faced with disturbances. However, for the studied storm, which was particularly extreme and with a returning period of a 100 years (Sanchez-Vidal et al., 2012), many other species of fishes were profoundly affected. In the studied zone, beaches were completely covered with stranded fishes of several species, but not *S. salpa* (personal observations). Additionally, a parallel project in our study area assessing the effects of the same storm on other fish populations, found that *Anthias anthias* (L.) and *Chromis chromis* (L.), which display a more site-attached behaviour, were severely affected and were swept ashore in great numbers (Garcia-Rubies et al., 2012). This has also been observed in other studies that have pointed out that more mobile fish species are generally less affected by physical disturbances than sedentary ones (Bortone, 1976; Walsh, 1983). So, more than the phylogenetic position of the species what seems crucial is the species' movement behaviour in relation to the disturbance. Given that disturbances generally operate across a limited range of scales, animals that can respond across different scales may be better suited to withstand a variety of disturbances (Elmqvist et al., 2003). Similarly, if different species in a functional group operate at different scales, they may provide mutual reinforcement contributing to the resilience of the function, while at the same time minimizing competition among species within the functional group (Peterson et al., 1998; Elmqvist et al., 2003). This is known as scale range redundancy and may be occurring within the Mediterranean herbivorous group, given the differences in mobility and behaviour.

Response diversity within functional groups has been suggested to be of crucial importance to ensure the resilience of ecosystem functions (Elmqvist et al., 2003). While our study did not assess whether the function provided by *S. salpa* and *P. lividus* (i.e. herbivory) changed as a result of the disturbance, it is known that both herbivores are important functional elements (Palacín et al., 1998; Vergés et al., 2009; Pagès et al., 2012). In our system, given the low number of herbivorous species, herbivory function would be easily eroded should both herbivores respond in a similar way to disturbances. However, we have shown that even faced with large infrequent disturbances such as the 2008 storm, at least one of the herbivorous species of the system would be able to maintain the herbivory function.

Acknowledgements

We would like to thank Josep Pascual, observer from l'Estartit meteorological station, for kindly letting us use his daily maximum wave height time series. We would also like to thank Rohan Arthur, Guillem Roca, Jordi Boada and Oriol Mascaró for interesting discussions. Frederic Bartumeus, Aitana Oltra, John Palmer, Marc Macias and Carlos Rivera helped with the statistical analysis. Núria Cot aided in the image analysis to compute patch areas. We are indebted with Àlex Lorente, responsible for the Medes Islands marine reserve that sadly deceased in a diving accident. He was always willing to make the reserve a pleasant and easy place to work. The Spanish Ministry of Science and Innovation funded this research (projects CTM2010-22273-C02-01 and 02). The Spanish Ministry of Education supported JP (scholarship AP2008-01601) and the Spanish National Research Council supported AG (scholarship JAEPre_08_00466).



9

General discussion

9.1 Main conclusions

Chapter 4

Predation pressure on a key herbivore can be modified both by the environmental context within which it finds itself and by the actions of another herbivore that modifies the plant traits that create this environmental context. Herbivores, particularly when acting as ecosystem engineers, may have the potential to mediate and increase predation risk, as they substantially modify habitat structure with consequences for refuge availability, among others.

Chapter 5

Sea urchins can perceive predator chemical cues and respond escaping from these stimuli altering its behaviour by switching among different movement patterns. Predation risk may be as important in determining animal movement patterns as feeding strategies, and should be taken into account when analysing trajectories in the field. As is for searching food, some movement patterns may be evolutionarily more optimal to escape or to search for shelter, and this may lead to changes in the population distributions of prey.

Chapter 6

The herbivorous fish *Sarpa salpa* display large home ranges and connect distant habitats with their highly mobile behaviour. In spite of their mobility, they also display a strong selectivity for the seagrass habitat, which seems preferred over the rocky and sand areas. Highly mobile species can connect distant habitats, and may perceive the seascape at a greater scale. Management plans and MPAs design should take these findings into consideration.

Chapter 7

Seascape attributes influence herbivory patterns in *Posidonia oceanica* seagrass meadows. The observed spatial heterogeneity in the herbivory process may be mediated by the interaction of mobility of the two main herbivores (sea urchin and fish) with seascape configuration and predation risk.

Chapter 8

The herbivores of Mediterranean macrophyte communities display contrasting responses to extreme storm events. Under catastrophic disturbances, the presence of different responses among the key herbivores of the system may be critical for the maintenance of functions. Differences in species mobility explain why the most mobile species (*S. salpa*) have the possibility to endure extreme storms, while the low-mobility species is subject to great population losses just relying on the structural complexity of the habitat to resist.

9.2 Herbivores can have strong community-wide effects

Until recently, the role of predators has been considered central to understanding much of community and interaction ecology, relegating herbivores to a secondary place. While it was known that terrestrial herbivores could be of importance in some particular ecosystems, the role of initiators of indirect community-wide effects was reserved to predators. However, in recent years, herbivores too are starting to be considered strong initiators of ecological interactions (Pringle et al., 2007). Two fields have been crucial in establishing that strong indirect effects can also be initiated by herbivores: the study of ecosystem engineering by megaherbivores such as ungulates (Pringle et al., 2007; Huntzinger et al., 2008; Parsons et al., 2013) and the study of trait-mediated indirect interactions initiated by phytophagous insects (Karban & Baldwin, 1997; Ohgushi, 2005, 2008). Our study on the indirect effects generated by fish herbivores in a *P. oceanica* seagrass meadow (**chapter 4**) merges both fields and conveys with the growing recognition that herbivores may play a greater-than-acknowledged role in structuring communities, through indirect effects. **Chapter 4** results show that herbivores, especially when acting as ecosystem engineers, may produce community-wide effects via the modification of the environment created by vegetation, within which other complex interactions may occur. In our study site, the change in canopy height mediated by *S. salpa* herbivory modifies the predator-prey interaction between the edible sea urchin, another key herbivore of the system, and its predators. The interaction described is unique in the sense that an herbivore changes the predation risk of another herbivore and potential competitor.

Moving to a more speculative field, in **chapter 7** we showed that seascape attributes, such as matrix composition or position within the meadow, influence fish herbivory impacts. It is thus possible that spatial heterogeneity in the herbivory process may lead to a seascape of canopy heights and thus a seascape of fear and predation risk for the benthic sea urchins living within seagrass shoots. Finally, linking with **chapter 8**, this could even have implications on the capacity of these sea urchins to deal with disturbances, since seagrass meadows with shorter canopies attenuate worse the impact of waves (Koch et al., 2006).

To sum up, habitat structure modification by *S. salpa* (**chapter 4**), which can in turn depend on seascape attributes (**chapter 7**), may influence the other herbivore of the system at least in two different ways: firstly, via an increase in their predation risk due to a pair of interaction modifications (trait- and environment-mediated) (**chapter 4**); and secondly, decreasing the capacity of hydrodynamic attenuation of the seagrass canopy, which sea urchins use for shelter (**chapter 8**).

Hence, while in the objectives we presented this system as a simple one, with just one producer, two herbivores and a guild of predators, the picture now, although maybe more complete, it is also much more complex. If an apparently simple network can complicate to such a great extent, it is difficult to imagine the infinite possibilities of interactions between species, behaviour, landscape and disturbances in specious interaction networks such the herbivore guilds of tropical rainforests (e.g. Morris et al., 2004).

9.3 Movement patterns of the two main herbivores

In **chapter 6**, we show that *S. salpa* is a highly mobile species, displaying large home ranges and the capacity of connecting distant and different habitats. Previous studies had already acknowledged the mobility of this species on the short term (i.e. one month, Jadot et al., 2006), but this study confirms that this mobility is maintained through the year, which makes this species one of the most mobile species of the demersal fish observed so far in the Mediterranean. This mobility is also observed at a smaller scale, with fishes displaying similar temporal and spatial patterns for the whole tracking period, consisting in spending the night at the deeper areas of the seagrass meadow (near the seagrass limit) and moving to the shallow parts during the day (most probably to feed). All in all, these results do not agree with the winter migration hypothesis, which proposed that *S. salpa* stayed in deeper waters (*c.* 40 m) for spawning and shelter during winter (Verlaque, 1990). However, as shown in **chapter 8**, in stormy days fishes moved from the highly used shallow areas into deeper waters, most probably to shelter from wave action and sand scouring. Since winter is the season with the highest storm occurrence (see Fig. 8.5a, **chapter 8**), it is reasonable to think that *S. salpa* may spend more time at deeper waters in that time of the year. Nevertheless, while, we show that this behaviour happens every time a storm with maximum wave heights above 2 m occurs, fishes return to their normal range of depths in hours or days. Thus, these short-term movement modulations as a consequence of storms should not be considered a spawning migration.

At another scale, relevant for the sea urchin movement patterns, we observed that sea urchin movements in a featureless environment were very variable but in general superdiffusive (**chapter 5**), which is an optimal strategy for searching for randomly and sparsely distributed resources (Bartumeus et al., 2005). We also identified that the chemical cues of one of their principal benthic predators (a gastropod) can determine a switch in normal sea urchin movements into straighter and faster trajectories. This study emphasises the importance of taking predation risk into account when studying the movement patterns of animals in the field, since the risk of predation, may influence the scale at which seascape is perceived by the animal. This aspect is of importance for the study of herbivory in macrophyte communities with a behavioural seascape approach (see next section, and **chapter** 7).

9.4 Interaction of herbivore movement behaviour and seascape attributes

Chapter 6 highlights the importance of assessing animal movement, and how connectivity within a seascape may depend on organisms' perception and response to seascape structure within a range of spatial scales. We would expect that animals with high mobility perceived the seascape as more connected, compared to less mobile species (Lima & Zollner, 1996). The high mobility observed for *S. salpa* may explain why, in **chapter** 7, we did not find differences in herbivory between seagrass patches close and separated tens of meters from a rocky reef. Our findings contrast with other studies, mostly done in tropical areas, reporting increased herbivory rates in seagrasses near coral reefs (or even halos), but with herbivory rates decreasing away from the reef (Valentine et al., 2007; Vergés et al., 2011). This suggests that the species responsible for the above-reported patterns in herbivory, may display strong site-fidelities, as has been widely found for most demersal fishes (Chapman & Kramer, 2000; Topping et al., 2005; Alós et al., 2012), with home ranges being particularly small for some coral reef species (Welsh & Bellwood, 2012b,a).

The integration in **chapter** 6 of the spatial and temporal habitat use, with both fish mobility and the seascape configuration identifies the fish *S. salpa* as a potential mobile link. While previous studies pointed out that *S. salpa* acted as a key herbivore in seagrass and rocky macroalgal habitats independently (e.g. Prado et al., 2007; Vergés et al., 2009), our results connect the use of both habitats by the same individuals or schools. Indeed, we consider *S. salpa* a mobile link organism since it is capable of commuting between different habitats, and given it is a generalist, it is capable of grazing (and probably defecating, transferring matter) both on macroalgae and on the seagrass leaves. This means that it may deliver its herbivorous function across the different habitats contained in a seascape mosaic without the perception of barriers among them. Indeed, in the seascape studied in **chapter** 7 we found that fishes grazed three times more the seagrass patches embedded in a rocky matrix than those surrounded by sand. This pattern may be due to the complementation or supplementation hypotheses (Dunning et al., 1992), further highlighting *S. salpa* potential mobile link role and its perception of the seascape at a broad scale. Similar results were found in a study with butterflies with low and high vagility (Ricketts, 2001). In that study, patches were perceived as connected for the most vagile species, while for the least vagile ones patches were perceived as isolated (Ricketts, 2001). Organisms are expected to alter their movements, as well as experience differential fitness benefits or costs, according to the nature, form, and spatial arrangement of habitat patches and edges. Thus, the functional connectivity of a landscape is likely to be both species and context-dependent (Belisle, 2005). We show that for *S. salpa*, functional connectivity is high. Indeed, in **chapter 6** we found that they displayed excursions on the order of kilometres (*c.* 2 km) even crossing large sand patches (unsuitable habitat for them), although most animals do not usually cross edges that are highly contrasting (i.e. hard edges), such as seagrass-sand edges (Chapman & Kramer, 2000; Haynes & Cronin, 2006).

Connectivity, understood as the degree to which landscape enables movement across habitat of a given species, may be some orders of magnitude higher for *S. salpa* than for adult *P. lividus* sea urchins, which only move on the order of tens of meters (Hereu, 2005) even on the long term (Palacin et al., 1997). In addition, adult sea urchins have been shown to be influenced by barriers such as hard edges (e.g. seagrass-sand, Dance, 1987), further limiting their movement across habitats. Nevertheless, their difficulty to cross hard edges may not only be a consequence of its low mobility, but also of the risks involved in crossing habitats lacking adequate protection against predators. At the level of behavioural decision-making, different perceptual ranges and movement capabilities may mean elevated or lowered mortality risk (i.e. from predators, as seen in **chapter 5**; or from disturbances, as seen in **chapter 8**) when leaving a patch in search of new grounds (Lima & Zollner, 1996). This limited capacity to explore the seascape may be in part offset by the planktonic dispersing phase that *P. lividus* has. In fact, we did not find differences in sea urchin abundance comparing seagrass patches near or far from a rocky reef (**chapter 7**). This aspect highlights the importance of their planktonic phase and their recruitment bottleneck (Prado et al., 2012), since it is improbable that adult sea urchins moved from rocky reefs to seagrass patches crossing tens of metres of bare sand. In contrast and as also seen in **chapter 7**, it is highly possible that sea urchins crossed the soft edge (less-contrasting) between the seagrass and the rocky macroalgal communities. Indeed, sea urchins have been shown to move from rocky habitats into seagrass patches (Ceccherelli et al., 2009). This may be explained by several arguments: (i) denso-dependent migration, due to the high recruitment in rocky areas (Prado et al., 2012); (ii) sea urchins may need to complement or supplement their diet with seagrass leaves (or their epiphytes, Tomas et al., 2005a) crossing the rock-seagrass edge. Whatever the reason, these aspects could further explain the contrasting herbivory rates found in seagrass patches embedded in rocky areas as opposed to the ones embedded in sand (**chapter** 7). Indeed, matrix type has been shown to affect edge-mediated behaviour and emigration rates of various species (Ricketts, 2001; Haynes & Cronin, 2003, 2006). This has been attributed to differential predation risk according to the matrix they are in.

9.5 Connectivity and the scale of function delivery

As seen, the sea urchin *P. lividus* and the fish *S. salpa*, the most important Mediterranean herbivores in macroalgal and seagrass communities, perceive and respond to seascape configuration at completely different scales. These differences in mobility between both species mean also different scales of function delivery. However, apart from the scale and movement capacity, habitat selection is of importance when considering the impacts of species on the seascape. For example, while *S. salpa* may be a generalist with enough mobility to impact on different ecosystems, they display an obvious selectivity for the seagrass meadow (where they spend 90% of time, **chapter** 6). This suggests these fishes impact more on the seagrass habitat than on the algal communities, which resonates with the results obtained in other studies in the same sites (Tomas et al., 2005b; Hereu et al., 2008). Hence, to understand the seascape-dependent distribution of herbivory impacts, it is important not merely to know the consumption rates, diets and preferences of the species within the system, but also herbivore behaviour, i.e. movements and habitat selection across time and space, along with the spatial configuration of the seascape mosaic.

Given that disturbances generally operate across a limited range of scales (e.g. until a given depth, for example; or along some kilometres), if different species in a functional group operate at different scales (if one species can swim deeper, or it can escape horizontally), they may provide mutual reinforcement contributing to the resilience of the function (Peterson et al., 1998; Elmqvist et al., 2003). This is known as scale range redundancy and, as pointed out in **chapter** 8, it may be present within the Mediterranean herbivorous group, given the observed differences in *P. lividus* and *S. salpa* mobility and behaviour (**chapters** 5 and 3 6). In addition, their different response to storms (**chapter** 8) has been called response diversity and is suggested to be of importance to ensure the resilience of ecosystem functions in environments subjected to disturbances (Elmqvist et al., 2003). While our study in **chapter** 8 did not assess whether the function provided by *S. salpa* and *P. lividus* (i.e. herbivory) changed as a result of disturbances, it is known that both herbivores are important functional elements (Palacín et al., 1998; Vergés et al., 2009; Pagès et al., 2012). In our system, given the low number of herbivorous species, herbivory function would be easily eroded should both herbivores be heavily affected by the storm. However, we have shown that even faced with large infrequent disturbances such as the 2008 storm, at least one of the herbivorous species of the system (*S. salpa*) would be able to maintain the herbivory function.

The study of not only species abundance or distribution, but also of ecosystem processes, such as herbivory, may be crucial in bridging behavioural and landscape ecology. As we show in **chapter** 7, this is due to the fact that distribution-abundance studies may not be sufficient for a complete understanding of ecosystem processes in different landscapes, since areas with very similar abundances of herbivores can show contrasting herbivory levels due to species and landscape-specific behaviours. These different approaches to the study of ecosystem functioning may be fundamental in order to predict the spatial heterogeneity of ecological processes, which in the case of herbivory ultimately influence plant production, nutrient cycling, plant reproductive success, biotic interactions and trophic pathways of the system. The results of this thesis highlight the insights that the study of behaviour and movement patterns of key species may add to the study of ecological functions such as herbivory within a landscape.

9.6 Future directions

How common are the indirect interactions described in chapter 4?

The interaction network we describe in **chapter** 4 is highly detrimental for the sea urchin population, which is headed to a local extinction in the study site where we conducted our experiments (Romero et al., 2012). While it is obvious that *S. salpa* modify seagrass canopy height in most seagrass meadows (Prado et al., 2007), are the described indirect effects present in other areas apart from Medes Islands MPA? From our results in **chapter** 4, it would seem reasonable to think that every meadow with *S. salpa* reducing canopies below 25 cm is susceptible of presenting this kind of interactions. Therefore it would be interesting to correlate canopy heights in different meadows with their sea urchin abundance. However, the abundance and biomass of predators present in Medes Islands are some orders of magnitude higher compared to most other Mediterranean areas (Sala et al., 2012). Thus, it may be difficult to find this kind of interactions outside MPAs. In any case, our results emphasise that only paying attention to the most conspicuous interactions can be dangerous when managing MPAs, since we may encounter unexpected outcomes in the long term due to interacting indirect effects. This is especially true when the predators and the initiators of indirect effects are equally affected by conservation measures, since they can interact with a positive feedback.

Sea urchin movements under light and chemical cues

In **chapter** 5 we show that sea urchins respond by switching their movement patterns when they detect predator chemical cues, but without a response to light differences. Several other ideas came up during the experiment that could not be conducted at that moment due to temporal limitations. We are interested in seeing whether these prey species would respond with the same type of escaping strategies should we subjected them to roving fish predator cues, which the urchins cannot outrun in the field. We are also curious on whether they would detect more contrasted shadows, how they would search for a refuge in the presence and absence of predator cues, whether they would switch their movement patterns with the presence of food cues, etc. These experiments could be further complemented using different size classes and urchins with varying levels of satiation. Moreover, it would be interesting to make the jump from the laboratory into the field, and from some hours of tracking period to a 24 h cycle or even several days, although this would mean some methodological challenges, such as a way to photograph sea urchins at night (when they are more active, Dance, 1987; Hereu, 2005).

How do *S. salpa* fishes living in areas without seagrass meadows behave?

In **chapter** 6, we show that *S. salpa* is a very mobile species with the capacity of commuting between distant habitats. However, it is also very evident their high selectivity for the *P. oceanica* seagrass meadow. Thus, the question is how would fishes behave in areas without seagrass? Would they display the diel temporal patterns we observed in the meadow area, in other seascape configurations? Or on the contrary, in a seascape with several meadows within fish range, how would fishes move and behave? Would they be faithful to a given meadow or would they spend several days in one meadow and some days in another?

Seasonality, herbivory in seagrass meadows and *S. salpa* movement patterns

In **chapter** 6 we show that *S. salpa* fishes display similar patterns in different seasons. Nevertheless, it has been thoroughly demonstrated that in the Mediterranean sea herbivory is very seasonal, with a peak in summer and low rates in winter (Prado et al., 2007). If *S. salpa* fish, the principal herbivore of *P. oceanica* seagrass meadows (Prado et al., 2007), do not migrate to deeper areas in winter (see **chapter 6**), how do these seasonal patterns arise? Our suspicion is that *S. salpa* activity may be highly dependent on temperature, as has been demonstrated for other fish species (Smith, 2008). Our experience in the field during these years, tells us that intense grazing by *S. salpa* does not occur until water reaches 19-20°C. So, is this actually the case? And if this is the case, is the grazing season longer in southern Mediterranean regions (e.g. North Africa)? And therefore, do seagrass meadows in these areas suffer high herbivory rates for more months (with implications for the plant and for the whole community, see **chapter 4**)? Pushing this argument further, will the foreseen temperature rise result in a generalised increase of grazing pressure?

Another explanation for the lower fish herbivory in seagrass meadows in winter would be a seasonal change in *S. salpa* diet, or the broadening of *S. salpa* diet in winter, as has been found for other fish species (Horn, 1983). In fact, our results on habitat use from **chapter 6** pointed to this direction, with higher habitat use of rocky habitats in winter and almost 100 % of use of the seagrass in summer, in spite of not being conclusive due to the low number of fishes in summer ($n = 1$). Thus, studies in this direction would expand our knowledge on fish seasonal foraging patterns, which could have implications on how algal and *P. oceanica* seagrass cope with the high levels of herbivory *S. salpa* can cause.

Does seascape-dependent spatial heterogeneity in herbivory imply differences in plant production or in plant reproductive success?

The herbivory rates we found in some areas of the seascape in **chapter 7** were well above the production rates at that time of the year. We did not find this production imbalance to imply reduced primary production, as has been found in other cases (Gera et al., in press). However, it could well be the case that we did not find differences at that time of the year (early summer), but since highly grazed plants have to endure the whole summer with less photosynthetic tissues, this may imply less production on the long term (as seen by Gera et al., in press). In addition, this could even lead to increased or decreased resources allocated to reproduction (flowers), as was shown by Planes et al. (2011) in highly grazed meadows inside MPAs.

Do the macroherbivores of Mediterranean macrophyte communities exhibit response diversity and functional compensation in the face of disturbances?

In **chapter** 8, we found that *S. salpa* and *P. lividus* display contrasting responses to storm disturbances, with fishes enduring the disturbance with insignificant losses compared to 50% decreases in sea urchin abundance. We surmise this could imply the maintenance of herbivory function by *S. salpa* even after great storms, owing to the observed ability of these fishes to escape from storm effects. To actually test this functional result, we would have to obtain herbivory rates in several zones before and after a great storm. We could then actually compare both rates and see whether this function was maintained.

Overall, we feel convinced that merging the behavioural and landscape approaches can result in new views in the ecology of functions such herbivory, in which at least two species interact among themselves framed by a given landscape configuration.

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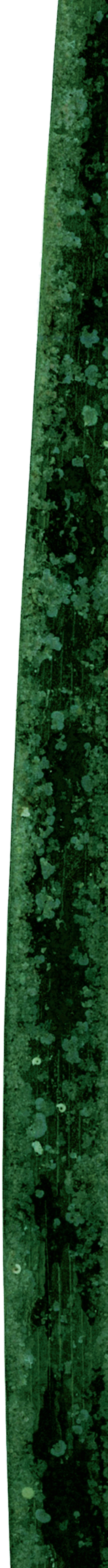

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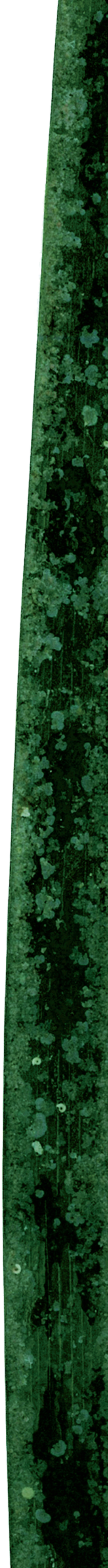
Appendix



A

Supplementary materials

A.1 Evaluating a key herbivorous fish as a mobile link: a Brownian bridge approach

BBMM implementation

To implement BBMM, the data set of each animal should contain a column of coordinate locations and a column with the time each location was reached. In passive acoustic telemetry, location coordinates are those of the receiver that is detecting a given transmitter. However, since the BBMM allows for uncertainty around the starting and ending locations (i.e. location error), the real location is not a constant position, but a Gaussian probability density function around that point (with a mean, i.e. the receiver coordinates; and a variance around that mean, i.e. receiver's detection range, in our case 250 m) (Horne et al., 2007). The column with the time stamps is used to produce a vector of time lags between locations. Since this is a vector of increments of time, its length is thus a row less than the column of time and coordinates. Care should be taken to remove from the data set simultaneous receptions from the same fish (i.e. leading to time lags equal to zero; e.g. if the fish was detected by two or more overlapping receivers at the same time, or for any other reason). See the first rows of SS91 data set (Table A.2) prepared for BBMM estimation of the UD.

Calculations were performed in R (R Development Core Team, 2012) using the package BBMM (Nelson et al., 2011), which computed the UDs for each fish by assigning a probability to each cell of a grid (in our case the grid = 226 × 226 cells, cell size = 20 m). To avoid assigning a space use probability to land cells, we subtracted all land probabilities *ad hoc* and renormalized the UD cell matrix sum to 1, given that utilisation distributions are probability density functions (Powell, 2000).

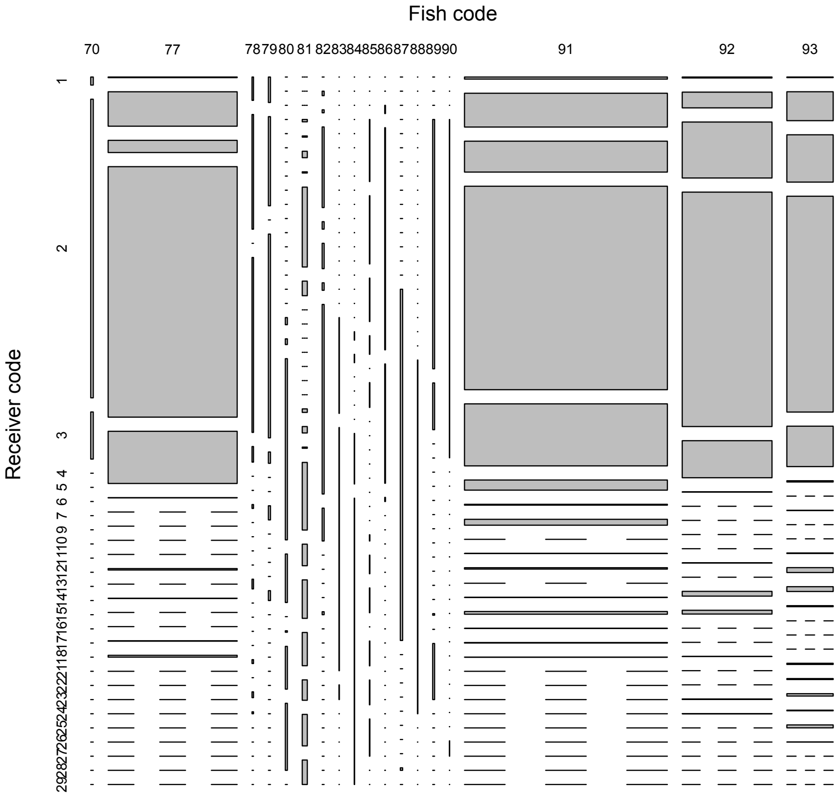


Figure A.1: Raw data distribution. Bar width on the x-axis relates to the number of total detections per fish. Bar length on the y-axis relates to the number of detections per receiver for that fish. Note that the vast majority of detections (95.5%) come from only fishes (SS77, SS91, SS92, SS93). These fishes plus SS70 were considered resident to our receiver network, since they spent within the array more than the 60% of days of their tracking period (see Table A.1). Note also that receivers 3, 4 and 5 accumulate most of detections. These receivers presented seagrass habitat ('meadow') within their range.

Table A.1: Summary of the monitoring data for the 18 successfully tracked fish. ID = fish code; TL = total length; DD = number of days detected; TP = tracking period (total period of detection); TD = total number of detections; RI = residence index; NR = number of receivers that detected each fish; AR = area of release; Rel. Date = date the fish was released (yyyy/mm/dd); HR size = home range size; Connect.I-C = did the fish moved between the islands and the coast?

ID	TL (cm)	DD (days)	TP (days)	TD	RI	NR	AR	Rel. Date	HR size (ha)	Connect. I-C
SS70	28	22	28	308	0.79 (resident)	3	4	2008/10/16	40.92	no
SS77	25	96	98	15473	0.98 (resident)	10	3	2008/10/16	166.24	yes
SS78	27.5	12	184	182	0.07 (non-resident)	9	3	2008/10/16	94.26	yes
SS79	27	18	206	250	0.09 (non-resident)	6	3	2008/10/16	71.48	no
SS80	27	20	93	248	0.22	7	1	2008/10/16	-	no
SS81	26	26	51	607	0.51 (non-resident)	16	1	2008/10/16	65.68	yes
SS82	22.5	3	3	237	1	9	3	2008/10/16	-	no
SS83	27	4	216	48	0.02	3	1	2008/10/16	-	no
SS84	24	7	95	42	0.07	4	1	2008/10/16	-	no
SS85	25	2	5	57	0.40	11	1	2008/10/16	-	yes
SS86	23	14	27	86	0.52 (non-resident)	4	2	2008/10/17	40.64	no
SS87	23.5	4	84	279	0.05	2	2	2008/10/17	-	no
SS88	23	1	1	45	1	1	2	2008/10/17	-	yes
SS89	22.5	3	179	227	0.02 (non-resident)	4	2	2008/10/17	967.04	yes
SS90	25	8	35	23	0.23	2	3	2008/10/16	-	yes
SS91	28	346	372	24330	0.93 (resident)	15	4	2008/10/16	167.96	yes
SS92	32	79	112	10764	0.71 (resident)	12	4	2008/10/16	580.88	yes
SS93	34	62	71	5557	0.87 (resident)	17	4	2008/10/16	313.80	yes

Table A.2: First rows of SS91 data set prepared for BBMM estimation of the UD. The first column corresponds to the time the fish reached each location (in Julian minutes in this case), the second column are the UTM coordinates on the x-axis and the third column the UTM coordinates on y-axis. The time lags between locations are the difference between the time the next location will be reached and present time.

Julian	x	y
20403030	518238.2	4654958
20403040	518238.2	4654958
20403043	518238.2	4654958
20403059	518238.2	4654958
20403074	518499.5	4654690
20403077	518238.2	4654958
20403082	518238.2	4654958
20403088	518238.2	4654958
20403093	518238.2	4654958
20403097	518238.2	4654958
20403102	518238.2	4654958
20403107	518238.2	4654958
20403121	518238.2	4654958
20403127	518238.2	4654958
20403136	518238.2	4654958
20403142	518238.2	4654958
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20403154	518238.2	4654958
20403159	518238.2	4654958

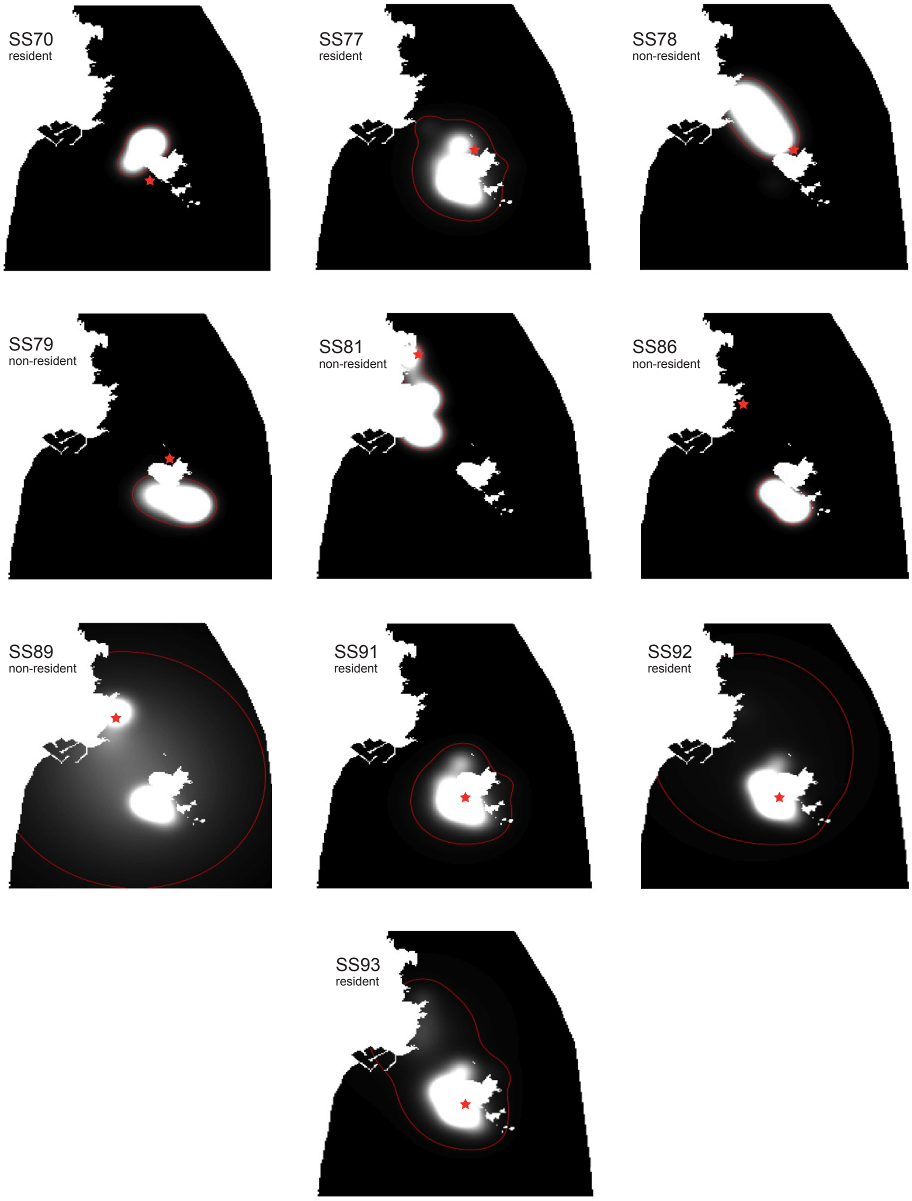


Figure A.2: Individual BBMM utility distributions of all fishes. Black colours indicate low probability and colors from grey to white indicate increasing probabilities of finding an individual. The red line encompasses the 95% probability of use for a given individual. Stars correspond to the respective sites of capture and release. Note that resident fishes used with a high intensity the areas corresponding to seagrass habitat in Fig. 6.1a (from **chapter 6**). In addition, 3 out of 5 non-resident fishes did also use these meadow areas. Note also, that while fish SS78 very frequently connected the islands with the coast, four other fishes (SS77, SS89, SS92, SS93) connected both areas regularly (both areas enclosed by the 95% isopleth [red line]).

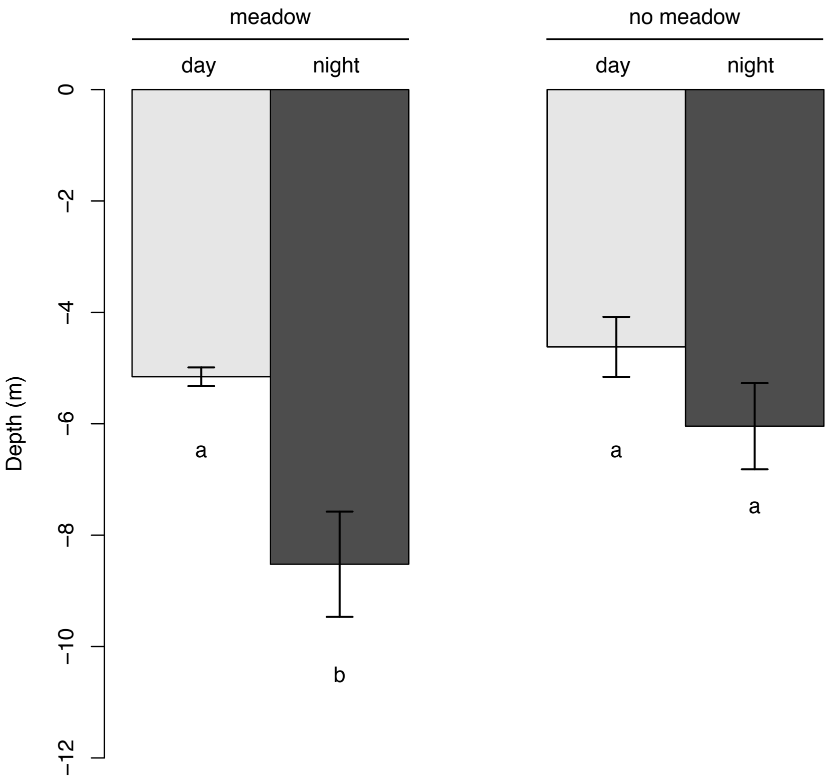


Figure A.3: Day and night mean depths for the resident population in meadow and no-meadow habitats. Different lower case letters indicate significant statistical differences. There were significant differences in fish mean depth according to the phase of the day in meadow habitat, but not in no-meadow habitat.

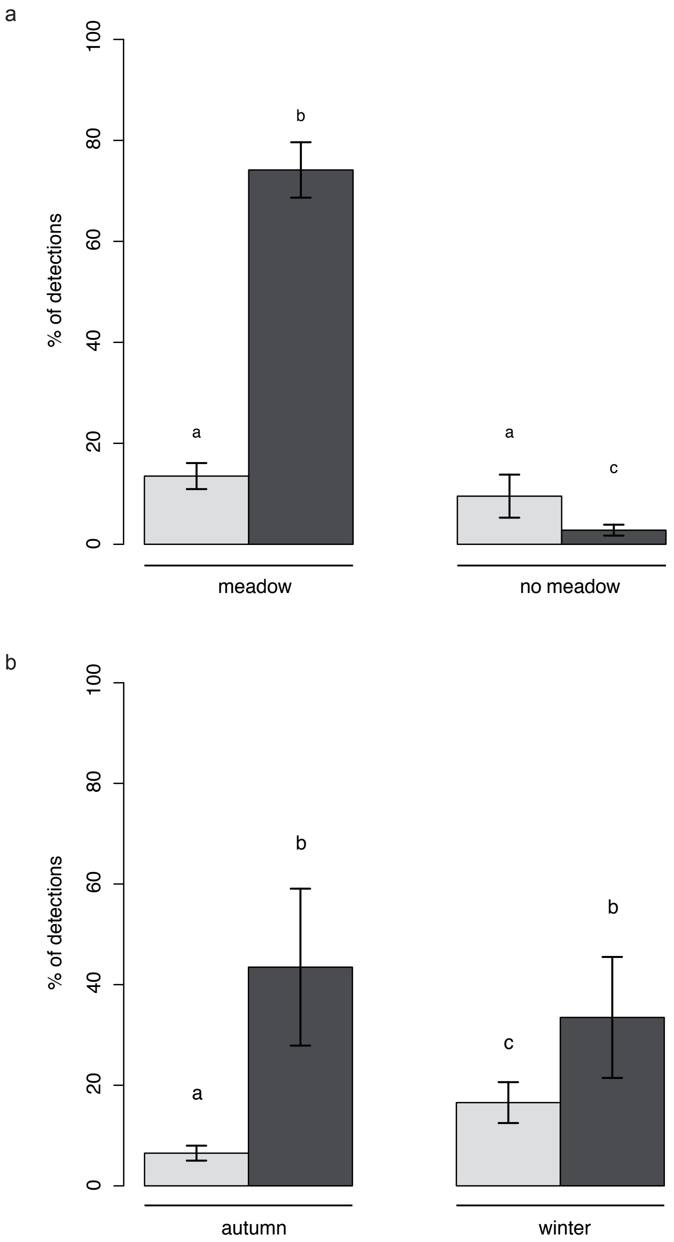


Figure A.4: Day (light grey) and night (dark grey) mean% of detections for the resident population (a) in meadow and no-meadow habitats and (b) in different seasons. Different lower case letters indicate statistical significant differences.

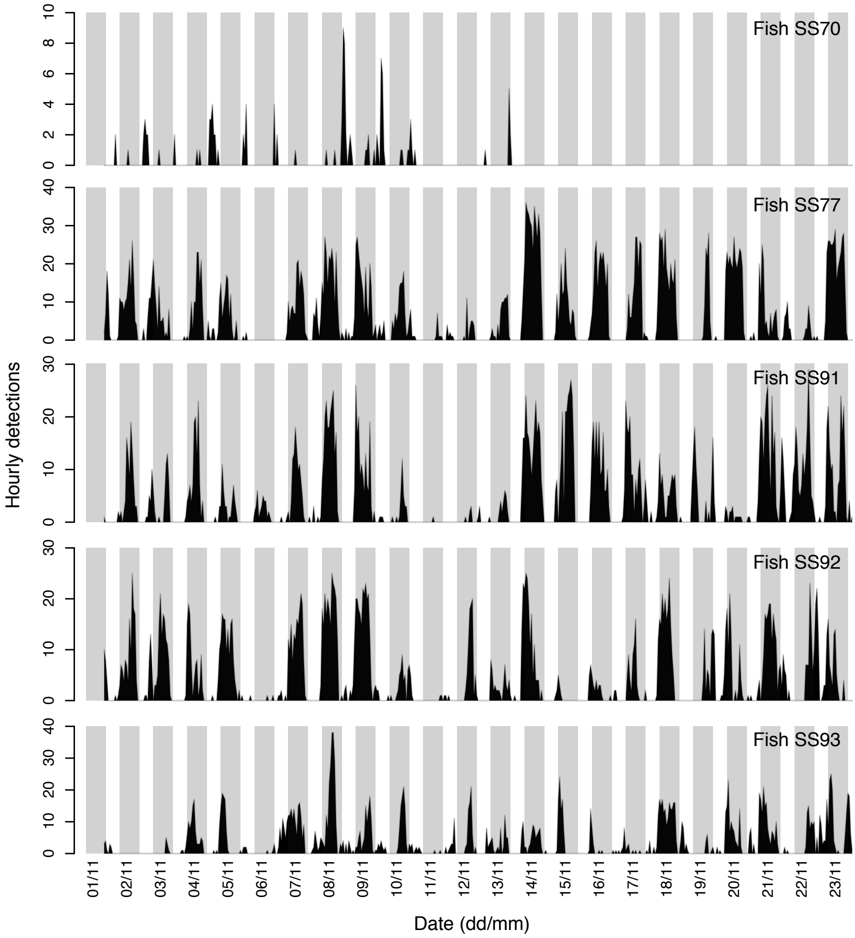


Figure A.5: Resident fishes' subset of the number of hourly detections. Vertical stripes indicate day (white) and night (grey) related to the local sunrise and sunset time. Note the higher number of nocturnal detections for fishes SS77, SS91, SS92 and SS93 and a reversed cycle (i.e. higher number of diurnal detections) for fish SS70.

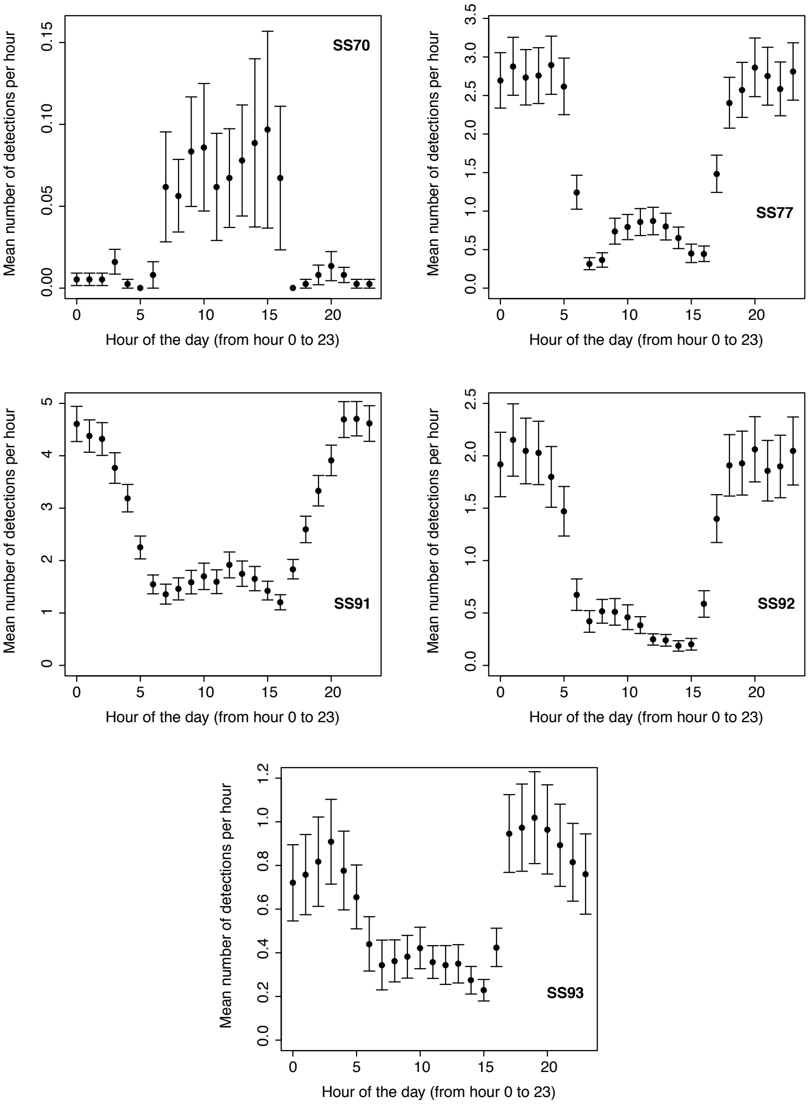


Figure A.6: Individual temporal patterns of the mean number of hourly detections for resident fishes along a 24 h cycle. Note the different scales on the y-axis. We observe that 4 out of 5 resident fishes behaved very similarly, with only fish SS70 with a reversed cycle, but with a lower contribution to the whole dataset compared to the rest of fishes (see Table A.1 and Fig. A.1). Note this temporal pattern (24 h cycle) remains visible even after taking the average of these 5 resident fishes (see Fig. 6.3a from **chapter 6**).

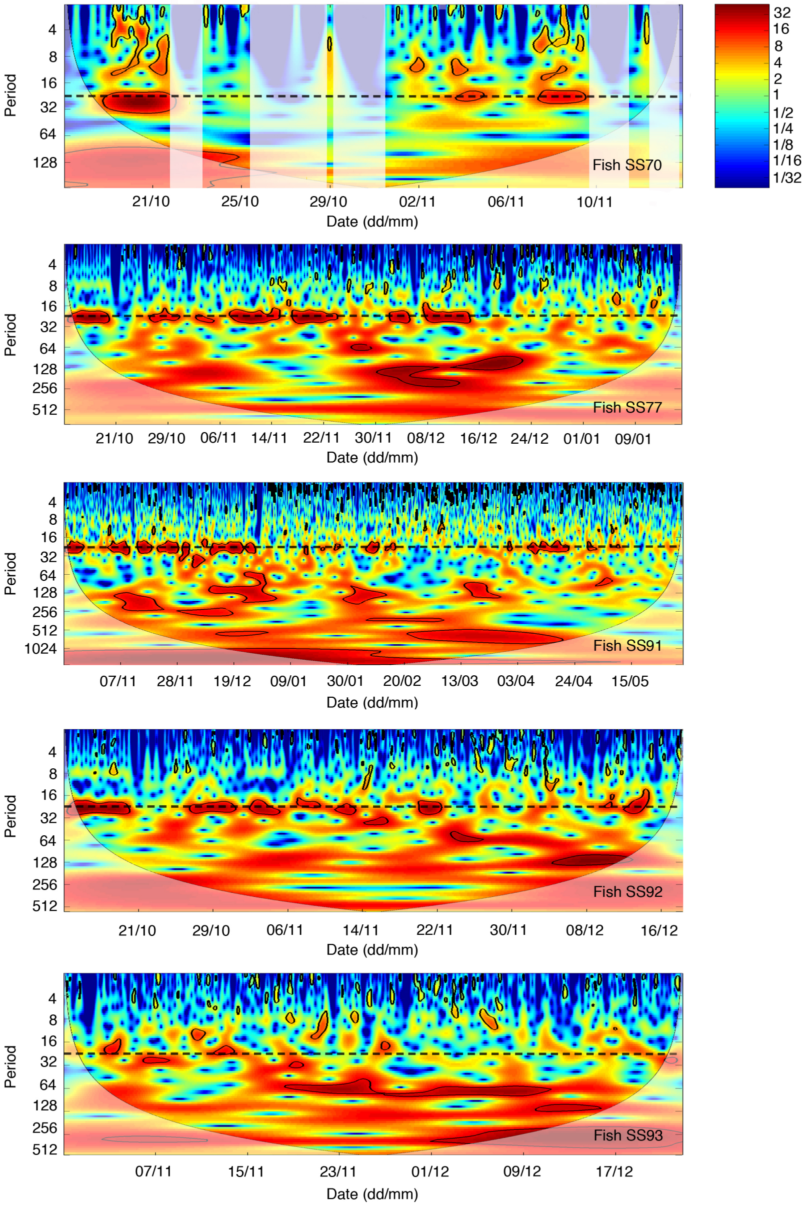


Figure A.7: Wavelet spectrum for the number of hourly detections of each resident fish individually. Significant patches on the 24 h period were detected for all residents (horizontal dashed line). The pattern was significant (with some non-significant patches) for most of the time series for fish SS77, SS91 and SS92. It was less evident for fish SS93. Fish SS70 had also a significant 24 h cycle but, with a reversal in the phase (see Fig. A.5, A.6). Since all resident fishes displayed similarities also on these analyses, the wavelet spectrum for the pooled population of resident fishes gave very similar results (see Fig. 6.3b from **chapter 6**). The thick contour designates the 95% confidence level. The cone of influence where edge effects might distort the picture is shown as a lighter shade. Light rectangles correspond to holes in the time-series without fish detections where assessing periodicity makes no sense. The scale bar represents the intensity of the time-frequency space over time.

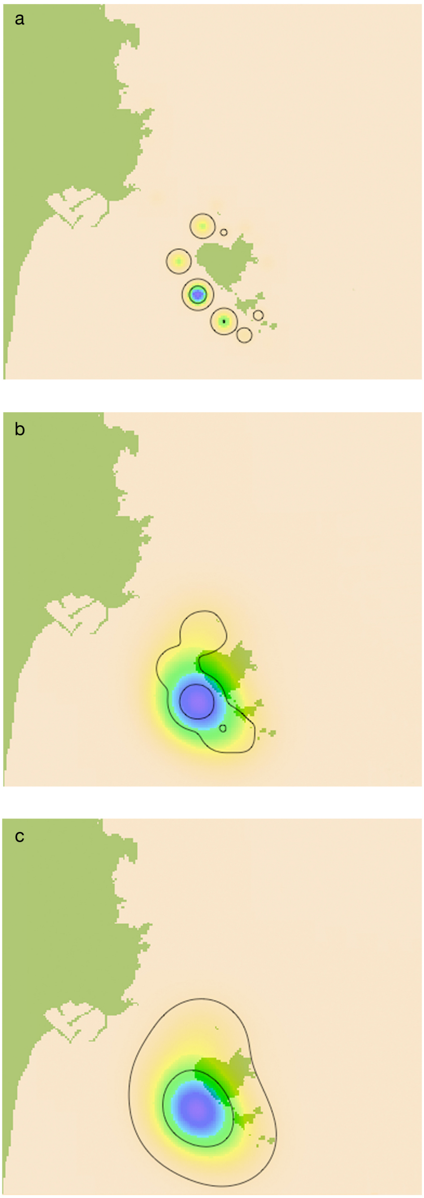


Figure A.8: Utility distributions of resident fishes obtained with the kernel density estimator (KUD). Differences between panels arise as a result of different smoothing parameters: (a) h = 50, (b) h = 100, (c) h = 250. Solid lines correspond to the 50% and 95% isopleths, and cooler colours indicate higher intensity of use. While the BBMM successfully identified connections between the islands and the coast (see Fig. 6.1b,d from **chapter 6**), KUD did not. In addition, the BBMM identified specific connections (bridges) between receivers with a higher intensity of use than others. This is not possible with the KUD, since it only takes location distribution into account. In contrast, the BBMM considers not only the locations but also the time dependence between them (the actual path the animal has followed), assumes the animal has moved following a conditional random walk between pairs of locations and allows for accounting for a location error (in our case we specified a telemetry error of 250 m).

A.2 Analizing animal movements using Brownian Bridge Movement Models

See Horne et al. (2007) for additional information.

Features

A Brownian bridge is a continuous-time stochastic model of movement in which the probability of being in an area is conditioned on starting and ending locations, the elapsed time beetween those points, and the mobility or speed of movement.

- It takes into account *biotelemetry error* (location error). Therefore the model considered incorporates uncertainty in the starting and ending locations.
- It takes into account the *time* series between relocations.
- It has a *Brownian Movement Model* behind (pure diffusive model).

Equations

BBMM is dependent on time-specific location data, the distribution of location errors and the Brownian motion variance parameter σ_m^2, which can be estimated by maximum likelihood.

The movement model behind this home range method comes from the bivariate normal distribution $N(\mu, \sigma^2 \mathbf{I})$:

$$\varphi(z; \mu, \sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} exp\left[\frac{-(z-\mu)^2}{2\sigma^2}\right]$$

To consider the uncertainty in the starting and ending locations they let them be random, with probability density functions $f_a(x) \sim N(a, \delta_a^2 I)$ and $f_b(x) \sim N(a, \delta_a^2 I)$ respectively, where x and y are position variables.

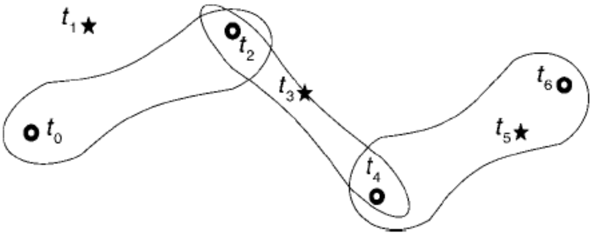
After some steps, we can obtain the probability density function of an animal using region A, $h(z)$

$$h(z) = \frac{1}{T}\int_0^T \varphi(z; \mu(t), \sigma^2(t))dt \tag{A.1}$$

The formula in equation (A.1) is the pdf for the bridge between 2 locations, and therefore the only thing we have to do to obtain the bridge for multiple locations is iterate it and sum it all up. This is what is done in fortran in the BBMM R package (Nelson et al., 2011). This is the resultant equation:

$$h(z) = \frac{1}{T_{total}} \sum_{i=0}^{n-1} \left\{ \int_0^{T_i} \varphi(z; \mu_i(t), \sigma_i^2(t)) dt \right\}$$

Until now, we have been bridging between consecutive locations. However, in order to estimate σ_m^2 we must do it between even locations to obtain independent time observations that will be used in the estimation.



This yields a sample of $n/2$ independent odd observations Z_1, Z_3 ,..., Z_{n-1}. Z_i is the ith observation $Z_i \sim N(\mu_i(t_i), \sigma_i^2(t_i)I)$ where

$$\mu_i(t_i) = Z_{i-1} + \alpha_i(Z_{i+1} - Z_{i-1}) \Longrightarrow \mu_i = Z_{i-1} + \frac{(t_i - t_{i-1})(Z_{i+1} - Z_{i-1})}{t_{i+1} - t_{i-1}}$$

$$\alpha_i = \frac{t_i - t_{i-1}}{T_i}$$

$$T_i = t_{i+1} - t_{i-1}$$

and

$$\sigma_i^2(t) = T_i\alpha_i(1 - \alpha_i)\sigma_m^2 + (1 - \alpha_i)^2\delta_{i-1}^2 + \alpha_i\delta_{i+1}^2$$

where δ_i^2 is the telemetry error on the ith location.
This allows them to construct the likelihood function for odd locations:

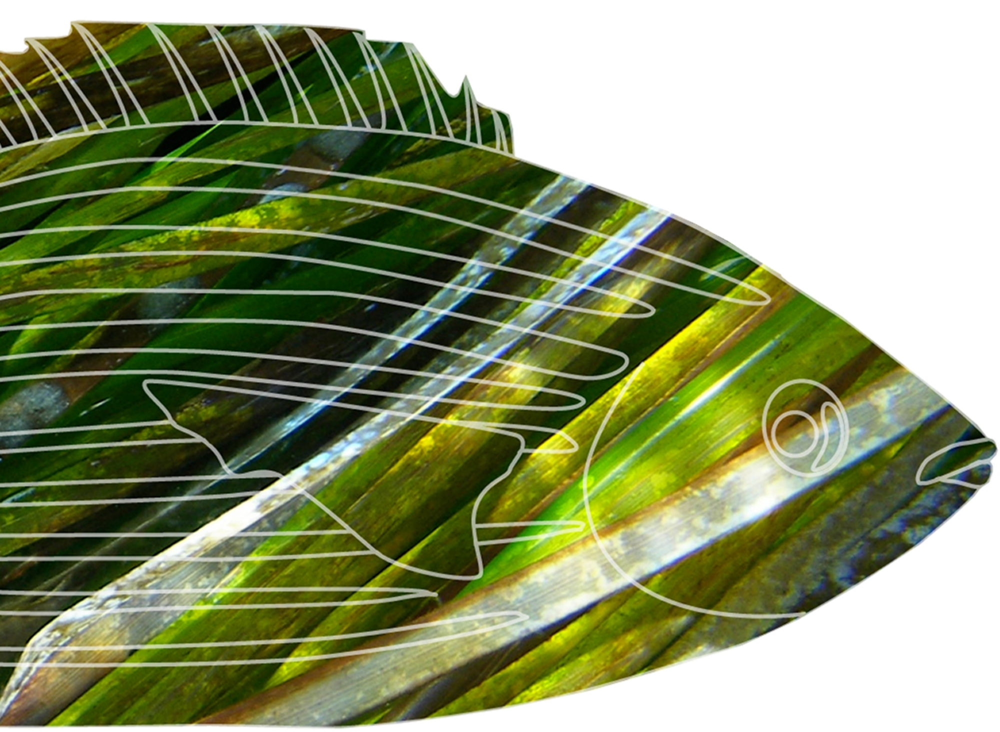
$$L = \prod_{n-1}^{i=1} \frac{1}{2\pi\sigma_i^2(t_i)} exp \left\{ \frac{-[Z_i - \mu_i(t_i)][Z_i - \mu_i(t_i)]^\intercal}{2\sigma_i^2(t_i)} \right\} \tag{A.2}$$

The following equation is the same as equation (A.2) but in the way it is implemented in the package BBMM:

$$L = -\sum_{n-1}^{i=1} \log \left[\frac{1}{2\pi\sigma_i^2(t_i)} exp \left\{ \frac{-[Z_i - \mu_i(t_i)][Z_i - \mu_i(t_i)]^\intercal}{2\sigma_i^2(t_i)} \right\} \right] \tag{A.3}$$

If δ is known, the only unknown parameter in equation (A.3) is σ_m^2, and therefore it can be obtained by optimizing the previous equation.

In effect, we are using the observed locations to find the value of σ_m^2 that best predicts the odd locations when a Brownian bridge is assumed between the even locations.



Estudi de l’**herbivorisme** en **macròfits marins** des de l’**ecologia** del **comportament** i del **paisatge**