IMPORTANCIA DE L'ENERGIA AUXILIAR EN LA DINAMICA DELS SISTEMES PELAGICS: TURBULENCIA I ZOOPLANCTON

Memòria presentada per Enric Saiz Sendrós
per optar al Grau de Doctor

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A la meva familia.

Agraïments

Primer de tot vull agraïr al Dr. Miquel Alcaraz la direcció d'aquesta Tesi i el constant suport i encoratjament que ha demostrat. La seva col.laboració i participació han estat decissives al llarg de totes les etapes d'aquesta tasca.

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Els Drs. C. M. Duarte, M. Estrada, R. Margalef i P.J. Wangersky han revisat alguns dels treballs originals que constitueixen els capítols de la Tesi. Els agraeixo les seves correccions i suggeriments.

El Sr. Gregorio Andreu, de SONY ESPAÑA SA, amablement va assessorar en alguns aspectes relatius a la videocinematografia. El Dr. C. Esparducer, Director de l'Hospital Materno-Infantil de la Ciutat Sanitària de la Vall d'Hebró, i els Drs. G. Enríquez i C. Aso, del Departament de Radiologia, van facilitar l'ús d'una ecosonda Doppler de l'esmentat Departament.

Finalment, Marta, t'agraeixo la paciència i suport que m'has donat durant aquests anys, i les hores de son dedicades a l'edició i correcció de la Tesi.

PROLEG

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L'organització de la tesi en capítols independents és conseqüència de la prèvia o futura publicació dels resultats obtinguts conforme s'obtenien i elaboraven. Aquesta estructuració ha fet que sovint s'hagi estat repetitiu en alguns conceptes, especialment a les introduccions respectives de cada capítol. Mentre que per la INTRODUCCIO general de la Tesi i la SINTESI final s'ha emprat la llengua catalana, pel motiu abans esmentat s'ha respectat l'ús de la llengua anglesa per la redacció de la resta dels capítols, afegint-hi un breu resum en català al final de cadascun d'ells.

A la **INTRODUCCIO** es revisen els coneixements actuals sobre turbulència i zooplàncton, es discuteix la seva importància i es plantegen les hipòtesis de treball bàsiques de la tesi i l'aproximació experimental utilitzada.

En el **CAPITOL I** s'estudia experimentalment mitjançant l'ús de microcosmos l'efecte de la turbulència de petita escala en el desenvolupament de poblacions de copèpodes del gènere *Acartia*. En una primera part es fa èmfasi en la relació entre consumidors i productors, observant-se canvis en l'estructura demogràfica de les poblacions i en l'eficiència tròfica del sistema. En una segona part s'estudien amb més detall les pautes de creixement i desenvolupament en condicions de turbulència i el paper que els canvis qualitatius en el fitoplàncton hi poden tenir.

En el **CAPITOL II** s'estudia la influència de la turbulència en el metabolisme del zooplàncton, estimant-se taxes d'excreció d'amoni i fòsfor en diferentes espècies del copèpode calanoide *Acartia*, i es discuteix la seva importància en relació als trets observats a nivell poblacional.

En el **CAPITOL III** es determinen les taxes d'ingestió i l'eficiència bruta de creixement en funció de la concentració de menjar en tres espècies congenèriques d'*Acartia*, i s'avaluen els efectes de la turbulència de petita escala en aquests processos i el diferent comportament de les espècies en funció del seu hàbitat.

El **CAPITOL IV** és un recull d'estudis o observacions videocinematogràfiques sobre com pot afectar la turbulència de petita escala al zooplàncton. Agrupa tant treballs amb entitat pròpia com estudis preliminars sobre possibles línies a seguir en un futur. Es determinen taxes d'encontre entre copèpodes i ciliats i s'estudien pautes de comportament i la seva freqüència. També s'assaja videocinematogràficament la quantificació de la intensitat de turbulència en un dels models experimentals emprats. D'alguna manera, pretén completar o aclarir aspectes sorgits mitjançant l'ús de microcosmos o tècniques clàssiques d'incubació.

A la **SINTESI** es repassen globalment els resultats obtinguts basant-se en els coneixements actuals, s'extreuen conclusions i hipòtesis sobre el paper de la turbulència de petita escala en l'activitat dels copèpodes calanoides, i es discuteix la seva repercusió en el funcionament dels ecosistemes pelàgics. Finalment es discuteixen, així mateix, estudis preliminars sobre l'aplicació de sondes Doppler en la quantificació de turbulència en models de laboratori.

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Antecedents

L'energia mecànica introduïda als sistemes aquàtics per l'acció del vent, l'escalfament pel Sol i l'acció gravitacional, indueix el moviment de masses d'aigua i una conseqüent generació d'energia cinètica turbulenta, distribuida en tot un ventall d'escales espacio-temporals, que caracteritza els sistemes aquàtics com uns ambients essencialment turbulents (Harris 1986).

La importància d'aquest moviment turbulent en la dinàmica dels ecosistemes aquàtics ha estat reconeguda des de fa molt de temps, especialment quan es relacionen processos de barreja (cicle estacional d'estratificació-barreja, fronts, marees, ventades, afloraments, ...) amb la producció primària i la successió i selecció d'espècies o grups biològics de fitoplàncton (p.e. Margalef 1978, Legendre 1981, vegeu Tett i Edwards 1984 per una revisió). És difícil de diferenciar en aquests casos, però, els efectes de la turbulència "per se" dels efectes deguts a canvis en la intensitat de llum i concentració de nutrients a l'abast dels organismes fitoplanctònics.

Turbulència i zooplàncton en el medi natural

L'estudi de la influència de la turbulència sobre les poblacions de zooplàncton en el medi natural s'ha orientat principalment des d'un punt de vista faunístic i descriptiu, tant en relació amb processos de transport per advecció com a l'estret acoplament amb els productors primaris.

Així, s'han observat biomasses elevades i canvis en la composició específica de comunitats de zooplàncton associades a sistemes frontals (Holligan et al. 1984, Herman et al. 1981, Boucher et al. 1987, Ibanez et al. 1987, Saiz et al. submitted), no només per un efecte purament mecànic de transport, sinó també com a conseqüència del propi comportament dels organismes (potser l'aspecte menys conegut). Similarment, s'ha descrit una dispersió en la distribució vertical del micro i mesozooplàncton (Turner i Dagg 1983; Jonsson 1989; Haury et al. 1990), i de l'ictioplàncton (Heath et al. 1988; Olla i Davis 1990) en relació a la turbulència. Boucher (1984) relaciona la pèrdua del comportament de migració vertical del zooplàncton en sistemes frontals a canvis en la distribució vertical del fitoplàncton.

Diversos treballs recents indiquen que aquests processos hidrodinàmics també poden influir en altres aspectes de l'activitat del zooplàncton. Així, Scrope-Howe i Jones (1985) (citat a Haury i Pieper 1988) descriuen increments en l'abundància de zooplàncton en el sistema frontal del Western Irish Sea, els quals corresponen principalment a poblacions compostes per estadis jovenívols i que s'atribuirien a un augment en la producció de zooplàncton en el front. D'altra banda, Harris i Malej (1986) estimen taxes específiques d'excreció d'amoni més altes a *Calanus helgolandicus* que habiten zones de barreja respecte els de zones estratificades.

Runge (1985) i Peterson (1986) consideren que els increments observats en l'activitat (alimentació, desenvolupament, fecunditat) dels copèpodes en relació amb aquests processos hidrodinàmics, depenen principalment de diferències en la composició qualitàtiva i específica del fitoplàncton, més que no pas de la seva concentració o biomassa. En aquest sentit, Peterson i Bellantoni (1987), Kiϕrboe i Johansen (1986) i Kiϕrboe et al. (1988, 1990) associen la variabilitat de la fecunditat en copèpodes calanoides amb l'estructura hidrogràfica del seu hàbitat, principalment com a conseqüència de l'augment en zones d'alta turbulència de la proporció de fitoplàncton (clorofil.la) $>$8-10 μm respecte al total, encara que no es descarten d'altres causes (Kiϕrboe et al. 1988, 1990).

Estudis experimentals

Paral.lelament a aquests treballs realitzats en el camp, on el control i l'aïllament dels factors físics, químics i biològics és impossible, en la darrera dècada s'ha incrementat la utilització experimental de meso i microcosmos, volums d'aigua de mida molt variable confinats tant al laboratori com al medi natural. Malgrat problemes, com l'alta relació superfície/volum i els canvis en els coeficients de difusió i advecció, el seu ús ha demostrat que són una eina útil en l'estudi de la dinàmica dels processos planctònics, a mig camí entre els sistemes naturals i el laboratori (Harte et al. 1980; Oviatt et al. 1980; Pilson i Nixon 1980), ja que a més del control de les variables permet la replicabilitat.

Paradoxalment, malgrat el fet que la turbulència, junt amb la llum i els nutrients, sigui un dels factors que més influeixen en l'estructura dels ecosistemes aquàtics, el seu estudi mitjançant aquesta aproximació no ha estat gaire intens, i els resultats existents sovint són interessants i suggeridors, però de difícil interpretació, en part a causa de problemes metodològics en la generació i quantificació de turbulència, i sobretot pel fort caràcter modulador que té l'estat de successió de les poblacions de fitoplàncton en el moment de confinar-les (Marrasé 1986, Estrada et al. 1987b).

En aquest sentit, Perez et al. (1977) demostren que la turbulència afecta de forma diferent el zooplàncton (forta davallada en l'abundància, fins a valors la meitat del control) i el fitoplàncton (gran increment en l'abundància) en microcosmos de 150 litres. Resultats semblants en d'altres experiments del mateix equip (Nixon et al., 1979) són interpretats com una menor pressió de depredació sobre el fitoplàncton, tant per una menor eficiència en l'alimentació com per una major mortalitat en condicions de turbulència (d'origen fisiològic o comportamental, o potser un artefacte mecànic produït pel sistema d'agitació).

Oviatt (1981), en mesocosms de 13000 litres, realitza un estudi integrat del mateix estil durant varis mesos. De l'aplicació d'una agitació continua en resulta una menor concentració de nutrients, una més alta concentració de clorofil.la (encara que els quocients producció/clorofil.la són similars), i una menor biomassa zooplanctònica.

L'autora conclou que la disminució de biomassa del zooplàncton només pot ser un artefacte degut a les mides del tanc i a la reducció en l'advecció horitzontal, provocant la destrucció de la segregació espacial dels diferents estadis de desenvolupament de les espècies presents i un conseqüent increment del canibalisme. La presència d'altes concentracions de fitoplàncton, però, no recolza aquesta hipòtesi.

Altres estudis en mesocosms també han demostrat un efecte de la turbulència en el zooplàncton, tant una reducció del control exercit pel zooplàncton sobre el fitoplàncton (Eppley et al. 1978), com canvis en la dominància d'espècies, abundància i biomassa total (Donaghay i Klos 1985). Malauradament, la presència de zooplàncton carnívor en alguns d'aquests treballs dificulta la interpretació dels resultats.

Dins d'una línia de treball més àmplia enfocada a la successió d'espècies i a la influència que la turbulència i aports periòdics de nutrients poden tenir-hi (vegeu Marrasé 1986 per a una compilació), Alcaraz et al. (1989) discuteixen els resultats obtinguts en experiments realitzats en microcosmos de 30 litres, ens els quals s'estudia específicament l'efecte de la turbulència i el zooplàncton (copèpodes) en la dinàmica de poblacions naturals de fitoplàncton. Només en presència d'agitació i copèpodes s'observen canvis en l'evolució temporal de la concentració de clorofil.la. Aquests canvis (retardament en el bloom inicial de clorofil.la o l'aparició d'un pic secundari) són atribuïts a un increment en el metabolisme del zooplàncton en condicions de turbulència, com a conseqüència de l'estimulació de les reaccions d'escapada en els copèpodes pels remolins turbulents. Les reaccions d'escapada són una pauta de comportament força general en el zooplàncton que se suposa adaptativa com a resposta enfront de depredadors i com estratègia per buscar microzones ("patches") més riques en aliment. Estimacions teòriques en copèpodes les suposen d'un cost energètic de 3 a 400 vegades més alt que el metabolisme estàndar (Strickler 1977, Morris et al. 1985, Alcaraz i Strickler 1988). Segons aquesta hipòtesi, doncs, l'increment metabòlic donaria lloc per una banda a altes taxes d'excreció i, com a conseqüència d'aquest aport de nutrients per via regenerativa, a l'aparició de blooms secundaris. D'altra banda, això comportaria una major pressió depredadora sobre el fitoplàncton, la qual cosa explicaria el retardament en l'aparició del pic inicial.

Els resultats obtinguts amb la utilització de meso i microcosmos són difícils d'explicar, però, basant-se només en els canvis qualitatius i quantitatius del fitoplàncton observats en sistemes naturals. Això fa pensar en altres mecanismes, potser del caire proposat per Alcaraz et al. (1989), pels quals la turbulència influeix en la dinàmica i l'activitat de les poblacions de zooplàncton. Ara bé, ¿hi ha d'altres indicis que suggereixin un possible efecte directe de la turbulència en el zooplàncton a unes escales temporals i espacials petites? Pot realment la turbulència de microscala (de $<10^{-2}$ m) afectar el zooplàncton?.

Alguns aspectes físics de la turbulència de microscala

Des d'un punt de vista físic, encara es discuteix l'escala mínima en la qual l'energia turbulenta pot actuar abans de dissipar-se. La teoria de la turbulència (vegeu Spigel i Imberger 1987 per una revisió) suggereix que en un flux turbulent l'energia del flux mig es transfereix mitjançant interaccions no-lineals cap a remolins successivament més petits, a través de salts d'energia, fins a arribar a unes escales espacio-temporals per sota de les quals els gradients en velocitat són difosos per la viscositat molecular tan aviat com es formen. L'escala espacial del remolí més petit (anomenada escala de Kolmogorov) és independent del mecanisme generador, depenent només de la taxa de dissipació i de la viscositat cinemàtica. Aquesta mida és típicament de l'ordre de mil.límetres a la capa de barreja (Spigel i Imberger 1987). D'altra banda, en el medi natural la turbulència és força discontinua, intermitent i confinada a taques ("patchiness"). Levandowsky et al. (1988) en una discussió sobre la viabilitat de la quimiorecepció en un medi turbulent, descriuen, coincidint amb Spigel i Imberger (1987), l'aspecte que pot tenir un fluid turbulent a petita escala: "...els remolins més petits, de l'ordre d'1 mm de diàmetre, sovint arrenglarats o apilotonats, es troben separats per volums d'aigua relativament grans amb fluxs aparentment laminars a la seva escala. Els remolins més petits poden arribar a ocupar menys de l'1% del volum del sistema, i els espais entre els remolins més petits, o rengleres d'ells, poden ser de l'ordre de centímetres o decímetres. L'aigua remanent en les regions fora dels remolins més petits pot eventualment ser endinsada cap a ells, en escales de temps de l'ordre de segons".

Altrament, en un treball recent Lazier i Mann (1989) argumenten que a escales petites la densitat d'energia disminueix ràpidament en funció de la mida del remolí, de manera que per a remolins 5 vegades l'escala de Kolmogorov el contingut d'energia seria poc important, de l'ordre d'un 1% del màxim d'energia. Segons els autors, el fet de no considerar això comporta una sobrestimació del grau de barreja turbulenta a petita escala (com p.e. Mitchell et al. 1985). Així, la turbulència de petita escala podria arribar a influir en el flux de difusió de partícules immòbils només quan aquestes medeixen al voltant d'1 mm per a turbulències febles, i de l'ordre de 100 μm per a intensitats majors. Hi ha evidències experimentals, però, que certs organismes fitoplanctònics molt menors, de l'ordre de 10-40 μm, poden veure's afectats tant en el seu creixement com en l'absorció de nutrients per la turbulència (Pasiack i Gavis 1975, White 1976, Savidge 1981, Thomas i Gibson 1990, Berdalet 1991).

En qualsevol cas, sembla factible des del punt de vista físic que els organismes mesozooplanctònics puguin ésser afectats pel grau de turbulència del medi, depenent de la intensitat, escala i espectre de la turbulència, així com de les característiques del propi organisme.

Noves perspectives

Al llarg de la dècada dels 80, el reconeixement de la importància que té l'estret acoplament entre processos físics i biològics, i així mateix entre llurs escales espacial i temporal, ha estat general (p.e. recull de treballs a Steele 1978, Denman i Powell 1984, Tett i Edwards 1984, Legendre i Demers 1985, Peterson 1986, Haury i Pieper 1988). Pren importància l'estudi dels processos fisiològics del plàncton a les escales de temps i espai en què viu l'organisme , i alhora es questiona el paper que la turbulència de petita escala hi pot jugar.

Rothschild i Osborn (1988) proposen que la turbulència de petita escala, en augmentar la velocitat relativa entre depredador i presa, incrementaria la seva taxa d'encontre. Com a conseqüència, en condicions de turbulència hi hauria un augment aparent de l'abundància de preses, és a dir, el depredador tindria la "impressió" que hi ha més preses al seu abast. Segons aquest model, aquests efectes són més evidents com més petita és la velocitat dels organismes i més intensa la turbulència. Evans (1989) ha corregit algun aspecte matemàtic del model, però les conclusions qualitatives són les mateixes.

El model de Rothschild i Osborn suposa un pas endavant en la comprensió dels processos que, a petita escala, poden influir fortament en propietats macroscòpiques de la dinàmica de poblacions. Encara no es coneix, però, quina és la resposta dels organismes a aquest efecte: com es comporta el depredador enfront d'aquest increment aparent? Pot realment aprofitar-ho? Aquestes respostes són fonamentals per esbrinar la importància real de la turbulència de petita escala en les transferències tròfiques als ecosistemes pelàgics.

Fins ara hem vist que la turbulència pot arribar a actuar a les escales de temps i espai en què tenen lloc els processos biològics del plàncton, i a més pot incrementar la taxa d'encontre entre partícules per un efecte purament mecànic. Finalment, ens falta considerar si els organismes zooplanctònics tenen la capacitat de respondre a aquests estímuls.

La resposta del zooplàncton a estímuls hidrodinàmics es coneix d'antuvi en relació a la capacitat reotàctica d'evitació de xarxes de plàncton. Experiments duts a terme amb copèpodes i altres organismes en diferentes condicions d'il.luminació i agitació, indiquen un augment en la proporció d'organismes capturats respecte la captura esperada tant en condicions de foscor com d'agitació (Singarajah 1975). La interpretació d'aquests resultats suggereix una interferència de la turbulència en els processos de detecció de gradients de corrents (reotaxis), disminuint doncs la capacitat d'evitació.

Recentment, Gill i Crisp (1985) han constatat la capacitat dels copèpodes per detectar estímuls hidrodinàmics (gradients de pressió, fluxs,..), similars als que podrien generar possibles preses o depredadors. Els òrgans mecanosensorials estan distribuïts principalment al llarg de les primeres antenes, en forma de pèls anclats a una base (estructures "e-hair") (Barrientos 1980, Gill 1985), i la seva abundància s'ha relacionat amb els hàbits alimenticis (Barrientos 1980, Paffenhöfer i Stearns 1988). Gill i Crisp (1985) demostren que la incidència de febles corrents a les antenes estimula la producció de reaccions escapada. La mateixa pauta de comportament enfront de la turbulència és la proposada per Alcaraz et al. (1989).

En una revisió dels coneixements actuals sobre la interacció a microscala entre els copèpodes calanoides i el fitoplàncton, Strickler (1985) reflexiona sobre la possible interferència de la turbulència amb els fluxs generats pels animals durant l'alimentació. Segons l'autor, aquest efecte seria més dràstic en aquells copèpodes amb un camp sensorial ampli, acostumats a re-direccionar futures partícules alimentícies en un ambient pobre en menjar. En aquest sentit, Omori i Ikeda (1984) i el propi Strickler (1985) citen algunes observacions pròpies no publicades en les quals l'alimentació s'inhibira en presència de turbulència. Aquest fet, junt amb l'especificitat de les pautes de comportament alimentici de cada espècie, podria jugar un paper molt important en la separació de nínxols ecològics en el plàncton (Strickler 1985). La verificació d'aquesta hipòtesi, doncs, és primordial per conèixer la importància de la turbulència com a modulador de les relacions tròfiques entre productors i consumidors als ecosistemes pelàgics, i per a qualsevol quantificació que es pretengui. En un pas posterior, caldria aclarir també quins tipus i intensitats de turbulència interfereixen, i si hi ha comportaments alimenticis que s'acoplin millor al grau i espectre de turbulència ambiental (selecció adaptativa).

Les preguntes formulades per Strickler (1985) ara per ara romanen només parcialment contestades. Mitjançant l'anàlisi videocinematogràfica, Marrasé et al. (1990) i Costello et al. (1990) han estudiat el comportament del copèpode calanoide *Centropages hamatus* exposat a condicions de calma i turbulència. Els resultats, malgrat certes limitacions (la restricció del moviment de l'individu mitjançant la fixació a un suport) i el seu caire preliminar, semblen confirmar el model de Rothschild i Osborn (1988) i la hipòtesi d'Alcaraz et al. (1989): l'increment de les taxes d'encontre entre depredadador i presa, la "impressió" per al depredador d'augment aparent de la densitat de preses, i així mateix un increment en la freqüència de reaccions d'escapada. Tanmateix, el model de Rothschild i Osborn considera els organismes des d'un punt de vista estrictament mecànic, com partícules inerts, i no té en compte el paper del comportament individual. En aquest sentit, Costello et al. (1990) i Marrasé et al. (1990) observen com la concentració de partícules-presa sembla modular la resposta de l'organisme-depredador, així com l'existència d'una certa inèrcia en el seu comportament enfront dels estímuls hidrodinàmics. Malauradament, l'anàlisi videocinematogràfica no permet esbrinar altres aspectes fonamentals: Representen els canvis de comportament variacions en les taxes d'ingestió? Quins canvis metabòlics hi tenen lloc?.

Molt recentment, Sundby i Fossum (1990) apliquen el model de Rothschild i Osborn a una sèrie temporal de continguts al digestiu de larves de bacallà, abundància de futures preses al mar i intensitat del vent en el moment de la pesca. Obtenen augments en les taxes d'encontre en funció de la força del vent (un augment en la intensitat del vent de 2 a 6 m s^{-1} pot comportar un increment teòric en la taxa d'encontre de l'ordre de 2.2 vegades) molt similars als observats en les dades de camp (2.8 vegades més plens els digestius per a una mateixa concentració de preses i vent més intens). Aquest treball, doncs, confirma també la hipòtesi de Rothschild i Osborn, i fa palès el paper molt important que la turbulència de petita escala pot jugar en els mecanismes reguladors del reclutament d'aquesta espècie.

Concloent, podem afirmar que hi ha prou evidències que la turbulència de petita escala pot afectar l'activitat del zooplàncton herbívor, així com la seva interacció amb el fitoplàncton. Es poden suggerir quatre mecanismes principals pels quals la turbulència podria actuar (Figura 1):

i) Diferències en la qualitat i quantitat del fitoplàncton d'ambients estratificats i turbulents podrien explicar un augment en l'activitat del zooplàncton en aquests darrers.

ii) Els estímuls hidromecànics de la turbulència incrementarien la freqüència de les reaccions d'escapada (o alguna altra pauta de comportament) provocant un augment en el consum energètic (metabolisme) de l'individu.

iii) L'increment en la probabilitat d'encontre degut a la turbulència podria afavorir la transferència tròfica entre productors i consumidors.

iv) La turbulència podria actuar com un factor evolutiu en la selecció de nínxols ecològics, mitjançant la interferència o afavoriment del comportament alimentici de diferentes espècies de copèpodes.

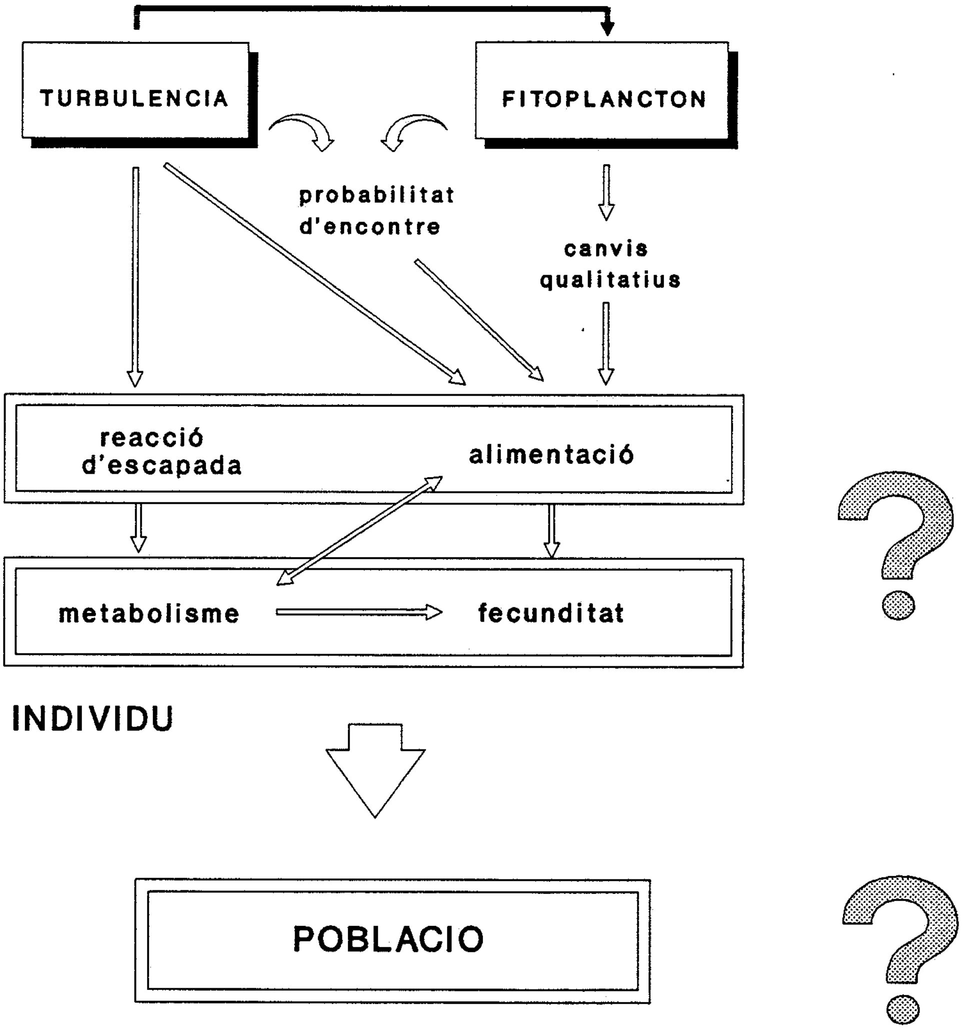

Figura 1. Possibles vies per les quals la turbulència de petita escala podria influir en l'activitat i dinàmica del zooplàncton.

Objectius i justificació

L'objecte principal d'aquest estudi és determinar els efectes de la turbulència de petita escala en els mecanismes de transferència d'energia entre productors i consumidors en els sistemes planctònics marins. La importància de les hipòtesis exposades a l'apartat anterior i, així mateix, la seva posterior aplicabilitat en l'elaboració de models de producció en sistemes pelàgics són evidents i justifiquen esmerçar esforços en el seu aprofundiment. En aquest sentit, Rothschild (1988) i Rothschild i Osborn (1989) fan especial èmfasi en la necessitat d'una revisió dels models de producció existents tenint en compte la turbulència del medi i els seus efectes. D'altra banda, la relevància del nostre estudi possiblement també es podria estendre als sistemes limnètics, donada la similitut en la dinàmica dels processos pelàgics.

Els objectius d'aquest treball, doncs, abasten problemes tant a nivell individual com poblacional, sense oblidar la interacció amb el fitoplàncton, i es poden resumir en els següents:

i) esbrinar la influència de la turbulència de petita escala en l'estructura i dinàmica de poblacions de copèpodes des d'un punt de vista macroscòpic mitjançant l'ús de models reduïts de laboratori (microcosmos);

ii) determinar a nivell individual els processos fisiològics i comportamentals responsables dels canvis observats a nivell poblacional.

Per aconseguir això, en una primera fase l'estudi s'ha concentrat en el desenvolupament de poblacions de copèpodes en diferentes condicions experimentals al laboratori mitjançant l'ús de microcosmos. En un següent pas, s'ha aprofundit en aquells aspectes de l'ecofisiologia dels copèpodes (metabolisme, alimentació, fecunditat i comportament) que podrien explicar els canvis observats a nivell poblacional. Això ha comportat la utilització d'una certa varietat de tècniques i metodologies amb la intenció de diversificar les aproximacions a un mateix problema.

L'estudi s'ha concentrat fonamentalment en els copèpodes calanoides, per la seva importància en abundància i biomassa i, així mateix, pel paper fonamental que juguen en la dinàmica dels sistemes aquàtics marins (Raymont 1983). D'altra banda, l'estudi s'ha restringit a espècies de copèpodes d'hàbitat costaner per tres motius principals:

i) a les zones costaneres es concentra la fracció més important de la producció primària marina, és a dir, quantitativament s'hi donen els processos més importants (Harris 1986);

ii) també és on els processos hidrodinàmics generadors de turbulència es fan palesos amb més intensitat; i finalment,

iii) per la facilitat d'obtenció d'exemplars vius.

En treballar experimentalment amb un factor, la turbulència, la naturalesa, control i mesura del qual són difícils, l'estudi ha estat en alguns aspectes merament qualitatiu en no quantificar-se la intensitat de turbulència. Malgrat tot, les condicions són fàcilment reproduibles per cada tipus d'experiment. L'ús de volums experimentals relativament petits (de 30 ml fins a 30 litres) imposa un límit superior en l'espectre de la turbulència generada, la qual cosa, des del punt de vista metodològic, afavoreix l'estudi, perquè evita la component d'advecció que trobem al medi natural. En aquest sentit, l'estimació de coeficients de dissipació d'energia turbulenta i coeficients de difusió vertical turbulenta en models de laboratori semblants als utilitzats i de mides molt diferents, confirma una forta similitud amb els valors obtinguts en sistemes naturals (Nixon et al., 1979; Marrasé, 1986; Marrasé et al., 1990), recolzant la validesa d'aquesta aproximació. D'altra banda, i conseqüentment, qualsevol pretesa extrapolació dels resultats obtinguts als sistemes naturals serà sempre de caràcter qualitatiu i amb les degudes precaucions.

CAPITOL I

EFECTES DE LA TURBULENCIA EN EL DESENVOLUPAMENT I EL CREIXEMENT DE COPEPODES CALANOIDES EN MICROCOSMOS

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EFECTES DE LA TURBULENCIA EN EL DESENVOLUPAMENT I EL CREIXEMENT DE COPEPODES CALANOIDES EN MICROCOSMOS

1.1. Effects of turbulence on the development of phytoplankton biomass and copepod populations in marine microcosms.

(Basat en l'article del mateix títol fet en col.laboració amb M. Alcaraz, C. Marrasé i D. Vaqué, i publicat a Mar. Ecol. Progr. Ser., vol. 49: 117-125, 1988)

1.2. Effects of small-scale turbulence on development time and growth of *Acartia grani* (Copepoda: Calanoida).

(Basat en l'article del mateix títol fet en col.laboració amb M. Alcaraz i publicat a J. Plankton Res., vol. 13, 1991)

1.1. EFFECTS OF TURBULENCE ON THE DEVELOPMENT OF PHYTOPLANKTON BIOMASS AND COPEPOD POPULATIONS IN MARINE MICROCOSMS

Introduction

Turbulence and herbivorous zooplankton play a prime role in the control of marine pelagic ecosystems. While turbulence (and its associated changes in light and nutrient availability) is a determinant factor to the primary production (Margalef, 1974; Legendre, 1981) and the selection of phytoplankton life-forms (sensu Margalef, 1978), herbivorous zooplankton form one of the most important components of pelagic food webs, and exert a modulating influence upon biomass, size spectrum and specific composition of phytoplankton populations through nutrient recycling (N and P excretion) and grazing pressure (Eppley et al., 1973; Ryther & Sanders, 1980; Conover & Mayzaud, 1984; Verity, 1985; Alcaraz, 1988).

Turbulence and zooplankton have been generally studied independently in natural systems, mainly due to the difficulties in controlling these parameters. As a consequence, the majority of studies dealing with turbulence have been made in the laboratory, using experimental enclosures where the conditions can be easily controlled, despite the problems associated with the measurement of turbulence (Perez et al., 1977; Estrada et al., 1987 a) and the temporal and spatial scale constraints (Harte et al., 1980; Oviatt et al., 1980; Pilson & Nixon, 1980).

The enclosure of natural plankton populations is often followed by a phytoplankton bloom and collapse (e.g. Oviatt, 1981; Marrasé, 1986; Estrada et al., 1987 a,b; Alcaraz et al., 1989). Both turbulence and herbivorous zooplankton have a quantitative influence upon phytoplankton biomass (turbulence increases the intensity of the bloom;

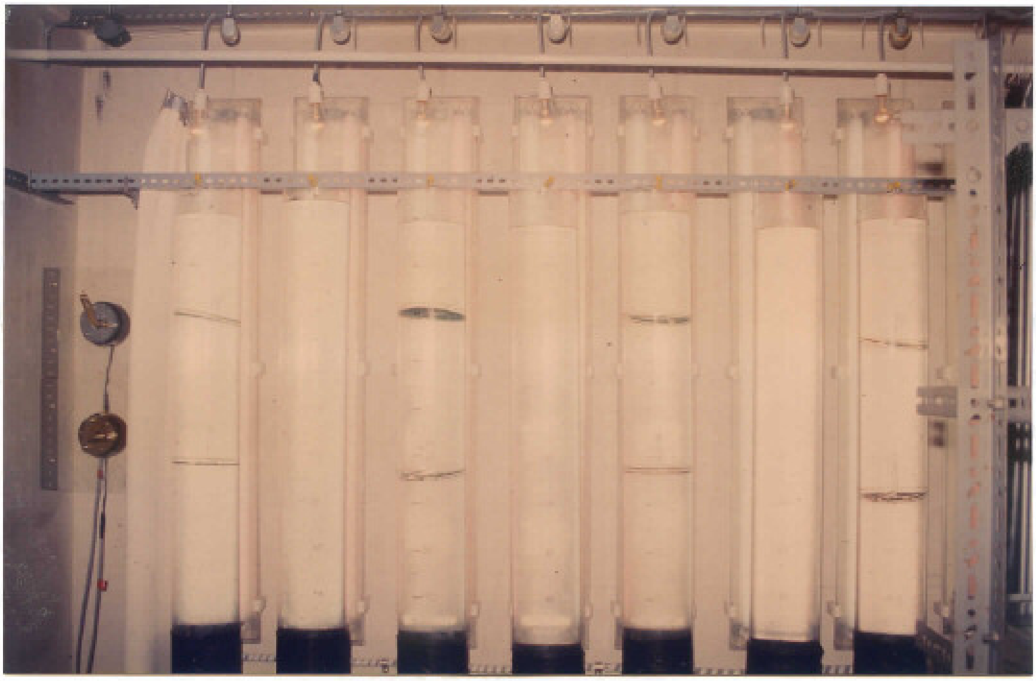
zooplankton tends to reduce it, Alcaraz et al., 1989). The interaction of the two factors, however, can have both quantitative and qualitative effects, for they can also modify the events, such as a delay in the occurrence of the peak, or the development of secondary blooms (Oviatt, 1981; Alcaraz et al., 1989).

Data on changes in zooplankton dynamics and metabolic activity due to turbulence are scarce, and their influence upon the evolution of phytoplankton biomass is uncertain (Oviatt, 1981; Alcaraz et al., 1989). In order to understand the effects of the smaller scale of turbulence (the turbulent motion which acts at distances $<10^{-2}$ m, Rothschild & Osborn, 1988) on the link between producers and consumers in pelagic ecosystems, a series of experiments using laboratory microcosms was performed. The goals of this paper are two-fold: (1) to test the hypotheses that turbulence induces changes in the population dynamics and demographic composition of zooplankton populations; and (2) to examine the implications of these changes on the coexisting phytoplankton biomass.

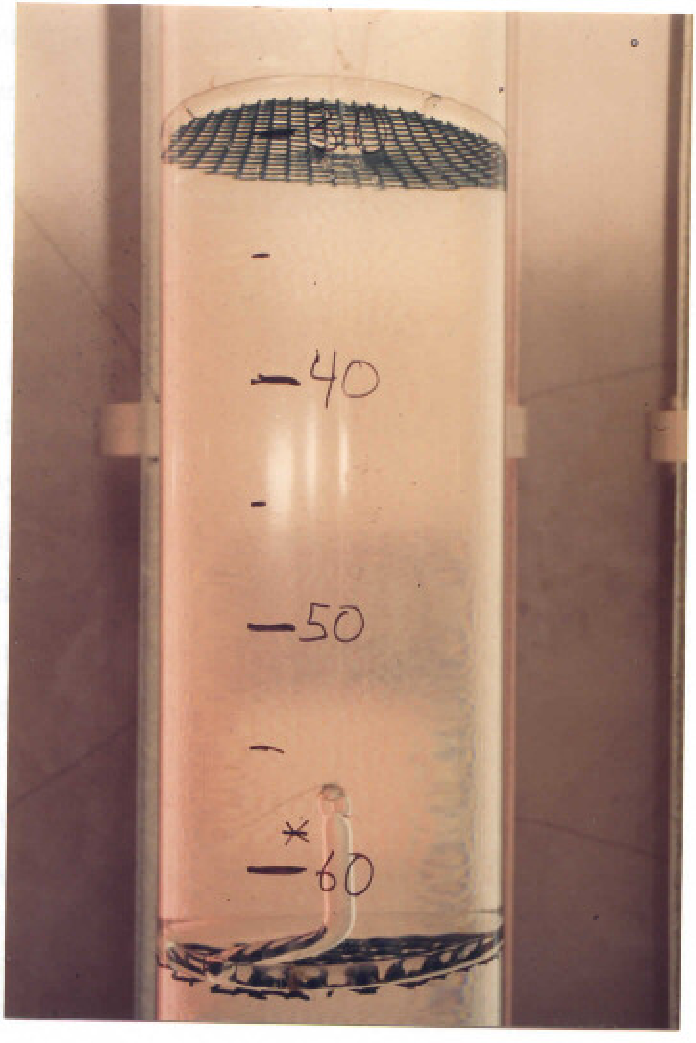
Material and methods

Description of the microcosms and experimental design

The laboratory microcosms are described in detail elsewhere (Marrasé, 1986; Estrada et al., 1987 a, b; and Alcaraz et al., 1989), and consisted of eight 30 l perspex tubes (200 cm high and 15 cm in diameter) placed in a temperature-controlled chamber (17 ± 1°C) (Picture 1.1.1). Two 35 W, 100 cm long fluorescent lamps (one of them GRO-LUX) plus a 20 W incandescent lamp per microcosm placed at 20 cm above the initial water surface, illuminated the upper half of each microcosm with a 12 h light / 12 h dark photoperiod and provided enough heat to create a stable thermocline. Water temperature in the microcosms ranged between 24 to 17°C (surface and bottom). Surface temperature in the microcosms was 2°C higher than that measured in the area of sampling when the experiments were run. PAR (photosynthetically active radiation) in the upper half of the microcosms was 650 to 500 μE m^{-2} s^{-1}.



Pictures 1.1.1 (above) and 1.1.2 (right), ilustrating the experimental microcosms and the oscillating grids.



Two experiments designed to test the effect of turbulence on the dynamics of herbivorous zooplankton, and the interaction of both variables on the changes in phytoplankton were performed: Expt 1 (23 April to 9 May 1987) and Expt 2 (22 June to 3 August 1987). The experiments started at different successional stages as shown by the nutrient and chlorophyll concentrations and the composition of zooplankton populations. Expt 1 corresponded to an early successional stage with high nutrient and low chlorophyll concentrations; in Expt 2 phytoplankton was in an advanced successional stage (high chlorophyll and low nutrient concentration).

There were four microcosms for each of two treatments: no turbulence with zooplankton (Q microcosms), and turbulence with zooplankton (A microcosms). Turbulence in A microcosms was generated by means of two circular netlon grids (6 mm and 12 mm mesh size) in each tube, oscillating vertically at 20 and 40 oscillations min^{-1} respectively, as shown in Picture 1.1.2. This system is assumed to generate the appropiate small scale range of turbulence. Estimated vertical eddy diffusivity coefficients in such conditions were 0.5 cm^2 s^{-1} for the unstirred and 1 to 5 cm^2 s^{-1} for the stirred microcosms (Estrada et al., 1987 a).

Coastal seawater collected from the Masnou harbour (20 km north of Barcelona) was used to fill the microcosms. Before filling the tubes, the water was thoroughly mixed and filtered through a 150 μm nylon netting to exclude the larger fraction of zooplankton. In Expt 2, to estimate the initial number of copepod eggs and naupliae not retained by the 150 μm netting, and so introduced initially in the tubes, 30 l of the same water as used to fill the microcosms was filtered through a 60 μm nylon netting and the different developmental stages of copepods counted. Zooplankton was collected simultaneously in the same waters by means of short (2 min) horizontal tows made with a 30 cm wide-mouth plankton net fitted with 250 μm mesh nylon netting. Zooplankton samples were diluted in seawater and transported to the laboratory in 10 l plastic carboys.

Organisms which were damaged or showing abnormal swimming behaviour were discarded. The sample was split into aliquots and added to the microcosms at a concentration about three times that observed in the field. Two aliquots were saved for identification and counting. Initial chlorophyll, nutrient and zooplankton concentrations in the microcosms for both experiments are given in Tables 1.1.1 and 1.1.2.

Expt 1 was designed to follow the short trend changes of populations, and zooplankton was allowed to reproduce throughout the experiment; whereas due to the long duration of Expt 2, adult organisms (mainly *Acartia italica*, Table 1.1.2) were removed 6 days after starting the experiment to avoid overlapping of generations. This was done by vertically screening the enclosures with 250 μm mesh nylon nettings adjusted to the inner wall of the microcosms and placed in the bottom of the microcosms prior to filling them.

TABLE 1.1.1. - Mean initial values of nutrients (μg-at l^{-1}) and chlorophyll (μg l^{-1}) concentrations in Expts 1 and 2. Q: unstirred; A: stirred. In parentheses: standard error of the mean.

Experiment		NO_3-N	NO_2-N	NH_4-N	SiO_4-Si	PO_4-P	chla
Expt 1	Q	4.46	0.26	2.55	71.66	0.80	4.45
		(0.13)	(0.07)	(0.27)	(0.05)	(0.08)	(0.13)
	A	4.34	0.19	2.16	1.68	0.93	4.68
		(0.04)	(0.006)	(0.09)	(0.03)	(0.04)	(0.09)
Expt 2	Q	0.39	0.50	0.24	1.52	0.54	19.80
		(0.08)	(0.009)	(0.03)	(0.11)	(0.03)	(0.87)
	A	0.33	0.50	0.24	1.53	0.48	20.44
		(0.11)	(0.006)	(0.06)	(0.02)	(0.04)	(0.53)

TABLE 1.1.2.- Mean composition of zooplankton added to microcosms in Expt 1 and 2.

Species	Stage	Expt 1	Expt 2
Acartia italica	♀	211	56
»	♂	64	12
»	C V-VI	-	60
»	C IV	-	1
»	C III	-	1
»	C I-II	-	-
»	N V-VI	-	-
»	N IV	-	6
»	N III	-	8
»	N I-II	-	20
»	Eggs	-	479
A. margalefi	♀	5	-
Other (Cirripede naupliae,copepodites,etc)		18	14

Sampling strategy and studied variables

The specific and demographic composition of zooplankton (eggs, naupliar and copepodite stages, adults and proportion of sexes), and mean size of each developmental stage, were followed at four day intervals (Expt 1) and eight to thirteen day intervals (Expt 2) by filtering the contents of one stirred and one unstirred microcosm through 60 μm nylon netting.

Biomass was estimated from the mean dry weight of each developmental stage, interpolated from the length-dry weight relation found for *Acartia clausi* (Durbin & Durbin, 1976) and from egg dry weight estimates by Kiφrboe et al.(1985). This procedure allowed sampling and examination of the developmental stages, from eggs to adults, in four intermediate periods of the experiments, at the cost of sacrificing the microcosms sampled. The quotient number of eggs/number of females, was adopted as a crude measure of fecundity, and the trophic efficiency (capacity of zooplankton in capitalizing primary producers) has been estimated through the ratio zooplankton C/phytoplankton C. Data for zooplankton dry weight/organic carbon and chlorophyll a/organic carbon relation have been obtained from Hardstedt-Romeo (1982) and Banse (1977) respectively. Although the frequency of zooplankton samplings and the limited number of observations preclude an accurate study of population dynamics or production, the method can be considered sufficient to describe the global effects of turbulence on the development of copepod populations.

Nutrient and chlorophyll a concentration were sampled 50 to 55 cm below initial water level, one hour into the light cycle. This sampling depth was adopted taking into account that in previous experiments, in which the temperature profiles were similar, data on chlorophyll and nutrient concentration at two depths (above and below the thermocline, 45 and 145 cm depth, respectively) showed no significant differences (Estrada et al., 1987 a; Alcaraz et al., 1989). Samples were obtained daily in Expt 1. In Expt 2 samples were taken every day for the first 10 days, and then less frequently (4 to 10 days). Temperature and photosynthetically active radiation (PAR) profiles were taken on several occasions. The main methodological procedures are listed in Table 1.1.3.

TABLE 1.1.3. - Methods used in the different measurements

VARIABLE	TECHNIQUE
Temperature	CRISON temperature probe (± 0.1 ºC)
PAR	LI-COR spherical quantum sensor
Nutrients	TECHNICON autoanalyzer (Strickland & Parsons, 1972)
Chlorophyll	Fluorescence (Yentsch & Menzel, 1963)
Zooplankton composition	Microscope counts
Zooplankton biomass	Microscope measurements of metasome length and conversion to dry weight (Durbin & Durbin, 1976; Kiørboe et al. 1985)

Results

Chlorophyll and nutrient concentrations

The time course of chlorophyll and nutrient concentrations followed a trend similar to that observed in previous experiments (Estrada et al., 1987 a,b; Alcaraz et al., 1989), with a rapid increase of chlorophyll after enclosing the water in the microcosms followed by the collapse of the bloom after nutrient depletion. There were no differences between Q and A tubes in the occurrence of chlorophyll peaks (Fig.1.1.1.). In Expt 1 the chlorophyll maximum occurred between the second and third day and reached significantly greater values in A tubes (Q tubes: 12.82±0.73 μg l^{-1}, A tubes: 16.8±0.38 μg l^{-1}; F_s=23.41, $F_{0.05(1,6)}$=5.99). In Expt 2, where the initial chlorophyll concentration was about five times higher (Table 1.1.1.), the maximum occurred the first day and did not differ significantly between Q and A tubes (Q tubes: 22.86±0.38 μg l^{-1}; A tubes: 21.81±1.53 μg l^{-1}; F_s=0.44, $F_{0.05(1,6)}$=5.99), but for the two days after the bloom, the chlorophyll concentration was higher in A tubes (second day, A: 16.45±0.70 μg l^{-1}; Q: 13.66±0.44 μg l^{-1}; F_s=11.51, $F_{0.025(1,6)}$=8.81; Third day: A: 7.24±0.43 μg l^{-1}; Q: 4.58±0.24 μg l^{-1}; F_s=29.0, $F_{0.01(1,6)}$=13.7). In both experiments the integrated phytoplankton biomass was higher in A tubes (Expt 1: A tubes: 64.42 μg l^{-1} ; Q tubes: 54.18 μg l^{-1}; Expt 2; A tubes: 138.41 μg l^{-1} ; Q tubes: 122.64 μg l^{-1}).

The concentrations of NO_3-N, PO_4-P, SiO_4-Si (not reported here because their trends were similar to those found in previous experiments, Alcaraz et al., 1989) and NH_4-N followed an opposite pattern to chlorophyll, with secondary increases due to regeneration. No significant differences were observed between A and Q tubes except for ammonia, whose secondary maxima were higher in A tubes (Fig. 1.1.2).

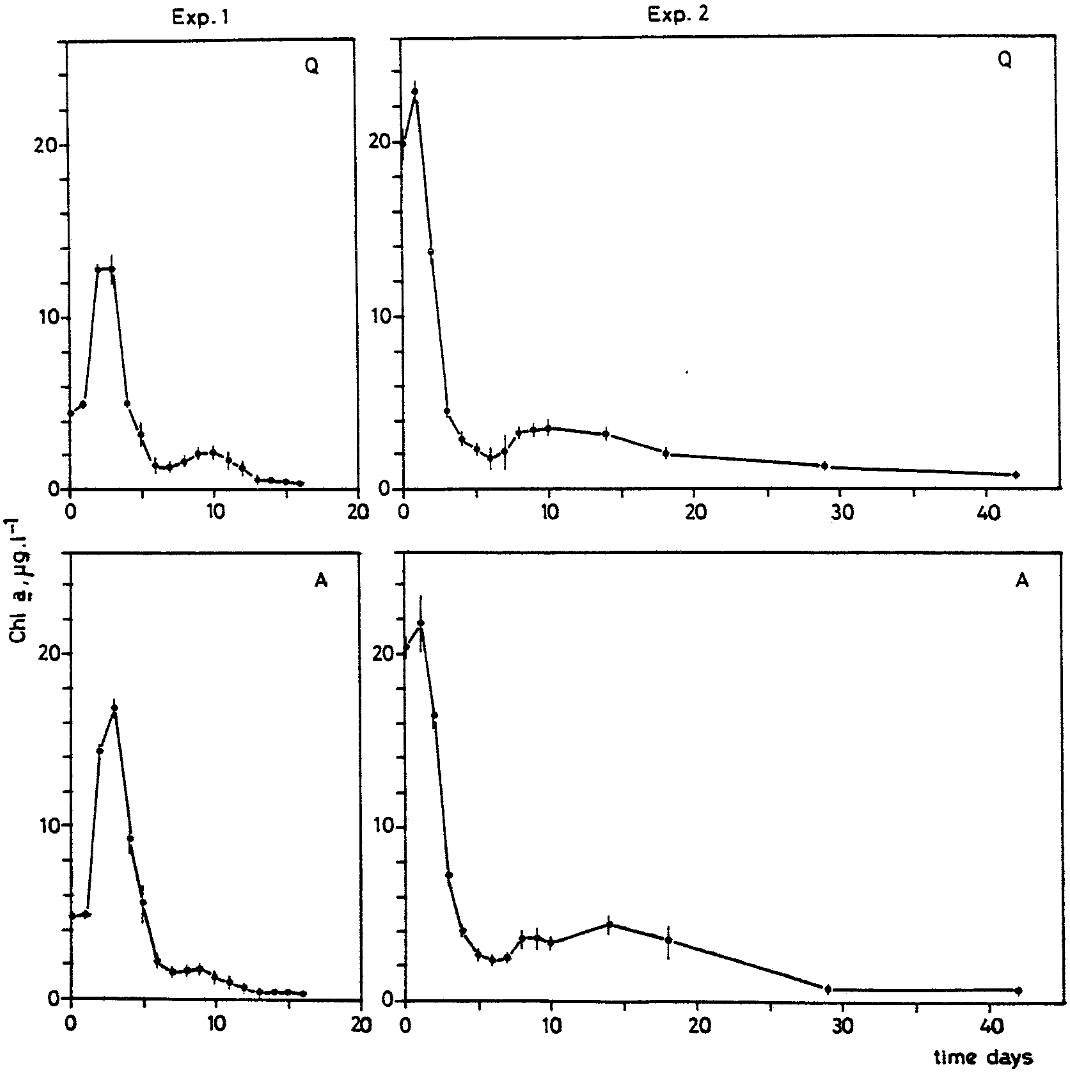


Fig. 1.1.1. Mean temporal variation of chlorophyll concentration in Expts 1 and 2. A: stirred microcosms; Q: unstirred microcosms. The vertical bars indicate the error of the mean.

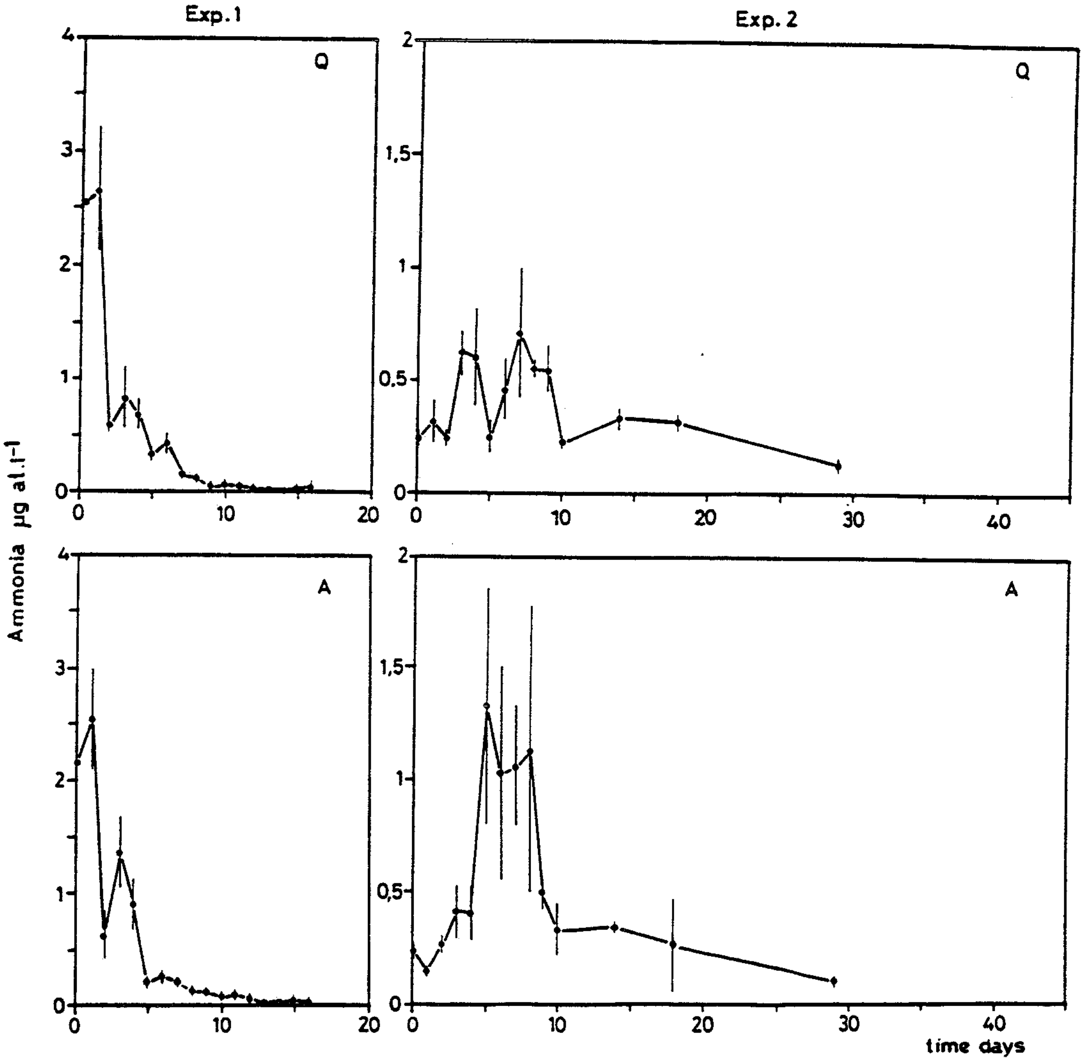


Fig. 1.1.2. Temporal variation of mean ammonia concentrations in Expts 1 and 2. A: stirred microcosms; Q: unstirred microcosms. The vertical bars indicate the error of the mean.

Zooplankton

Changes in the zooplankton populations has been expressed in terms of number of individuals and biomass (dry weight) for each developmental stage. The measured mean size and estimated biomass of each developmental stage, from eggs to adults, are represented in Table 1.1.4. In both experiments the mesozooplankton populations introduced in the microcosms consisted mainly of calanoid copepods. *Acartia italica* was the dominant species in the Masnou harbour when the experiments started (spring-summer), and the populations in the microcosms became practically monospecific. Because of their minor importance, other taxa (e.g. rotifers and tintinnids) also present in the microcosms were ignored.

TABLE 1.1.4.- *Acartia italica* mean length (mm) and biomass (μg dry weight) corresponding to each developmental stage. Values calculated according the length-dry weight relation given by Durbin & Durbin (1976) for *A. clausi*. Dry weight of eggs from Kiørboe et al., (1985).

	Eggs	NI-II	NIII	NIV	NV-VI	CI-II	CIII	CIV	CV-VI	♂	♀
mm	0.08	0.155	0.160	0.195	0.235	0.265	0.375	0.475	0.560	0.588	0.622
μg	0.04	0.04	0.103	0.181	0.310	0.430	0.480	1.000	1.630	1.900	2.350

Sex ratio (♂/♀+♂) appears to be modified by turbulence with a similar trend in both experiments (Table 1.1.5). In A (turbulent) tubes the proportion of males tended to decrease in comparison to Q (no turbulence) tubes.

The ratio number of eggs/number of females also differed between stirred and unstirred conditions, showing in general lower values in A microcosms, at least for the first two weeks after the experiments began (Table 1.1.5).

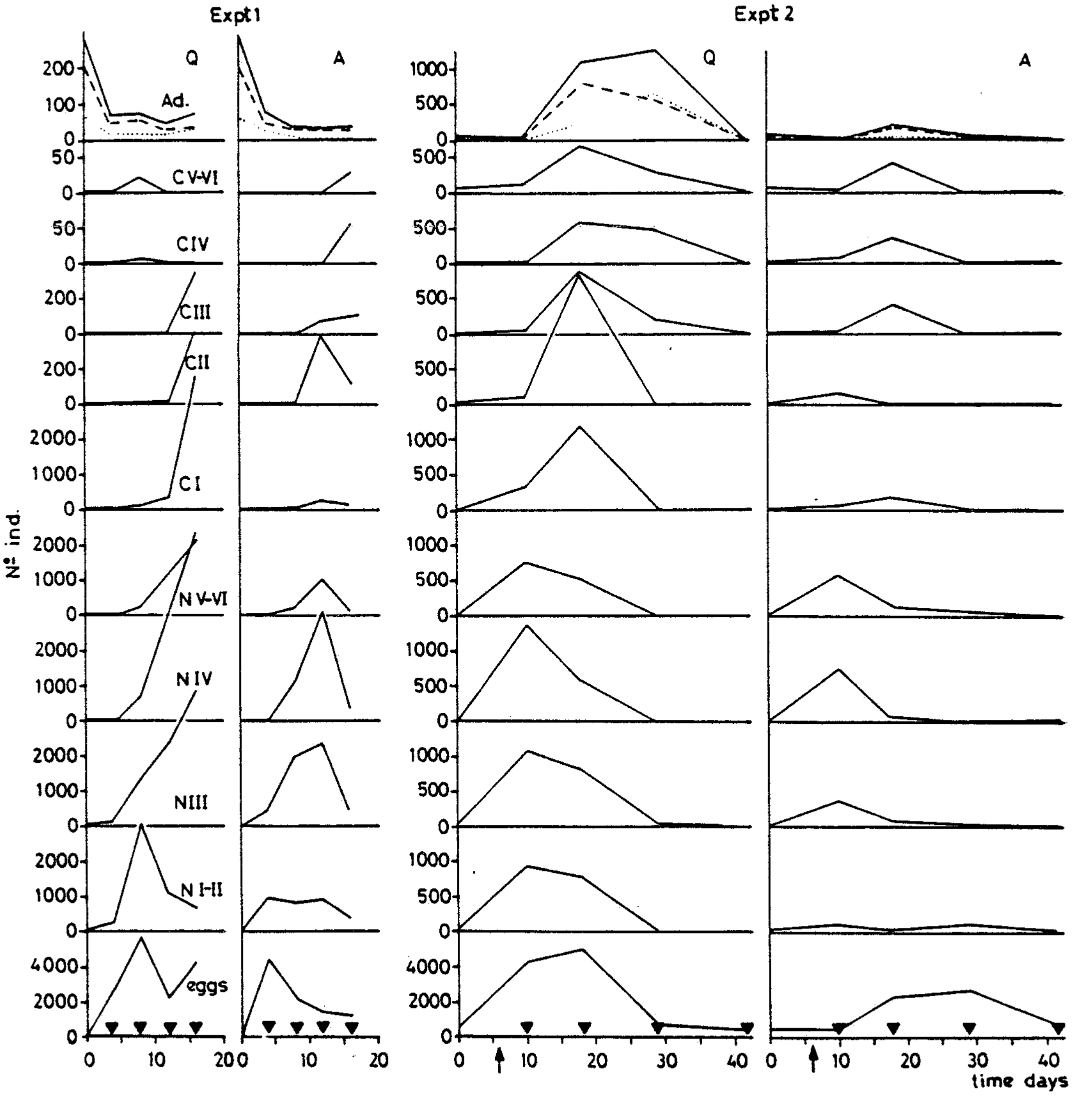


Fig. 1.1.3. Mean evolution of the different developmental stages of A. italica in Expts 1 and 2. A: stirred microcosms; Q: unstirred microcosms. In adults, continous line: total number, dashed line: females, dotted line: males. Arrows in experiment 2 indicate when adults were removed from the microcosms. Triangles indicate the time of sampling.

Copepod development seems to have been accelerated in A microcosms (Fig. 1.1.3). In general, for Expt 1, the maxima of the successive stages appear earlier in A tubes. In Expt 2, the adult peaks of abundance appear earlier in A tubes, but this trend was not always observed in the other developmental stages. A clearer effect seems to be the earlier end of abundance peaks in A tubes.

TABLE 1.1.5.- Mean sex ratio (♂/♀+♂) and instantaneous values of the quotient no. eggs/no. females in Expts 1 and 2. Q: unstirred; A: stirred. In parentheses, standard error of the mean.

Expt	Day	Sex ratio (♂/♀+♂)		Eggs female^{1}	
		Q	A	Q	A
1	0	0.23	0.23	-	-
	4	0.29	0.36	61.6	89.8
	8	0.26	0.17	111.0	72.6
	12	0.40	0.07	84.8	50.3
	16	0.48	0.19	119.7	41.4
	Mean	0.33	0.20	94.2	63.5
		(0.04)	(0.04)	(11.4)	(10.9)
2	0	0.17	0.17	-	-
	10	0.39	0.16	230.5	108.0
	18	0.30	0.11	6.5	14.5
	29	0.52	0.33	1.2	2.7
	42	-	-	-	-
	Mean	0.34	0.19	79.4	41.7
		(0.07)	(0.04)	-	-

Zooplankton biomass was always significantly lower in A tubes (Fig. 1.1.4). This effect, which was more evident in the longer lasting experiment (Expt 2), was also discussed by Oviatt (1981), although in our experiments zooplankton biomass maintained values from 7 to 16 times higher than those reported by Oviatt. On average, the values of the ratio consumers/producers (μg zooplankton C per μg phytoplankton C), were generally lower in A tubes for both experiments (Table 1.1.6), as also observed by Oviatt (1981).

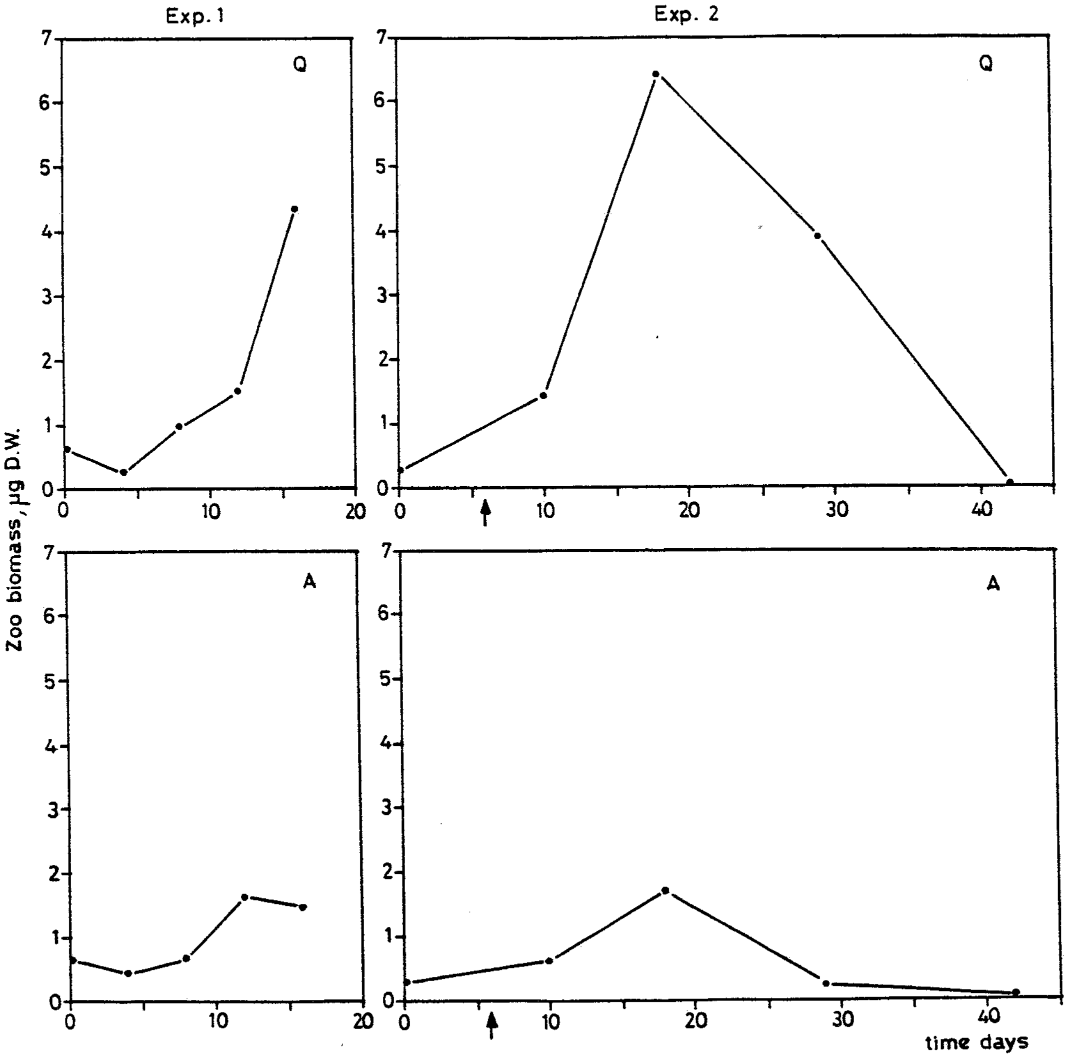


Fig. 1.1.4. Mean temporal variation of zooplankton biomass (μg dry weight per tube) in Expts 1 and 2. A: stirred microcosms; Q: unstirred microcosms. Arrows in Expt 2 indicate when adults were removed from the microcosms.

TABLE 1.1.6. - **Mean ratio consumers/producers (μg C zooplankton/μg C Phytoplankton) in Expts 1 and 2. In parentheses, standard error of the mean. Zooplankton dry weight/carbon relation from Hardstedt-Romeo (1982) and chlorophyll a/phytoplankton carbon relation from Banse (1977).**

Expt	Day	Ratio consumers/producers	
		Q	A
1	0	0.031	0.029
	4	0.012	0.010
	8	0.132	0.095
	12	0.280	0.600
	16	3.210	1.070
	Mean	0.731 (0.619)	0.361 (0.208)
2	0	0.003	0.003
	10	0.091	0.041
	18	0.677	0.108
	29	0.722	0.081
	42	0.005	0.018
	Mean	0.300 (0.164)	0.050 (0.020)

Discussion

In previous experiments, the interaction zooplankton-turbulence mainly affected the timing and intensity of changes in phytoplankton biomass during the first two weeks of the experiments (i.e. delayed phytoplankton blooms and occurrence of secondary ones in A tubes, Alcaraz et al., 1989).

In the two experiments described here this effect was less conspicuous, probably due to the increased PAR and temperature (which induced higher rates of change in phyto and zooplankton populations in comparison to previous experiments), as well as to differences in the initial plankton populations.

The higher integrated phytoplankton biomass achieved when turbulence and zooplankton interact was attributed by Oviatt (1981) to a reduction of zooplankton biomass (and hence grazing pressure) due to disrupting effects of turbulence on reproduction or feeding mechanisms, although a similar effect can be generated by turbulence alone (stirred tubes without zooplankton; Marrasé, 1986; Estrada, et al., 1987, a,b; Alcaraz et al., 1989).

Even though we have no data on feeding or metabolic rates, the higher ammonia concentrations observed in A tubes suggest an increased metabolism in copepods due to turbulence. Similar metabolic trends were reported by Harris & Malej (1986) in natural systems for *Calanus helgolandicus*, whith higher specific excretion rates of ammonium in mixed and frontal zones in comparison to stratified ones. This supposed higher metabolism could be driven by changes in the swimming behaviour (higher frequency of escape reactions induced by turbulence, Alcaraz et al., 1989). The turbulence spectrum created by the oscillating grids in our microcosms, as well as the details of the interaction between hydrodynamism and copepods are unknown.

Nevertheless it has been demonstrated that turbulence (mixing) affects the escaping capacity of copepods (Singarajah, 1975), and that the hydrodynamic stimuli are perceived by the antennal sensors of copepods (Gill & Crisp, 1985). In the present case this effect could be even more important as a consequence of the higher proportion of antennal mechanoreceptors of *Acartia* in comparison to other calanoid copepods (Barrientos, 1980; Paffenhöfer & Stearns, 1988).

Higher mechanosensitivity of males, or a lower capacity to withstand metabolic stress, might be the reasons for the differences of sex ratio observed in Q and A microcosms. Similar reductions in the male proportion in laboratory cultures of *Acartia tonsa* when submitted to periodical stirring and harvesting were reported by Heinle (1970), but were attributed to the reduction on population density.

The postulated higher metabolic rates of copepods in A tubes could have also an ageing effect comparable to that reported by Shaw & Bercaw (1962) for other crustaceans when temperature increases, thus explaining the apparent acceleration of the demographic changes in A tubes in comparison to Q tubes. This was not always observed in Expt 2 probably due to the longer time lag between samplings in comparison to Expt 1.

The decrease of male proportion could be the ultimate reason for the reduction of zooplankton biomass in A tubes. A significant correlation occurred between sex ratio and the quotient number of eggs/number of females in the short term experiment 1 ($r = 0.73$, $n = 8$). The lower fecundity of copepods of the genus *Acartia* when the proportion of males decreases has been described by Wilson & Parrish (1971) and Alcaraz (1977), and the control exerted by sex ratio on the population density of *A.italica* in natural systems by Alcaraz & Wagensberg (1978). The lack of correlation between proportion of male and eggs/female in Expt 2 might be attributable to the reduced fecundity due to food limitation (Checkley, 1980).

Therefore, turbulence appears to have three major influences on marine planktonic systems: (1) enhanced phytoplankton biomass; (2) reduced consumers biomass, through changes in the demographic composition of populations (lower proportions of males and higher development rates); and (3) presumably increased metabolic activity of consumers (feeding rates and excretion rates).

The ultimate effect of turbulence would be a reduction of the trophic efficiency of the system (lower consumers biomass per unit chlorophyll or phytoplankton biomass) and accelerated turnover rates, therefore enhancing nutrient regeneration.

RESUM

Mitjançant l'ús de microcosmos experimentals de 30 litres de capacitat s'han estudiat els efectes de la turbulència en la dinàmica de poblacions de copèpodes planctònics i en la biomassa de fitoplàncton.

Van ser duts a terme dos experiments emprant poblacions naturals de fito i zooplàncton originàries del Port de Masnou (20 km al nord de Barcelona); les poblacions van ser mantingudes en els microcosmos per períodes compresos entre els 15 i els 40 dies. Es van establir dues condicions experimentals: microcosmos sense pertorbar, quiets o Q, i microcosmos amb turbulència, agitats o A.

Havent confinat el plàncton, s'originà un bloom (pic) en la concentració de clorofil.la, de major magnitud en els microcosmos A, i una posterior davallada. L'evolució temporal en l'abundància dels diferents estadis de desenvolupament d'*A. italica*, el copèpode dominant de la comunitat, indicà diferències entre els microcosmos Q i A pel que fa a la "proporció sexual" (♂/♂+♀), "fecunditat" (ous/♀), "biomassa total de zooplàncton" i "quocient biomassa de consumidors/biomassa de productors".

La turbulència tendeix a reduir la biomassa de zooplàncton, fent-se palesos canvis demogràfics en la població (menor proporció de mascles). El desenvolupament de les poblacions confinades en els microcosmos A (sotmesos a turbulència) també esdevingué més ràpid.

Creiem que el desenvolupament més curt en el zooplàncton confinat en els microcosmos A és conseqüència d'un increment en l'activitat metabòlica del zooplàncton, o bé per un increment en les reaccions d'escapada dels copèpodes per acció directa del moviment turbulent de l'aigua en els mecanorreceptors antenals, o bé per una estimulació de

l'alimentació. La hipòtesi d'un augment metabòlic es veu recolzada per les majors concentracions d'amoni observades en els microcosmos A. Les conseqüències ecològiques finals de la introducció d'energia turbulenta al sistema estudiat serien una reducció en l'eficiència tròfica del sistema i una acceleració en les taxes de renovació.

1.2. EFFECTS OF SMALL-SCALE TURBULENCE ON DEVELOPMENT TIME AND GROWTH OF *ACARTIA GRANI* (COPEPODA: CALANOIDA)

Introduction

Turbulence plays a prime role in the regulation of primary production, spatial distribution, and selection of "life forms" of phytoplankton (Margalef, 1978; Legendre, 1981; Tett and Edwards, 1984; Mackas et al., 1985; Estrada et al., 1987, 1988). At smaller scales, turbulence increases encounter rates between planktonic predators and prey (Rothschild and Osborn, 1988; Evans, 1989), modifies copepod feeding activity (Perez et al., 1977; Oviatt, 1981; Strickler, 1985; Costello et al., 1990), and appears to enhance their development rates and metabolism (Alcaraz et al., 1988, 1989; Marrasé et al., 1990). These multiple effects may result in changes in biomass and demographic parameters of copepod populations (i.e. sexual proportion or age structure) (Alcaraz et al., 1988), thereby modulating population dynamics and consequently the pressure exerted by copepods on phytoplankton.

Alcaraz et al. (1988) suggested that turbulence accelerates zooplankton development and metabolism. Their experimental design, however, was not appropriate for zooplankton development and growth rates. Here we examine whether small-scale turbulence significantly enhances the development and growth of planktonic copepods. To achieve our goal, we used 10 l laboratory microcosmos to observe the development, under non-limited food conditions, of a cohort of *Acartia grani*, a common coastal copepod in temperate seas, and compared the differences in development and growth rates of individuals under agitated versus calm water conditions.

Material and methods

Microcosms and experimental design

The laboratory microcosms were a modified version of those described by Estrada et al. (1987) and Alcaraz et al. (1988). They consisted of fifteen 10.3 l perspex tubes (100 cm high and 11.5 cm inner diameter) placed in a temperature-controlled chamber (20±1°C). A 35 W, 60 cm fluorescent lamp illuminated each microcosm over their whole length with a 12:12h light:dark photoperiod with a photosynthetically available radiation ranging from 500 to 650 μE m^{-2} s^{-1}.

The microcosms were filled with seawater from Masnou harbour (20 Km N of Barcelona) which had been filtered through a 39 μm nylon netting to exclude eggs and the different stages of copepods, as well as other zooplankters, and were allowed to acclimatize overnight. The experimental organisms (*Acartia grani*) were obtained simultaneously with the collection of seawater, by means of short (5 min) horizontal tows made with a 38 cm wide-mouth plankton net fitted with 250 μm mesh nylon netting. Samples were diluted in seawater and transported to the laboratory in 10 l carboys.

Two experimental conditions were considered, and included two sets of seven microcosms each: no turbulence ("Q" microcosms, unstirred) and turbulence ("A" microcosms, stirred). An additional microcosm (the "initial" microcosm) provided data concerning the new cohort at the start of the experiment. Turbulence was generated by two oscillating (20 oscillations min^{-1}) circular netlon grids of 6 mm mesh size per tube. A similar setup (Estrada et al., 1987) provided a range of vertical eddy diffusivity coefficients ("Q" microcosms, 0.5 cm^2 s^{-1}; "A" microcosms, 1 to 5 cm^2 s^{-1}) comparable to those found in natural systems (Denman and Gargett, 1983).

Adult males and females of *Acartia grani* were sorted from the zooplankton samples, placed in 1 l jars filled with 39 μm filtered sea water and left overnight in a Ferris-

Wheel at 1 rpm. Then, 15 parental populations, each consisting of 13 males and 13 females of *A. grani*, were introduced into the microcosms in chambers designed to keep adults apart from eggs and to remove the adults from the microcosms easily, thereby providing a new cohort without generational overlap. The chambers were plexiglas cylinders (15 cm high, 5 cm diameter) bottom screened (150 μm mesh netting) and suspended half submerged in the upper part of each microcosm. After two days, the chambers with the parental populations were carefully removed. Following the removal of the adults, the abundance of the new cohort (eggs plus first naupliar stages) was determined in one of the microcosms (the "initial" microcosm) by gently filtering its contents through 39 μm netting. In the "A" microcosms, the stirring systems were switched on and turbulent conditions started (Day 0).

Every two days, 50 ml of a nutrient solution was added to each microcosm, providing an increase of 5 μM of nitrate, 0.2 μM of silicate and 0.5 μM of phosphate, in order to ensure non-limiting food conditions throughout the experiment.

Sampling strategy and variables studied

Food availability was estimated daily in all microcosms by the concentration and size spectrum of particulate matter (Coulter Counter model TA fitted with a 140 μm tube). Chlorophyll a concentration was determined occasionally when microcosms were sampled for zooplankton (see below).

The development and growth of *Acartia grani* were studied following the time course of the age structure of the population. At two day intervals, the whole contents of each of two microcosms, one stirred and one unstirred, was filtered through 39 μm nettings to collect the copepods, as in the "initial" microcosm. Prior to this procedure, water samples were taken for chlorophyll a determination by flourescence in acetone extracts (Yentsch & Menzel, 1963). This provided us with only two chlorophyll concentration values, one from the stirred and one from the unstirred "sacrificed" microcosms, at each zooplankton sampling.

The instar composition of *A. grani* was estimated in either total samples or in aliquots, for the most abundant developmental stages. Individuals were counted and measured using a stereomicroscope. Metasome length (adults and copepodites), total length (nauplii) or diameter (eggs) were used to estimate specific biomass from a modified length-dry weight relation described for *A. clausi* by Durbin and Durbin (1978) and from egg dry weight estimates by Kiφrboe et al. (1985). For further details of the procedures see Alcaraz et al.(1988).

Development times corresponding to the different naupliar and copepodite stages were estimated as the time corresponding to the gravitational center of pulses of successive instars (Rigler and Cooley, 1974). To avoid any differences in the absolute number of individuals, we analyzed stage composition on the basis of frequency data (after arcsin transformation; Sokal and Rohlf, 1969; Landry, 1983).

Growth patterns were described by comparing the specific body masses with the relative specific development time (i.e., the ratio between the development time of the instar and that corresponding to adult females for each condition, Ivanova, 1971; Miller et al., 1977). This procedure allowed us to compare growth patterns independent of the absolute development time of the species.

Results

Food availability

Particulate matter concentration (as volume, mm^3l^{-1}, Figure 1.2.1) increased after enclosement and experienced a subsequent decline, followed by a later increase. For most of the experiment "Q" and "A" microcosms had similar food concentrations, but after the 10th day variability increased and particulate volume concentrations were higher in "A" microcosms.

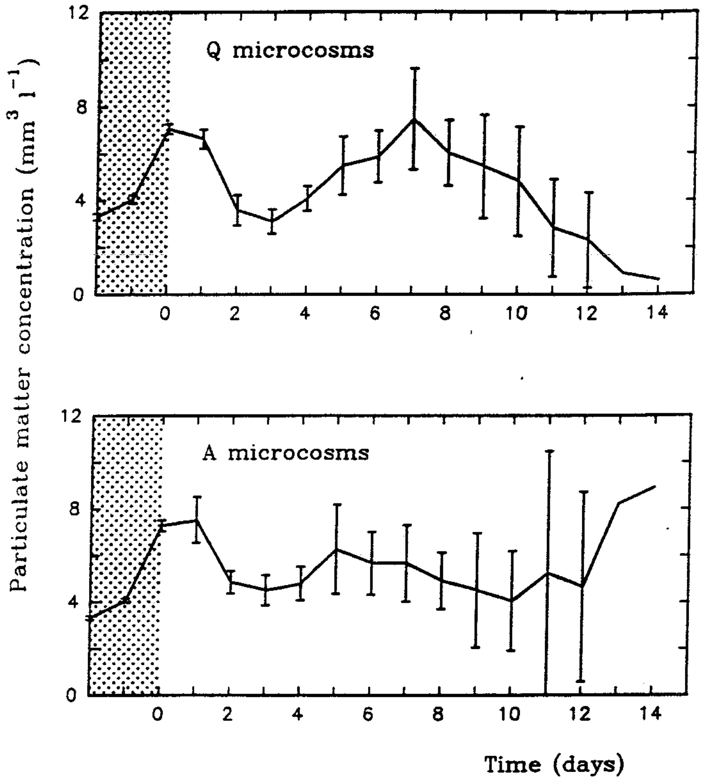


Fig. 1.2.1. Temporal evolution of particulate matter concentration throughout the experiment in "Q" and "A" microcosms. Bars indicate ± 95% confidence interval. Days are counted from the start of turbulence and adult removal. The egg-laying period (2 days) is indicated by the stippled area.

The size spectrum of particles was similar in "A" and "Q" microcosms until the 7-8th day (Figure 1.2.2). Afterwards they diverged, the proportion of >10 micron particles raising in "A" microcosms.

Data on chlorophyll a̲ concentration, in spite of the small number of samples and the sampling interval, showed a conspicuous initial peak of chlorophyll prior to the start of turbulence conditions (Day 0, Figure 1.2.3) corresponding to that one in particulated matter. After the subsequent decrease, values slightly rised, but no conspicuous difference was found between "Q" and "A" microcosms. For most of the experiment chlorophyll a̲ concentration was above 2 $\mu g\ l^{-1}$ for both conditions.

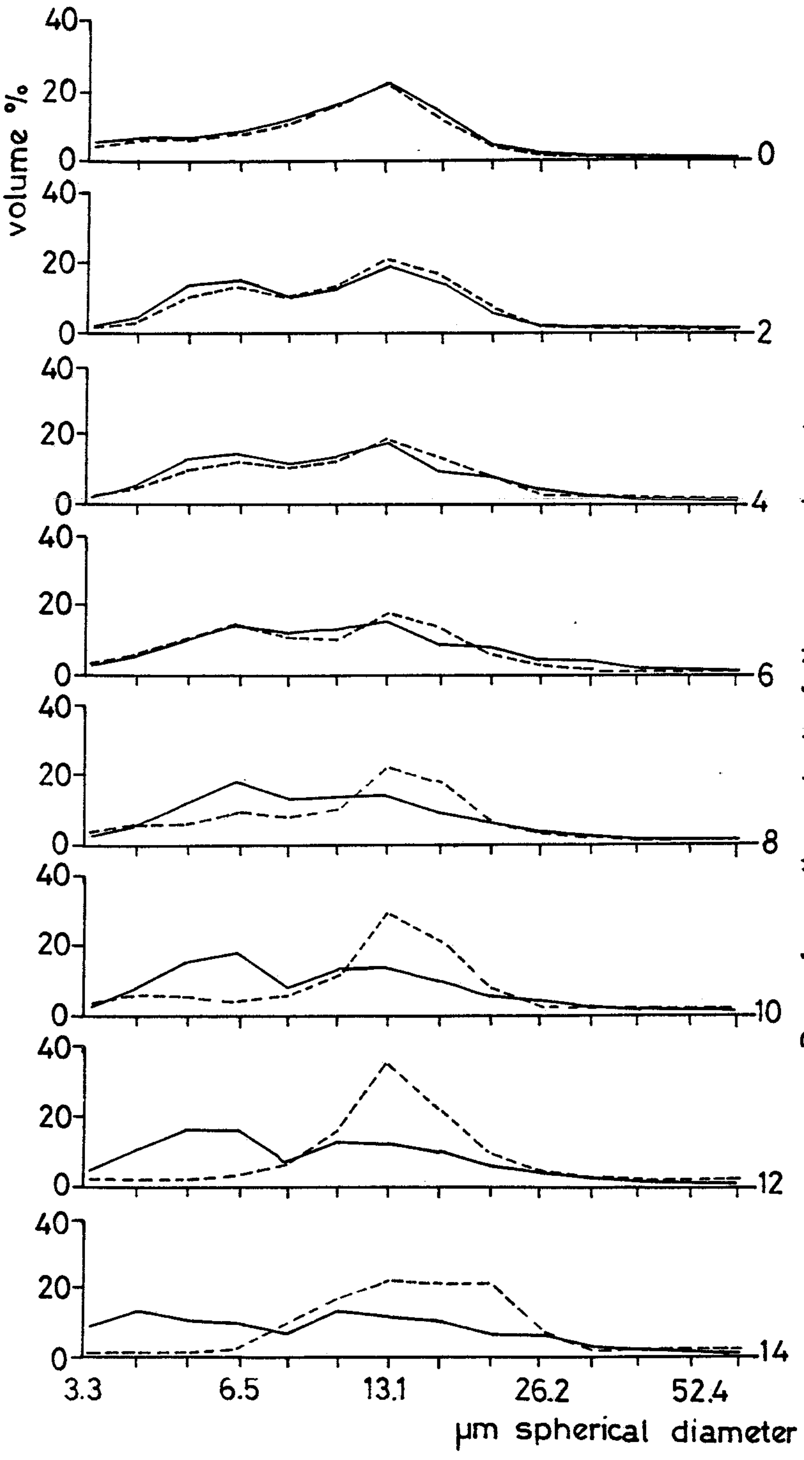


Fig. 1.2.2. Size spectrum of particulate matter as percentage of total volume, in "Q" (continuous line) and "A" (broken line) microcosms. The X axis represents the mean ESD (equivalent spherical diameter) for each Coulter Counter channel.

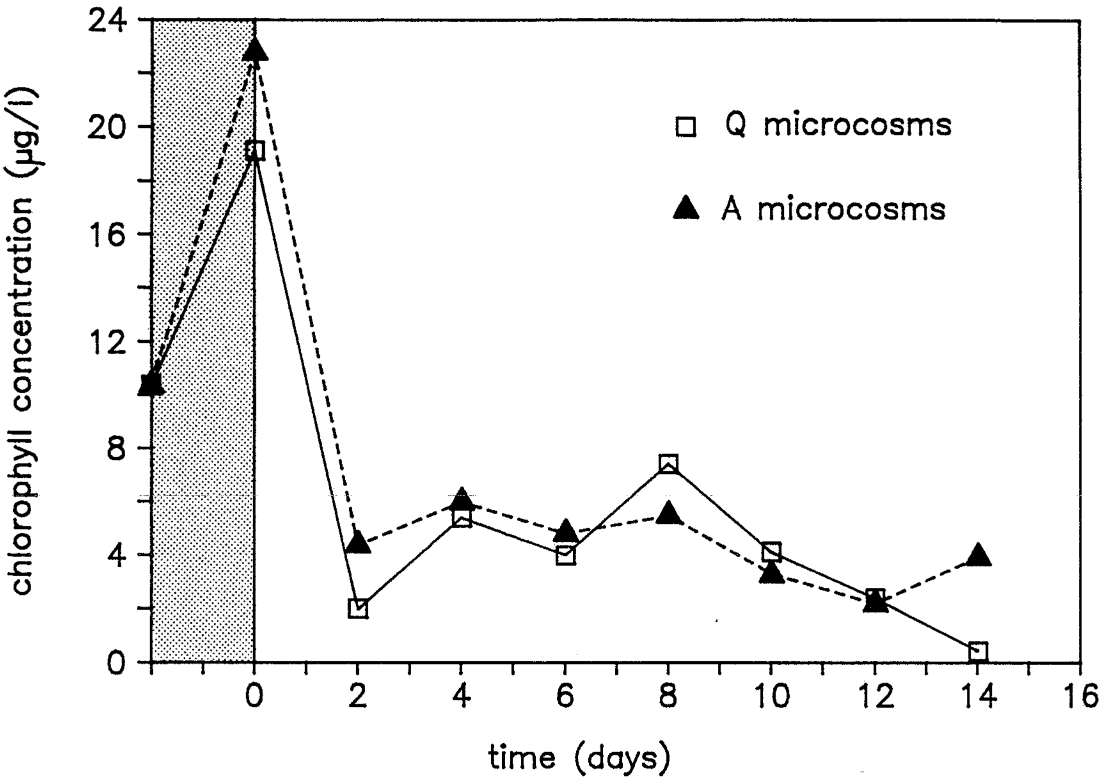


Fig. 1.2.3. Temporal variation of chlorophyll concentration. Days are counted from the start of turbulence and adult removal. The egg-laying period (2 days) is indicated by the stippled area.

Development and growth of *Acartia grani*

The abundance peaks for the different instars in stirred conditions preceded those in unstirred conditions (Figure 1.2.4), as found by Alcaraz et al. (1988) for *A. italica.* Consequently, instar development times were consistently shorter in "A" microcosms (two-tailed Wilcoxon rank test, $P<0.005$). However, to avoid possible indirect effects of turbulence that could result in a shorter total development time in "A" microcosms (maybe a stimulating effect of stirring on egg hatching by i.e. changes in oxygen availability, Uye et al., 1979), we compared instar development time as a percentage of time required to develop adult females in each condition. This analysis also demonstrated a quickening effect of turbulence on development (two-tailed Wilcoxon rank test, $P<0.011$). The gap in development time between "A" and "Q" microcosms increased until NV-VI, then decreased toward adulthood (Figures 1.2.5 and 1.2.6).

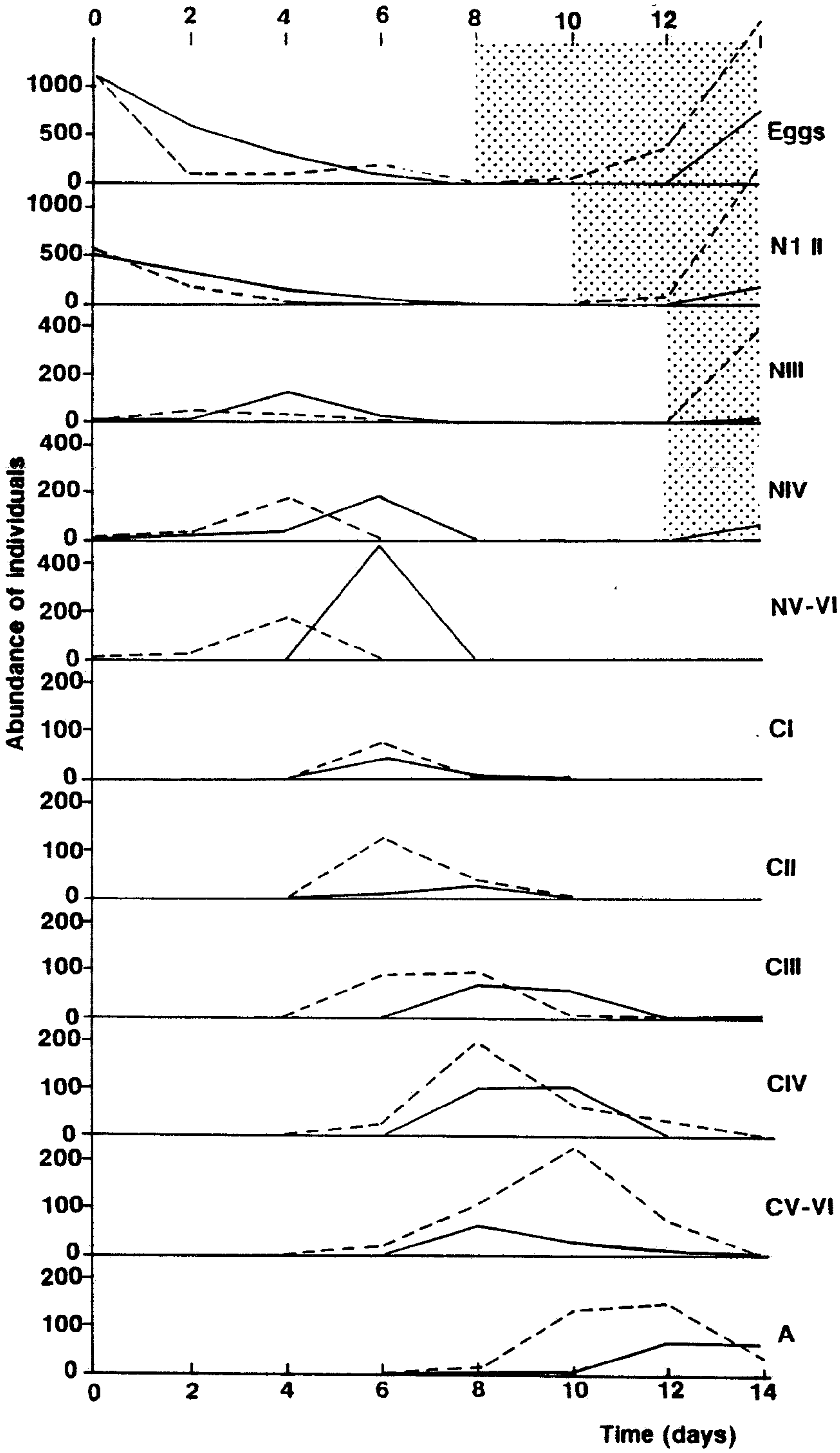


Fig. 1.2.4. Mean numbers over time of the different developmental stages of Acartia grani in "Q" (continuous line) and "A" (broken line) microcosms. The dashed area indicates the starting of a second cohort.

Stage-specific sizes of *A. grani* (Table 1.2.1) agreed with those reported by Vilela (1972) for the same species in a similar temperature range. For organisms at copepodite II or older, possible differences in size between treatments were checked. Adult males were significantly smaller in "A" microcosms (Table 1.2.1). The same tendency was observed for adult females, although the differences between "Q" and "A" microcosms were not significant, as occurred in the case of copepodite stages.

TABLE 1.2.1. - Size (μm) and estimated specific mean biomass (μg dry weight). From egg to CI instar, mean values and size ranges correspond to data pooled for "Q" and "A" conditions. From CII afterwards, mean values and standard deviations for each condition: not turbulent ("Q") and turbulent ("A") microcosms.

Instar	Length		Biomass	
Egg	77.8		0.04	
NI-II	123.0 (101-145)		0.049	
NIII	158.0 (145-171)		0.099	
NIV	184.5 (171-198)		0.154	
NV-VI	235.0 (198-272)		0.307	
CI	337.2±15.1		0.385	
	(Q)	(A)	(Q)	(A)
CII	450.9±23.2	441.4±20.0	0.938	0.879
CIII	555.3±19.3	555.9±23.7	1.776	1.782
CIV	677.0±32.4	672.5±28.2	3.259	3.194
CV-VI♂	787.2±16.2	788.2±21.6	5.176	5.197
CV-VI♀	863.5±32.1	855.3±26.3	6.873	6.675
♂	883.7±25.8	873.6±23.2*	7.378	7.123
♀	1013.7±32.5	1006.6±37.2	11.235	10.997

* Significant at the 0.01 level.

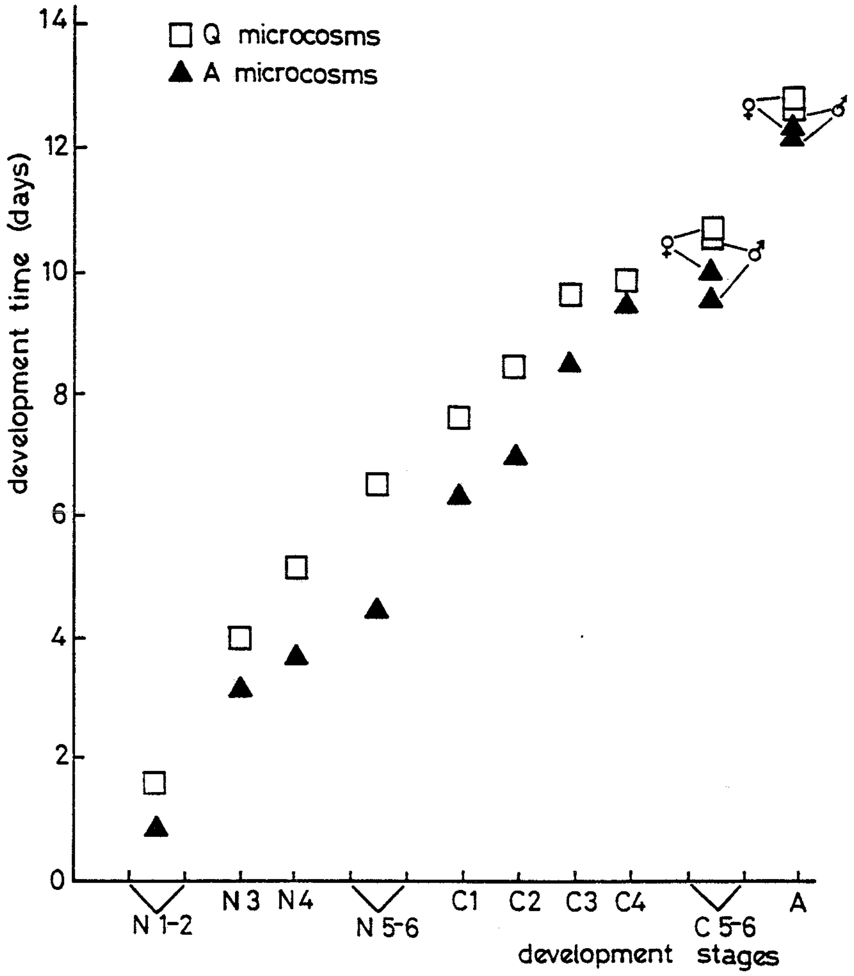


Fig. 1.2.5. Mean specific developmental times estimated from stage frequency data under turbulent and non-turbulent conditions.

Growth was exponential throughout development, but shifted in the transitions from nauplius V-VI to copepodite I and from copepodite V-VI to adult (Figure 1.2.6), following a pattern similar to that described by Ivanova (1973) and Miller et al. (1977). In general, copepodites had higher growth rates (estimated from the slope of the linear regression equations for log body mass versus relative development time, Table 1.2.2) than nauplii (2.5 and 1.5 times higher in "Q" and "A" microcosms respectively). Naupliar growth rates were higher in "A" microcosms than in "Q" microcosms (1.3 times), but for copepodites the trend was in the opposite direction (1.3 times lower in "A" microcosms).

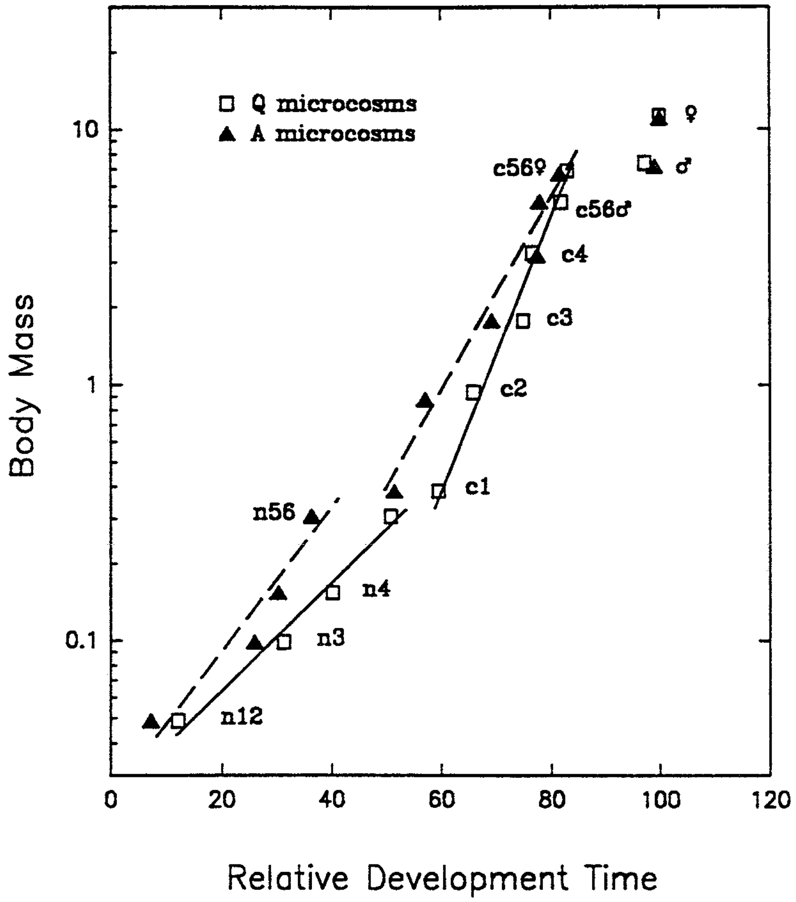


Fig. 1.2.6. Growth pattern of Acartia grani in "Q" and "A" microcosms. Continuous and broken lines are the fitted regression lines for "Q" and "A" microcosms data respectively.

TABLE 1.2.2. - Growth rates (regression slopes ± standard error) from the linear relationship between log body mass and relative instar development time (Figure 1.2.6).

	Growth rates	r^2
"Q" microcosms		
Nauplii	0.020±0.002	0.98
Copepodites (CI to CV-VI)	0.051±0.004	0.98
"A" microcosms		
Nauplii	0.025±0.006	0.91
Copepodites (CI to CV-VI)	0.038±0.003	0.97

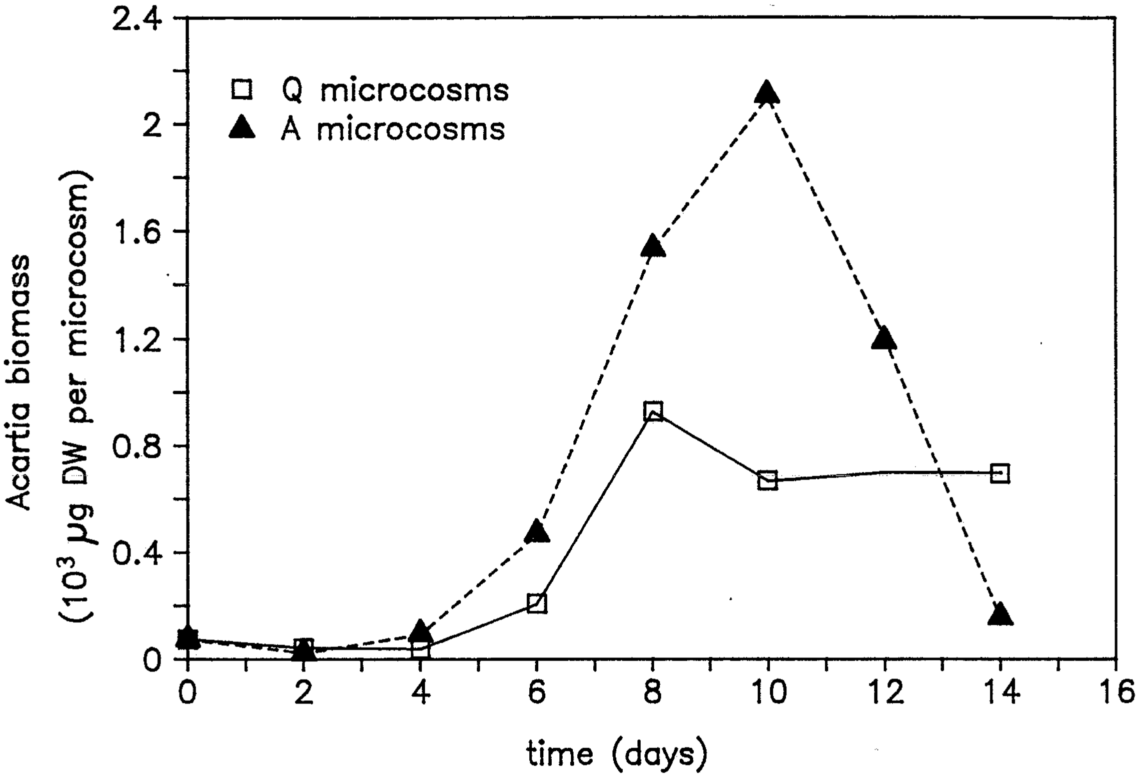


Fig 1.2.7. Acartia **integrated biomass temporal variation for unstirred ("Q") and stirred ("A") microcosms.**

Biomass temporal variation and consumers/producers ratio

Zooplankton biomass time course for "Q" and "A" microcosms is represented in Figure 1.2.7. For both conditions there was a marked increase in biomass about the 6th day, although trends differred. While for "Q" microcosms values reached a plateau and kept quite constant for the remainder of the experiment, in "A" microcosms the peak in biomass reached values 2-3 times higher than in "Q" microcosms but collapsed to values quite low at the end of the experiment (about 3-4 times lower than in "Q" microcosms on day 14th).

The "consumers/producers" ratio was estimated relating *Acartia* biomass with both particulated matter concentration (in volume) and chlorophyll concentration (Figure 1.2.8). Both quotients showed a similar trend, with and earlier increase followed by a collapse in "A" microcosms, while in "Q" microcosms the peaking was higher and delayed to the end of the experiment.

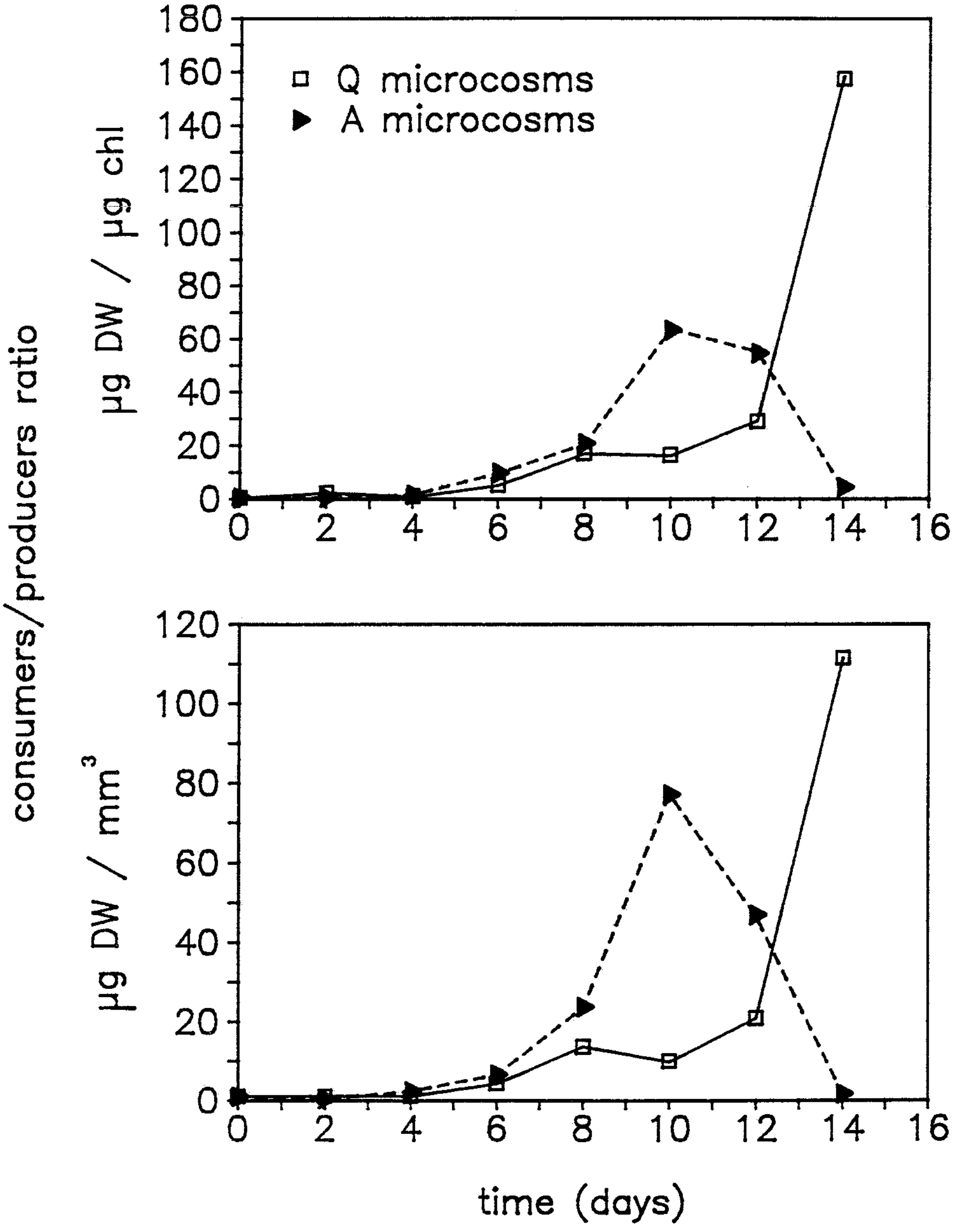


Fig 1.2.8. Temporal variation of the consumers/producers ratio estimated for chlorophyll (above) and particulate matter (below).

Discussion

Isochronal development (equal duration of all life history stages) has been considered as an evolutionary strategy for *Acartia* and other copepods occupying neritic and estuarine habitats, where predation would concentrate on adults (Miller et al., 1977). Although the instar-development time relationship for *A. grani* followed approximately a linear trend, there were step transitions at the stages experiencing the deepest morphological changes (i.e., NV-VI and CI; CIV and CV-VI). Differences in food availability throughout the experiment do not seem to explain this lack of linearity, because in most of the experiment particulate matter concentration was >2-3 mm^3l^{-1}, well above the saturation level reported for ingestion, egg production and specific growth rates of different *Acartia* species [1.7 mm^3l^{-1} for *A. clausi* (Ayukai, 1987); 1.8 mm^3l^{-1} for *A. tonsa* (Kiφrboe et al., 1985, Berggreen et al., 1988)]. As a consequence, the development of *A. grani* cannot be considered as strictly isochronal (sensu Landry, 1983) in our experiment.

Development times were significantly shorter in "A" microcosms for the different stages in our experiment. Although changes in food quality and quantity due to turbulence as in the shift in food size spectrum in natural systems reported by Kiφrboe et al.,1990 could also play an important role in copepod life history, in our experiment the particulate matter concentration and size spectrum were similar until the 7-8th day, when CI copepodites had just molted and the dissimilarities in development were more marked. Consequently, the changes in development observed in this period must be mainly attributed to a direct effect of turbulence, sensu Alcaraz et al. (1988). Afterwards, when differences in particulate matter started to manifest themselves, discrepancies in development time smoothed progressively. It is not clear whether or not differences in particulate matter concentration were really of importance in this period. If they were, poorer food conditions at the end of the experiment in "Q" microcosms should have caused longer development times and curtailed sizes of later stages (Klein Breteler et al., 1982; 1990). But in spite of that, in this period instar development times in "Q" and "A" microcosms tended to be equal and sizes were not significantly shorter in "Q" microcosms. Thus, we must conclude that even though differences in food availability could play a minor role in the faster development observed in our experiment, a direct effect of turbulence must be the main explanation for the differences found.

Regarding the changes in growth rates found in "A" microcosms, they seem to reflect the more conspicuous differences in development rate in late nauplii and early copepodites mentioned above. On the other hand, the fact that in both treatments copepodite growth rates were higher than the naupliar ones, contrasts with the constant relationship found for other *Acartia* species in a wide range of food concentrations, from starvation to saturation (Berggreen et al., 1988), and agrees with the development pattern showed by *Acartia grani* in our experiment.

The occurrence of the maximum acceleration of development in nauplii and the progressive decrease for the successive copepodite stages, points to possible differences in the way turbulence affects copepods throughout life. How turbulence really does affect copepods is still unclear, but recent works (Costello et al., 1990; Marrasé et al., 1990; Alcaraz and Saiz, in press) indicate that either an enhanced grazing activity due to higher encounter rates in turbulent situations or an increased metabolism due to a higher frequency of escape reactions might play an important role. Either mechanism could be responsible for an acceleration of development, in a way similar to increasing temperature (Landry, 1975; Ikeda, 1985; Uye, 1988).

The temporal variation of *A. grani* biomass differed from previous experiments with *A. italica* (Alcaraz et al. 1988). Zooplankton biomass was higher in "A" microcosms than in the "Q" ones until the end of the experiment. The time course of the consumers/producers ratio reflected the changes in copepod biomass and development time observed, with higher values under turbulence conditions; however, the marked different trend followed by particulate matter (and chlorophyll) between "Q" and "A" microcosms at the end of the experiment reverted this tendency. The mentioned discrepancy with previous experiments conducted with *A. italica* (Alcaraz et al. 1988) could be partially explained by the periodical supply of nutrients, that could have supported a better quality food in "A" microcosms than in the mentioned previous experiments, although no evidence is available. Furthermore, differences in size of the experimental set-up (10-l microcosms in our experiments versus the 30-l ones in the experiments reported by Alcaraz et al. 1988) probably were associated to a higher turbulence intensity in our experiment. We feel that a turbulence intensity-dependent response or species-dependent differences in the response to turbulence (i.e. different effects on behaviour, metabolism, feeding and growth efficiencies) are probably the main responsibles for the dissimilar behaviours exhibited by *A. grani* and *A. italica* populations. In any case, turbulence induced not only an accelerated development in the population of *A. grani* studied, but turbulence also tended to support a higher copepod biomass and a higher trophic efficiency.

The importance of small-scale turbulence in natural plankton communities is still uncertain, particularly for zooplankton (Marine Zooplankton Colloquium 1, 1989). Although there is no reason to expect qualitative differences between the effects of small-scale turbulence in laboratory microcosms and natural systems, this point is not yet resolved. The measurement of turbulence itself is one of the main problems (Soloviev et al., 1988). Changes in size, quantity or quality of particulate matter (Kiϕrboe et al., 1990) mediated by small-scale turbulence could affect copepod activity indirectly, and one must be cautious in interpreting experimental data.

RESUM

S'han estudiat els efectes de la turbulència de petita escala en el desenvolupament i creixement del copèpode calanoide *Acartia grani*, comú en zones semiconfinades de la Mediterrània Occidental, mitjançant l'ús de microcosmos de 10 litres de capacitat. En el microcosmos sotmesos a agitació (turbulència) s'escurçaren els temps de desenvolupament dels diferents estadis i es produiren canvis en les taxes de creixement. Canvis en la "qualitat" de les poblacions naturals de fitoplàncton confinades podrien explicar en part els resultats observats, però es fa palesa l'acció d'efectes directes que podrien afectar el metabolisme i l'activitat dels copèpodes. Aquestes influències semblen manifestar-se en diferent grau al llarg del desenvolupament, essent més evidents en els darrers estadis nauplius i en els primers estadis copepodit.

Canvis en l'evolució temporal de la biomassa total de zooplàncton confinada en els microcosmos i del quocient de biomasses "consumidors/productors" confirmen la tendència dels processos a accelerar-se en condicions de turbulència. La major eficiència tròfica del sistema en condicions de turbulència, però, suggereix una resposta diferent d'*A. grani* en condicions de turbulència respecte l'observada prèviament en *A. italica*.

CAPITOL II

EFECTES DE LA TURBULENCIA EN EL METABOLISME DE COPEPODES CALANOIDES

CAPITOL II

EFECTES DE LA TURBULENCIA EN EL METABOLISME DE COPEPODES CALANOIDES

2.1. Enhanced excretion rates induced by small-scale turbulence in *Acartia* (Copepoda: Calanoida).

(Basat en l'article del mateix títol fet en col.laboració amb M. Alcaraz)

2.1. ENHANCED EXCRETION RATES INDUCED BY SMALL-SCALE TURBULENCE IN *ACARTIA* (COPEPODA: CALANOIDA)

Introduction

Zooplankton metabolism and activity has been shown to be highly dependent on physical environmental factors. Temperature has been traditionally the most studied physical factor influencing zooplankton (McLaren 1963, Mayzaud 1973a), although light (Fernández 1977), salinity (Marshall 1973) and others (see Le Borgne 1986) have also shown to be relevant. However, little attention has been paid to the role that turbulent water motion plays on zooplankton, especially at the microscale. Only very recently it has raised an increasing interest in the study of the effects of small-scale turbulence on zooplankton activity (Strickler 1985, Alcaraz et al. 1988, 1989, Rothschild & Osborn 1988, Marine Zooplankton Colloquium 1 1989, Costello et al. 1990, Marrasé et al. 1990, Saiz & Alcaraz 1991). One of the main problems of its study arises from the field, where the effects of turbulence alone cannot be discerned from changes in food size and composition related to hydrographic structures (Peterson & Bellantoni 1987, Kiϕrboe et al. 1990). In spite of the difficulties in its measurement and its laboratory simulation (Nixon et al. 1979, Caldwell 1983), experimental approaches in the laboratory (Oviatt et al. 1981, Alcaraz et al. 1988, 1989, Marrasé et al. 1990) and indirect data from the field (Harris & Malej 1986, Sundby & Fossum 1990) seem to confirm the ecological importance of small-scale turbulence itself in controlling zooplankton activity.

At present, two main mechanisms have been proposed by which small-scale turbulence can affect zooplankton activity: (i) by an increase in the encounter probability between planktonic organisms and their food (Rothschild & Osborn 1988, Evans 1989, Costello et al. 1990), whether or not associated with enhanced ingestion rates (Nixon et al. 1979, Oviatt et al. 1981, Strickler 1985, Marrasé et al. 1990); and (ii) by the enhancement of zooplankton metabolism through mechanical stimulation, by an increase in the frequency of escape reactions, a metabolically high-expense swimming behaviour (Alcaraz et al. 1988, 1989, Marrasé et al. 1990).

In laboratory experiments (Alcaraz et al. 1988, Saiz & Alcaraz 1991) a shorter development time for copepods grown in microcosms with turbulence was observed, associated with an increase in ammonia concentration. This was explained assuming a mechanical stimulation of metabolic activity [point (ii) above], similar to the way increasing temperature enhances metabolic rates. Recent work using videocinematography (Costello et al. 1990; Marrasé et al. 1990) verified experimentally for *Centropages hamatus* the increase in the frequency of escape reactions under turbulence, as suggested by Alcaraz et al. (1988), but whether or not this really results in a substantial increase in metabolism is still unknown. The metabolic expenditure of escape reaction behaviour has not been experimentally measured yet, and the available estimates derived from hydrodynamic models range from 3 to 400 times higher than the standard metabolism (Strickler 1977, Morris et al. 1985, Alcaraz & Strickler 1989). Here we attempt to determine whether turbulence really enhances metabolism of copepods by its mechanical effect alone. We measured ammonia and inorganic phosphorus excretion rates of three species of planktonic copepods of the genus *Acartia* under non-turbulent (undisturbed or standing) and turbulent (unquantified level generated by a shaker) conditions.

Method

Copepods were obtained by means of short horizontal net tows made in the harbours of Barcelona and Masnou, on the Catalan Coast (Spain, Western Mediterranean), and transported to the laboratory in 10-l plastic containers filled with in situ seawater. In the laboratory, the containers were placed in a temperature-controlled chamber

(17.5 ± 1 °C) under dim light. Copepods were allowed to acclimatize to the experimental temperature in the buckets for at least 36 hours. Periodically, part of the water from the containers was removed and replaced by clean filtered sea water, and a suspension of phytoplankton (*Isochrysis, Thalassiosira*) added to ensure a food supply. Copepods used in the experiments usually were not kept in the laboratory for longer than a week.

Turbulence was generated by a reciprocal shaker oscillating at 90 to 100 strokes min^{-1} with an amplitude of 2.5 cm. No quantifications of turbulence intensity were performed. The turbulence induced at this rate of shaking proved not to be harmful for copepods, and animals survived well for several days after the experiments. Standing flasks were considered as non-turbulent conditions.

Excretion rates were determined by the incubation method (Omori & Ikeda 1984). Previous to the experiment, copepods were placed for about 1 hour in filtered sea water to empty their guts. After that, adult females of *Acartia margalefi* and *A. clausi*, and males and females of *A. grani* were sorted under a stereomicroscope, and placed in the experimental flasks. These consisted of 25 or 50 ml screw-cap polyethylene vials 3/4 filled with air-satured sea water filtered twice through GF/F glass fibre filters. The concentration of organisms in the experimental flasks ranged from 0.7 to 2.3 ind ml^{-1}, depending on the species size, and several flasks without copepods were used as control. In each experiment the number of flasks per condition (non-turbulent, standing flasks; turbulent, shaker flasks) ranged from 1 control and 3 experimental flasks, up to 4 control and 10 experimental flasks. Flasks were wrapped in aluminium foil, incubated at the experimental conditions for about 24 hours and then ammonia and phosphorus concentration were measured. In some cases the initial ammonia and phosphorus concentrations in control and experimental flasks were also determined. Although mortality was negligible, when significant mortality (>5%) occurred, the data were rejected.

Analyses of ammonia were performed usually on replicate samples, using the method of Koroleff (1970) adapted to 5 or 15 ml samples. Soluble reactive phosphorus was determined only in two experiments with *A. margalefi*, in 15 ml samples, following Koroleff (1983). The results were expressed as per individual as well as on a weight (body nitrogen) basis. The metasome size of experimental copepods was measured under a stereomicroscope in order to estimate their nitrogen content, which was calculated using the nitrogen-metasome size relationships given by Bergreen et al. (1988) for *A. tonsa*. These estimates proved to be very close to previous determinations carried out in our lab for *A. clausi* and *A. margalefi* (Alcaraz, unpubl. data).

In order to consider the possible existence of experimental artifacts induced by differences in bacteria abundance between experimental conditions, subsamples from experiments where we analyzed simultaneously ammonia and inorganic phosphorus were preserved in formalin and the number of bacteria counted after DAPI staining (Coleman 1980).

Results

Mean values of metasome size and estimated body nitrogen for the species studied are shown in Table 2.1.

Turbulence tended to increase excretion rates significantly (two-tailed Mann-Whitney test, Table 2.2) for all species except *A. clausi*, which also showed higher but not significant excretion rates. Ammonia excretion was on average 59% higher under turbulence, although this trend was very variable, values ranging from 14% to 122% higher. For phosphorus excretion, rates were about 63% higher under turbulence.

TABLE 2.1 - Average body size and weight of the species studied, and number of experiments performed.

Species	Expt	Size (μm)	Body Weight (ng N)
A. margalefi ♀ (early summer)	2	519	229.5
A. margalefi ♀ (early winter)	4	607	326.6
A. clausi ♀	1	852	975.9
A. grani ♂	1	771	730.4
A. grani ♀	3	917	1210.5

The percent of body nitrogen excreted as ammonia is indicated in Table 2.3. Ammonia excretion under starving conditions represented a small fraction of estimated body content of nitrogen, values ranging between 3 and 15% of body nitrogen. The turnover of body nitrogen was faster for the smaller sizes.

Simultaneous ammonia and inorganic phosphorus excretion rates for *Acartia margalefi* were well correlated (Spearman rank correlation coefficient $r=0.780$, $n=14$, $P<0.005$). Atomic N:P ratios tended to be lower under turbulence (Mean±95% CI: Non-turbulence 42.24±11.34; Turbulence 31.87±2.70), but differences were not significant (Mann-Whitney test). There were no significant differences in the abundance of bacteria between experimental conditions (Mann-Whitney test). Furthermore, no correlation was found for these experiments between excretion rates and abundance of bacteria (N excretion rate - bacteria: $r=-0.066$, $n=13$, $P<0.819$; P excretion rate - bacteria: $r=-0.500$, $n=13$, $P<0.083$, Spearman Rank correlation coefficient).

TABLE 2.2 - Nitrogen and phosphorus weight-specific excretion rates for the species studied. Average and range of values for each experiment performed are represented. The number of replicates in each experimental condition (NT: non-turbulence, T: turbulence) is also indicated.

Species	NT	T	NON-TURBULENCE	TURBULENCE
			N excretion (ng NH_4-N/mg Body N/day)	
A. margalefi ♀	4	4	116 (107-122)	133 (124-137)
	3	3	108 (96-116)	170 (153-182)
	5	5	51 (41-82)	64 (53-95)
	10	10	47 (30-65)	73 (47-114)
	3	3	20 (13-29)	32 (27-40)
	8	9	21 (10-46)	47 (18-72)
Pooled	33	34	53 (10-122)	77 (18-182)**
A. clausi ♀	3	3	49 (44-59)	62 (55-68)
A. grani ♂	6	6	43 (23-73)	71 (51-112)*
A. grani ♀	6	6	22 (5-44)	46 (16-69)
	6	6	37 (26-46)	52 (44-63)
	6	6	28 (20-35)	42 (29-57)
Pooled	18	18	29 (5-46)	48 (16-69)**
			P excretion (ng PO_4-P/mg Body N/day)	
A. margalefi ♀	4	4	5.3 (4.84-6.40)	9.8 (8.62-11.02)
	3	3	7.7 (5.47-9.58)	11.1 (9.60-11.97)
Pooled	7	7	6.3 (4.84-9.58)	10.3 (8.62-11.97)**

* $P<0.04$
** $P<0.01$

Weight-specific ammonia excretion was inversely related to body nitrogen for both non-turbulent and turbulent conditions (Figure 2.1). The variables were significantly correlated ($n=22$, $r=0.493$, $0.05>P>0.01$), and the regression equation on pooled data was

$$\log Y = -0.437 \log X - 0.094$$

where Y: ng NH_4-N ng body N^{-1} day^{-1}, and X: ng body N

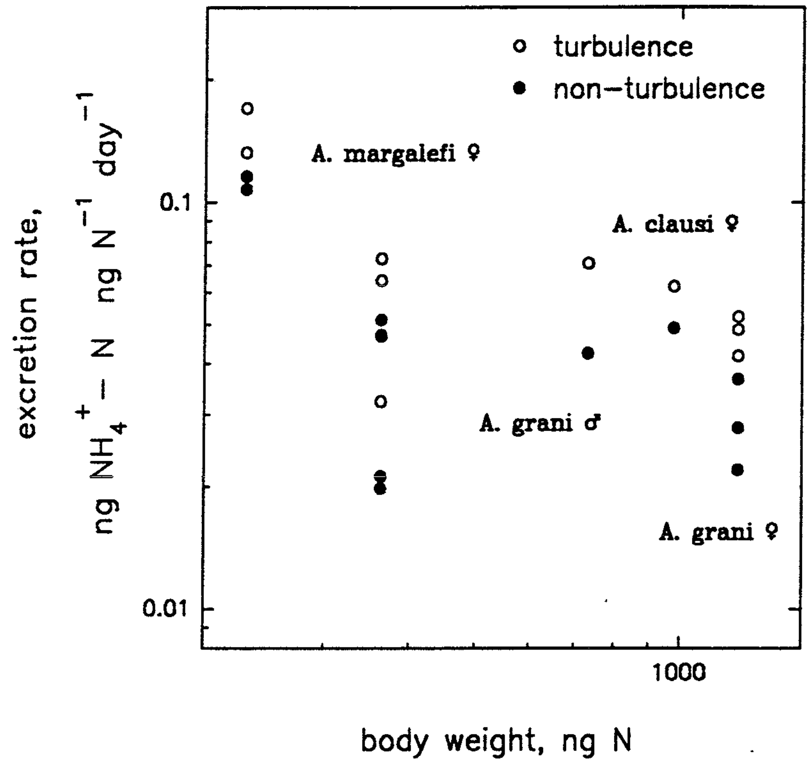


Fig. 2.1. Plot of weight-specific ammonia excretion rate versus body weight for all the species studied.

Discussion

Estimated excretion rates for ammonia and inorganic phosphorus agreed with values reported in the literature for species of the same genus in similar experimental conditions (Ikeda 1974, Kiϕrboe et al. 1985). The excretion rates exhibited by *Acartia margalefi* (early winter form) showed high variability, that probably could be explained by differences in past life history of copepods (e.g. recent food conditions).

The inverse relationship between weight-specific excretion and body size has been widely reported for copepods and zooplankton in general (Ikeda 1974, Fernández 1978). The regression coefficient was similar to those reported for mixed zooplankton (-0.475 to -0.419, Ikeda et al. 1982; -0.402, Verity 1985). However, this value was higher than the value of -0.25 reported by Banse (1972) for small invertebrates, the average value according to the surface law of von Bertalanffy (Le Borgne 1986).

The atomic N:P ratios were close to the values estimated for proteins (Ikeda 1977), indicating the protein-oriented catabolism of *Acartia* under starving conditions. This could be due to the reduced reserves of lipids of neritic copepods like *Acartia* (Ikeda 1974, Mayzaud 1976). However, our values were slightly higher than others reported for copepods. This does not seem to be related to bacterial activity in our experiments, although some influence on phosphate excretion cannot be excluded. Other factors can also explain the divergence of our values from those of the literature. As mentioned by Ikeda (1977), most of atomic N:P ratios reported have a quite narrow range (7 to 19, see Corner & Davies 1971 and Le Borgne 1986 for a review), that seems to be a consequence of the use of unfiltered sea water and unsorted zooplankton (with injured and dead animals). Thus, values reported by Ikeda (1977) ranged from 3.6 to 143.

Our measurements did not take into account the excretion of N and P organic compounds. In preliminary trials, we were unable to detect urea excretion in *Acartia*, which agrees with the mainly ammonotelic excretion (84% of total nitrogen in *Acartia* clausi) reported by Mayzaud (1973b). Although organic forms of phosphorus seem to account for most of phosphorus excretion in copepods (67% for *Acartia*, Hargrave & Geen 1968), it clearly depends on food availability (Butler et al. 1979) and even has been suggested to represent unassimilated dietary phosphorus (Le Borgne 1986).

Small-scale turbulence significantly increased both ammonia and inorganic phosphorus excretion. Only data for *A. clausi* seemed to be less consistent, probably as a consequence of the reduced number of replicates. The percentage of increase was shown to be very variable, but averaged about 60% for both ammonia and phosphorus. This represents a substantial enhancement of metabolism. Assuming a $Q_{10}=2$ (Mayzaud 1973a), this would represent a metabolic rate increase equivalent to a temperature raise of about 6.7°C. No obvious difference in the response of the species studied or between males and females of *A. grani* was apparent.

Since the experiments were conducted under "no food" conditions, our results seem to confirm the mechanosensorial hypothesis proposed by Alcaraz et al. (1988). This agrees also with the observations of Marrasé et al. (1990) about a higher frequency of escape reactions under turbulence in *Centropages hamatus*. However, their study indicated a shift in the response of *C. hamatus*. The increase in the frequency of escape reactions declined several minutes after the start of turbulence. According to our results, in *Acartia* this effect should last longer. In our experiments we did not detect any possible changes in behaviour, but this genus is known to have a higher proportion of antennal mechanoreceptors than other copepods (Barrientos 1980); this could explain the intense reaction of these copepods to turbulence. Future studies on the behaviourial response of *Acartia* to turbulence and time-series experiments on excretion would shed light on the time-scale at which turbulence really affects copepod metabolism and behaviour. Furthermore, experiments under controlled levels of turbulence will allow us to determine the role that this turbulence enhanced metabolism plays in natural systems.

RESUM

S'estudià l'excreció de nitrògen i fòsfor inorgànics en tres espècies congenèriques d'*Acartia*, i la possible influència de la turbulència en llurs taxes. També es va determinar en alguns casos la possible influència de l'activitat bacteriana en les taxes d'excreció mesurades. Les taxes d'excreció es van determinar mitjançant incubacions d'unes 24 hores de durada en aigua de mar filtrada.

Es va observar una relació al.lomètrica inversament proporcional entre les taxes específiques i la biomassa corporal de cada espècie, amb un exponent de -0.437. Les incubacions realitzades en condicions de turbulència presentaren taxes d'excreció de l'ordre del 60% (en promig) més altes que les incubacions en condicions no perturbades (en calma o quiets), tant per l'amoni com pel fosfat. Els quocients atòmics N:P assoliren valors alts, de l'ordre de 30-40, però les diferències entre tractaments no foren significatives.

No hi va haver diferències en l'abundància de bactèries entre tractaments. La influència bacteriana en l'excreció no es va fer palesa significativament en cap dels casos, encara que no pot descartar-se del tot una certa correlació negativa amb les taxes d'excreció de fòsfor inorgànic.

Les taxes d'excreció més elevades en condicions de turbulència observades en els nostres experiments concorden amb l'evidència obtinguda en experiments amb microcosmos, i confirmaria hipòtesis prèvies relatives a l'increment metabòlic del zooplàncton en condicions de turbulència per l'estimulació mecànica de les reaccions d'escapada.

CAPITOL III

EFECTES DE LA TURBULENCIA EN L'ALIMENTACIO, LA FECUNDITAT I L'EFICIENCIA BRUTA DE CREIXEMENT DE COPEPODES CALANOIDES

CAPITOL III

EFECTES DE LA TURBULENCIA EN L'ALIMENTACIO, LA FECUNDITAT I L'EFICIENCIA BRUTA DE CREIXEMENT DE COPEPODES CALANOIDES

3.1. Effects of small-scale turbulence on feeding and egg production rates of three *Acartia* species (Copepoda: Calanoida).

(Basat en l'article del mateix títol fet en col.laboració amb M.Alcaraz i G.-A. Paffenhöfer)

3.1. EFFECTS OF SMALL-SCALE TURBULENCE ON FEEDING AND EGG PRODUCTION RATES OF THREE *ACARTIA* SPECIES (COPEPODA: CALANOIDA)

Introduction

In recent years, interest on the effects of turbulence on zooplankton behaviour and activity has increased, especially at the microscale (Nixon et al. 1979, Oviatt et al. 1981, Strickler 1985, Alcaraz et al. 1988, 1989, Rothschild & Osborn 1988, Marine Zooplankton Colloquium 1 1989, Costello et al. 1990, Marrasé et al. 1990, Sundby & Fossum 1990). Initial indirect evidence has been provided by microcosms studies. Thus, Perez et al. (1977), Oviatt et al. (1981) and Alcaraz et al. (1988, 1989) reported experimental evidence of small-scale turbulence effects on development and feeding activity of confined zooplankton populations. Although the higher copepod activities observed in the field in relation to hydrodynamical features (frontal systems, stratification-mixing) have been attributed mainly to changes in food quality (i.e. size and chemical composition, Peterson & Bellantoni 1987, Kiϕrboe 1989, Kiϕrboe et al. 1990), the possibility of direct effects has also been proposed (Strickler 1985, Alcaraz et al. 1988, 1989). Recent experimental studies on mechanoperception and behaviour (Gill & Crisp 1985, Costello et al. 1990, Marrasé et al. 1990), theoretical models (Rothschild & Osborn 1988, Evans 1989) and new field data (Sundby & Fossum 1990) have strengthened these direct-effect hypothesis. Accordingly, there appears to be three main ways by which small-scale turbulence could affect copepod activity:

i) increasing metabolism by mechanical stimulation of escape reactions, proposed by Alcaraz et al. (1988, 1989) and supported by studies on mechanoreception and experimental data of Costello et al. (1990) and Marrasé et al. (1990);

ii) by increasing encounter probability, suggested by Rothschild & Osborn (1988) and Evans (1989), and verified experimentally by Marrasé et al. (1990) and Costello et al. (1990). Field support has been provided recently by Sundby & Fossum (1990) studying gut contents of cod larvae; and

iii) as an evolutionary niche selection factor, by interfering or enhancing feeding behaviour of different copepod species, proposed by Strickler (1985) and also by Alcaraz et al. (1989).

Here we attempt to determine whether or not small-scale turbulence itself can affect the feeding activity of copepods, and in which way egg production rates (as an estimator of efficiency in transforming ingested food into production) can be influenced. In order to do that, we conducted a series of experiments with three congeneric species occupying habitats of different hydrodynamism: *Acartia tonsa*, from an estuarine system in the Western Atlantic affected by strong semidiurnal tidal currents, and *Acartia clausi* and *Acartia grani*, from semi-enclosed areas in the Western Mediterranean. *A. clausi* is abundant in winter and the early spring bloom, while *A. grani* is a dominant species during early summer and the autumn bloom. To minimize possible indirect effects induced by changes in the quality of the food offered due to turbulence, we chose a common diatom, *Thalassiosira weissflogii*, typical of unstratified waters and unaffected by small-scale turbulence (E. Berdalet, unpublished data). Experiments were carried out over a wide range of food concentrations, to test possible dependence on food concentration in the response of the copepods to turbulence, as reported by Marrasé et al. (1990).

Materials and methods

i) *Acartia tonsa* experiments.

A. tonsa individuals were collected at the Skidaway River, Savannah (Georgia, USA), and left overnight diluted in a bucket with natural sea water. Salinity was slowly increased by adding offshore filtered sea water up to 32-37 ppt. Temperature in the laboratory was 20±1°C. After this period, adult females were sorted and acclimated to the experimental food concentrations for 24-36 hours in 2-l jars placed on a Ferris-Wheel rotating at 0.2 rpm under dim light, with a 12 h light/12 h dark photoperiod.

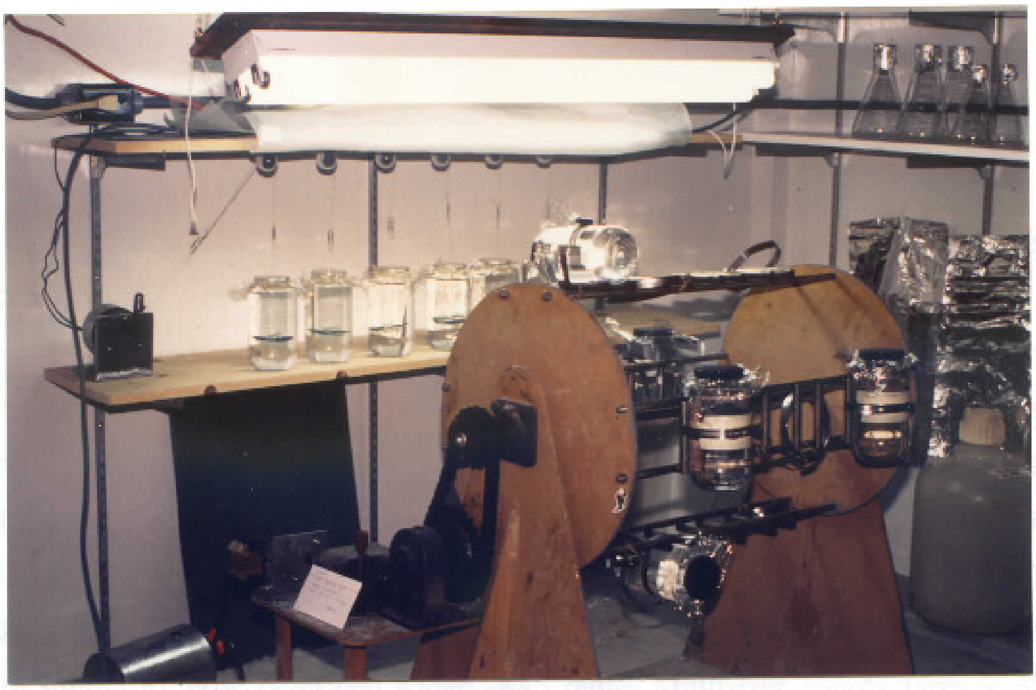
Turbulence was generated by a small grid (6 cm ϕ netlon grid of 0.5 cm mesh size) oscillating at 18 strokes per minute inside each standing jar along a range of 8 cm, in a similar set-up to that used by Alcaraz et al. (1988) (Pictures 3.1 and 3.2). A Ferris-Wheel rotating at 0.2 rpm was considered as non-turbulence (calm) conditions. Light intensity was about 22-23 μE m^{-2} s^{-1}, and was similar in both conditions in order to avoid light-induced changes in feeding rates (Stearns 1986).

Experiments were conducted over food concentrations ranging from 0.1 to 1.2 mm^{3}l^{-1} of *Thalassiosira weissflogii*. In general, there were four experimental and two control jars for each experimental condition. Eight to 10 females were added to each 960 ml experimental jars. Incubations lasted approximately 24 hours. Initial and final samples were taken for Coulter Counter analysis and microscopic counts in duplicated settled samples. At the end of each experiment, the animals were checked and the contents of the jar filtered through a 28 μm mesh size net to retain the eggs.

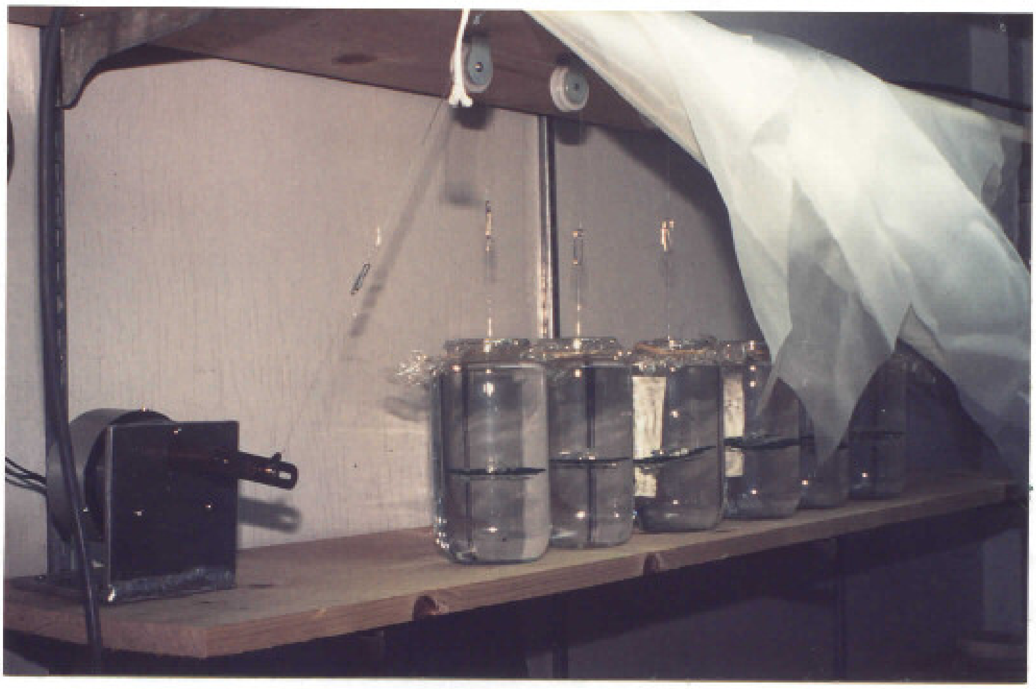
Settling chamber counts and average cell volumes estimated from Coulter analysis were used to calculate average food concentrations, clearance and ingestion rates according to Frost (1972). Empty shells and exceptionally nauplius I stages were accounted for egg production rates.

ii) *Acartia clausi* and *Acartia grani* experiments.

In general procedures were similar to those described above. Experiments were carried out in a temperature controlled room at 17.5±1°C. Light intensity was lower than for *A. tonsa* experiments, 7-12 μE m^{-2} s^{-1}. The grids used to generate turbulence were



Picture 3.1 (above) shows a general view of the experimental set-up. A detail of the jars under turbulence conditions (oscillating grid) is showed in Picture 3.2 (below).



coarser (1 cm mesh size), and experiments were run at two levels of turbulence, 9 and 20 strokes min^{-1} for *A. clausi* (first and second series respectively). For *A. grani*, experiments were performed only at 20 strokes min^{-1}.

Animals were collected in Barcelona Harbour (Western Mediterranean, Spain) by means of short, horizontal tows. After a food acclimation period of about 24-36 hours on a Ferris-Wheel at 0.2 rpm, 7-12 adult females were placed in 927 ml jars filled with a suspension of *T. weisflogii* (over a concentration range of 0.1 to 2.0 mm^{3}l^{-1}). Three additional experiments were performed on males of *A. grani*. The following procedures were similar to those described above. As Coulter Multisizer counts agree well with settling chamber counts (previously compared by linear regression analysis, $r^2=0.92$, $n=80$), data from Coulter Multisizer were used in all calculations.

iii) Statistical analysis

In order to take into account small differences in average food concentration between experimental conditions and jars in a experiment, statistical comparisons of feeding activity were performed on a grazing efficiency index, calculated as:

$$G = \frac{I * n}{C * V} * 100$$

where I is ingestion rate, C average food concentration, V experimental volume (ml) and n number of individuals. This index provides an estimate of the proportion of the available food which was ingested per copepod in each experimental jar.

The percentage of empty shells (empty shells/total eggs laid) was used to estimate egg cannibalism. In the few cases that some nauplius I were present, their corresponding empty shells were accounted as not eaten eggs. This represented a minor problem because incubations did not usually last for longer than 24 hours.

The quotient Egg production rate/Ingestion rate (E/I) was used to compare differences in efficiency transforming ingested food into eggs (gross-growth or production).

Mann-Whitney two-tailed tests were performed for each species considering pooled data of all experiments or, when saturated ingestions were achieved, grouping experiments in two sets: for non-saturating and saturating food levels.

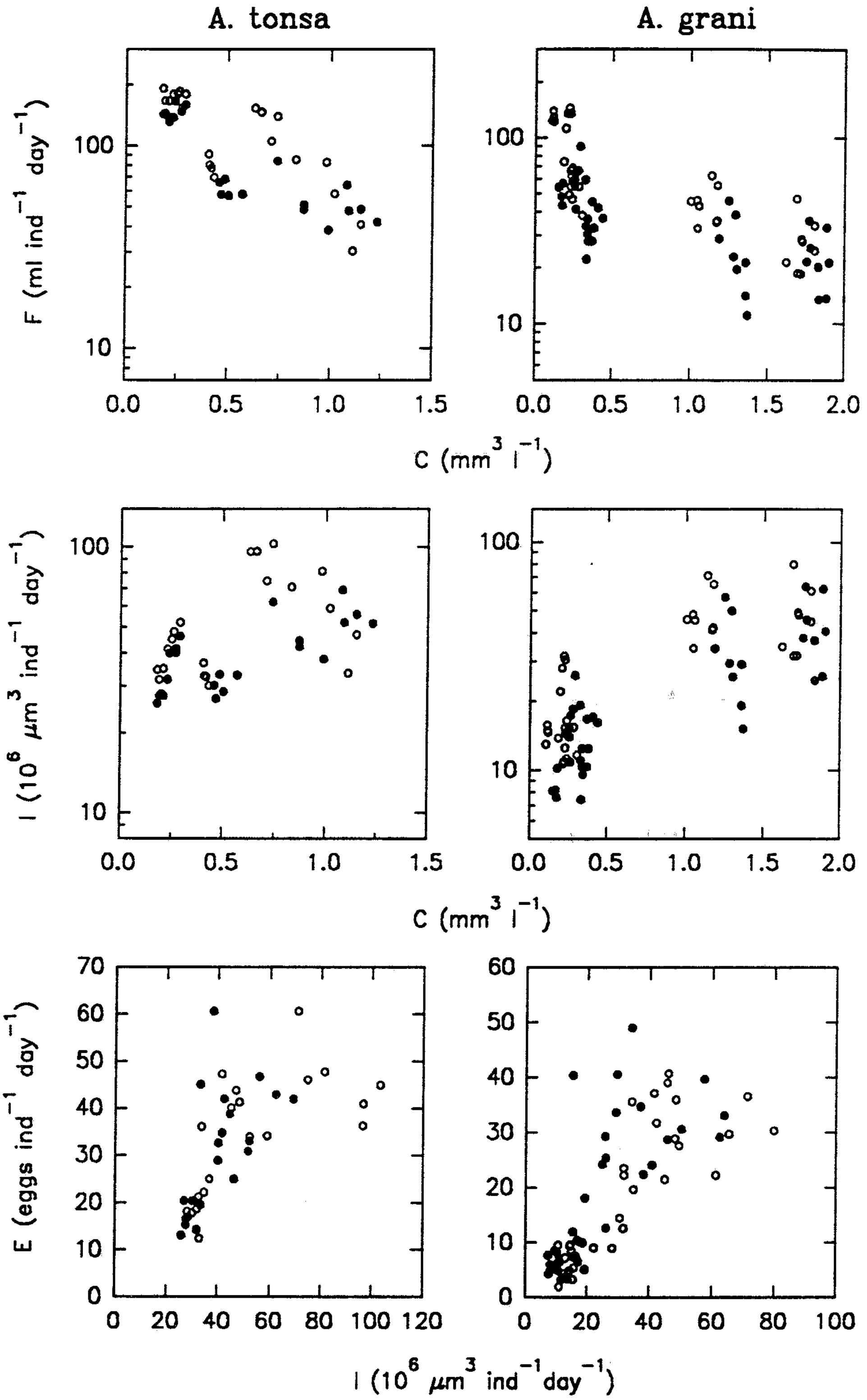
Results

Feeding and egg production under calm conditions

The trends on feeding and egg production observed for *A. tonsa* and *A. clausi* in our experiments agree with general patterns observed by other authors. Regarding to *A. grani* (males and females), only data on pigment gut contents and gut evacuation rates are available in the literature (Bautista et al. 1988).

Clearance rates for *A. tonsa* (see Figure 3.1) peaked at low food concentrations and decreased at higher food levels, as reported by Paffenhöfer & Stearns (1988) and Stottrup & Jensen (1990). Rates of ingestion did not reach saturating levels at the range of food concentrations tested for this species in our experiments.

A different pattern was observed for *A. clausi* (Figure 3.2), with clearance rates quite constant at food concentrations ranging from 0.2 to 1.5 mm^3l^{-1}, and decreasing at higher food levels. This trend is similar to that reported by Ayukai (1987) for the same species fed on *T. decipiens*. Values for the second series of experiments conducted with this species (Grid 20 str min^{-1}) tended to be higher, specially at low food concentrations. The first series was performed during April-May 1990 and the second one during January-February 1991; differences in past life history and size probably can explain this variation.



5.1 ~ 20
0.2 ~ 10
1.6 ~ 4n

Figure 3.1. Clearance (F) and ingestion (I) rates in relation to average food concentration (C), and relationship between egg production (E) and ingestion (I) rates for A. tonsa and A. grani. Filled circles: non-turbulence (Ferris-Wheel), Hollow circles: turbulence (Grid).

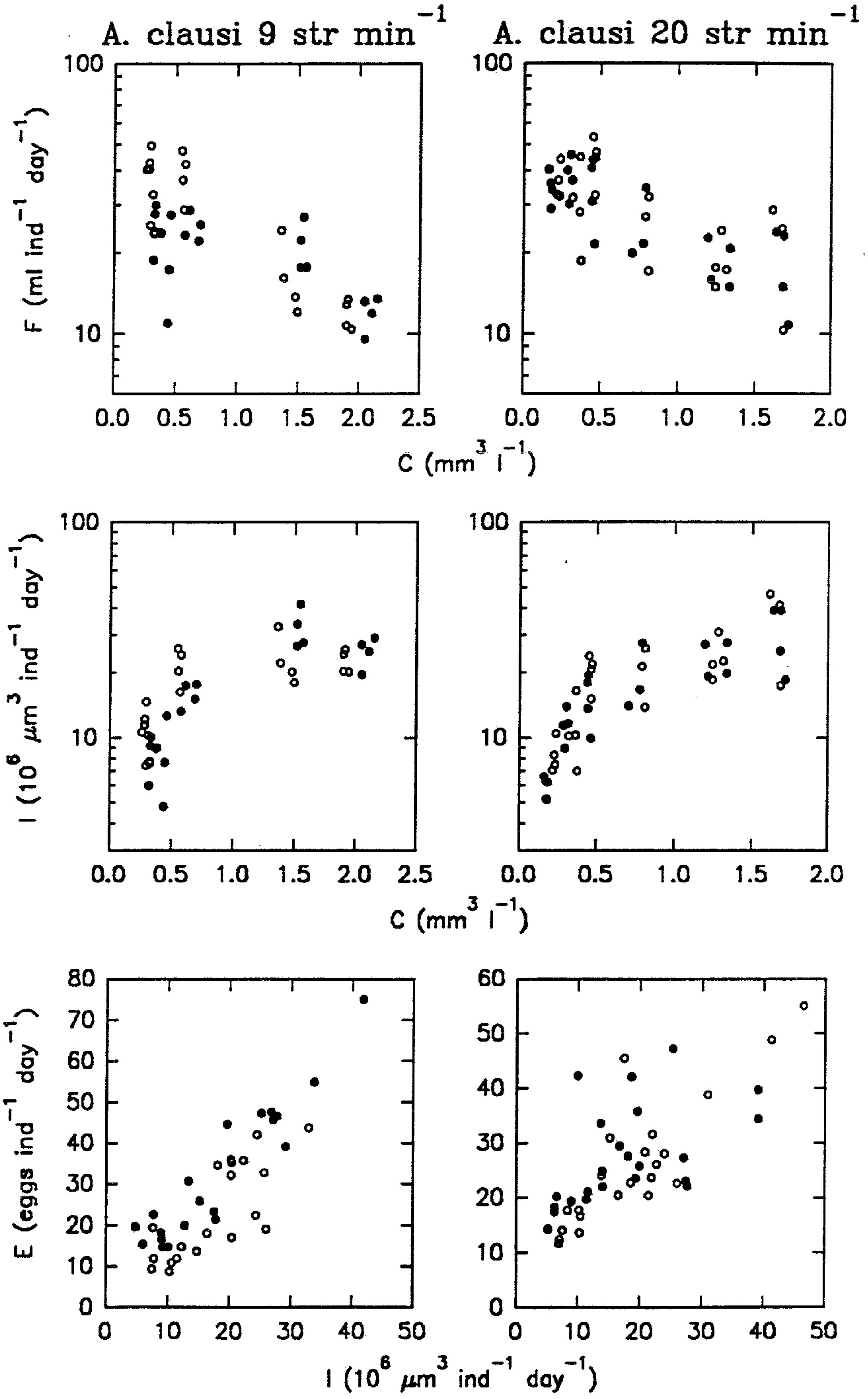


Figure 3.2. Clearance (F) and ingestion (I) rates in relation to average food concentration (C), and relationship between egg production (E) and ingestion (I) rates for both series of experiments conducted on A. clausi. Filled circles: non-turbulence (Ferris-Wheel), Hollow circles: turbulence (Grid).

Feeding activity in relation to food concentration for *A. grani* (Figure 3.1) was similar to the pattern of *A. tonsa*: the peaking of clearance rates at low food concentration and subsequent decrease at higher concentrations, as well as a sigmoidal relationship for ingestion, with saturated ingestion rates for food concentrations >1.0-1.5 mm^3l^{-1}. The three experiments performed on males (not represented in Figure 3.1, see Table 3.1) showed values much more lower than for females.

Egg production rates followed the same relation to food concentration than ingestion rates (figure not shown). The maximal number of eggs produced per female and day was about 40 to 50 eggs for all three species (Figures 3.1 and 3.2). The quotients E/I were similar for *A. tonsa* and *A. grani*, but differed from *A. clausi* values found for both series (Mann-Whitney two-tailed test, $P<0.001$). No significant difference was found for *A. clausi* between both series of experiments under non-turbulent conditions.

Egg cannibalism (estimated as percentage of empty shells found) was in general low and independent of ingestion under non-turbulent conditions (Figure 3.3). The lowest values (<5%) were for *A. tonsa*, while *A. grani* and *A. clausi* (first series) showed a higher proportion of empty shells, up to 10%. The second series of experiments performed with *A. clausi* showed conspicuous higher values, weakly dependent on food ingestion (Spearman rank correlation coefficient: -0.56, $P<0.01$), exceeding 10% up to about 40% at low food concentration.

TABLE 3.1 - Geometric means ± 95% CI (in parenthesis) for clearance (F), ingestion (I) and egg production (E) rates of A. tonsa and A. grani ♂ under calm (Ferris-Wheel 0.2rpm) and turbulent (Grid) conditions. The range of average food concentrations (C) for each experiment is also represented. (* There were only two experimental jars per condition. Figures in parenthesis represent the range of values). Units as in Figure 3.1.

ACARTIA TONSA

FERRIS-WHEEL 0.2rpm				GRID 19 str min^{-1}			
C	F	I	E	C	F	I	E
1.08-1.23	50.5 (29.6-86.2)	57.1 (37.9-86.1)	35.0 (23.5-52.1)	1.02-1.15	41.5 (18.5-95.8)	45.3 (22.4-91.5)	37.8 (27.3-52.2)
0.99-1.15*	43.2 (34.8-48.6)	46.1 (38.0-55.9)	53.2 (46.7-60.7)	0.83-0.98*	84.2 (83.0-85.4)	75.9 (70.9-81.3)	53.8 (47.7-60.6)
0.57-0.87	59.0 (39.8-87.6)	44.4 (29.3-67.3)	42.1 (38.1-46.5)	0.63-0.74	134.73 (103.0-176.3)	92.1 (73.4-115.6)	41.9 (35.3-49.7)
0.46-0.50	62.0 (53.4-72.1)	29.6 (25.7-34.1)	19.3 (16.8-22.1)	0.40-0.43	79.3 (66.8-94.2)	32.9 (28.9-37.5)	18.5 (11.5-29.8)
0.24-0.29	156.9 (145.2-169.6)	41.9 (37.5-46.7)	30.1 (23.9-37.9)	0.23-0.29	181.4 (177.3-185.7)	46.6 (39.8-54.5)	40.4 (32.5-50.1)
0.18-0.23	139.4 (129.8-149.7)	28.1 (24.4-32.3)	14.7 (12.6-17.3)	0.18-0.21	165.4 (134.6-203.2)	32.2 (27.4-37.9)	19.6 (14.9-25.6)

ACARTIA GRANI ♂

FERRIS-WHEEL 0.2rpm			GRID 20 str min^{-1}		
C	F	I	C	F	I
2.00-2.29	7.0 (4.8-10.3)	15.0 (10.3-21.8)	1.76-2.04	11.5 (8.6-15.4)	21.7 (16.7-28.1)
0.27-0.31	26.2 (17.7-38.9)	7.7 (5.4-11.2)	0.24-0.29	54.2 (41.2-71.3)	14.2 (11.0-18.2)
0.25-0.27	24.3 (17.3-34.1)	6.3 (4.8-8.3)	0.18-0.22	39.4 (25.8-60.3)	7.8 (4.1-14.8)

Feeding and egg production under turbulent conditions

Geometric means and 95% confidence intervals for clearance, ingestion and egg production rates under calm (Ferris-Wheel rotating at 0.2 rpm) and turbulent (Oscillating grid at 9, 19 or 20 str min^{-1}) conditions for all three species studied are summarized in Table 3.1, 3.2 and 3.3. In general, mean values of clearance and ingestion were higher under turbulence, except for *A. clausi* experiments at 20 str min^{-1}. Egg production mean rates tended to be lower under turbulence for *A. clausi*, and did not differ clearly for the other two species.

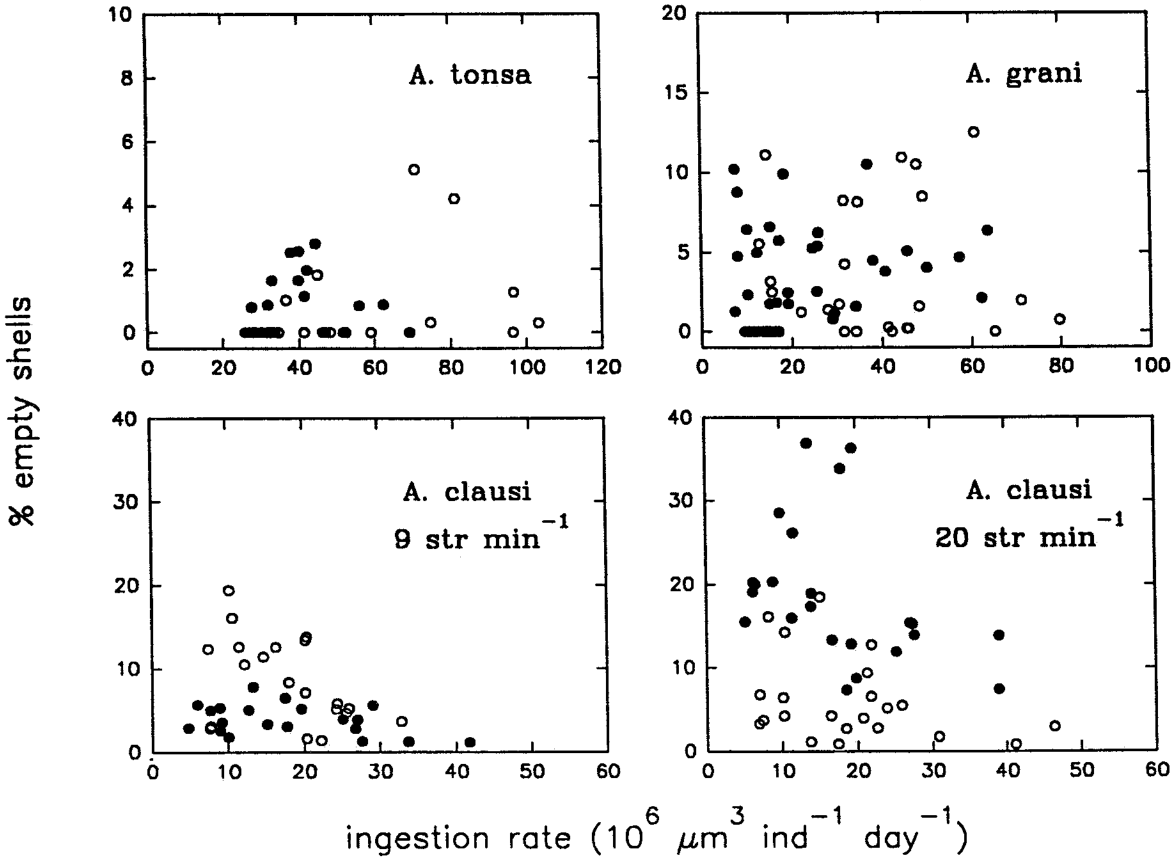


Figure 3.3. Egg cannibalism (% empty shells) in relation to ingestion rate (I) for the species studied. Filled circles: non-turbulence (Ferris-Wheel), Hollow circles: turbulence (Grid).

TABLE 3.2 - Geometric means ± 95% CI (in parenthesis) for clearance (F), ingestion (I) and egg production (E) rates of A. grani ♀ under calm (Ferris-Wheel 0.2rpm) and turbulent (Grid) conditions. The range of average food concentrations (C) for each experiment is also represented. Units as in Figure 3.1.

FERRIS-WHEEL 0.2rpm				GRID 20 str min^{-1}			
C	F	I	E	C	F	I	E
1.77-1.88	24.0 (11.7-49.1)	44.1 (22.0-88.3)	30.4 (24.3-37.9)	1.69-1.80	30.2 (16.3-55.9)	52.1 (28.0-97.2)	26.0 (20.4-33.1)
1.76-1.90	20.0 (12.9-31.1)	36.4 (23.8-55.7)	24.8 (20.9-29.3)	1.62-1.80	23.1 (17.2-31.0)	39.5 (25.8-54.8)	22.6 (17.9-28.4)
1.25-1.36	26.5 (10.9-64.3)	34.5 (14.9-79.5)	28.3 (16.8-47.7)	1.14-1.18	45.8 (28.7-73.2)	53.3 (33.8-84.0)	33.6 (28.3-40.0)
1.19-1.37	19.9 (10.3-38.2)	25.8 (14.5-45.9)	40.5 (31.7-51.8)	1.00-1.06	41.5 (32.1-53.7)	43.1 (33.6-55.1)	37.7 (34.0-41.9)
0.33-0.44	34.7 (26.4-45.6)	13.3 (8.8-20.1)	6.8 (5.9-7.9)	0.24-0.31	49.0 (36.1-53.7)	12.7 (10.4-15.5)	4.6 (2.9-7.3)
0.33-0.37	30.3 (18.9-48.6)	10.5 (6.1-18.0)	8.7 (7.0-10.7)	0.22-0.28	58.3 (46.2-73.5)	14.1 (10.4-19.1)	8.3 (6.5-10.6)
0.26-0.38	41.4 (27.4-62.6)	13.4 (9.0-19.9)	4.2 (3.1-5.7)	0.19-0.23	60.5 (45.0-81.2)	13.0 (10.4-16.3)	3.1 (1.8-5.3)
0.26-0.29	69.6 (52.7-91.9)	18.9 (13.2-27.1)	11.2 (9.3-13.4)	0.20-0.23	131.4 (110.5-156.1)	27.8 (21.5-35.9)	11.0 (7.5-16.1)
0.15-0.18	50.5 (41.6-61.2)	8.5 (6.9-10.4)	5.2 (4.1-6.5)	0.10-0.18	128.7 (117.3-141.1)	14.5 (12.8-16.5)	7.5 (5.0-11.2)

TABLE 3.3 - Geometric means ± 95% CI (in parenthesis) for clearance (F), ingestion (I) and egg production (E) rates of *A. clausi* under calm (Ferris-Wheel 0.2 rpm) and turbulent (Grid) conditions. The range of average food concentrations (C) for each experiment is also represented. Units as in Figure 3.1.

FERRIS-WHEEL 0.2rpm				GRID 9 str min^{-1}			
C	F	I	E	C	F	I	E
2.05-2.15	11.9 (9.3-15.3)	24.9 (19.0-32.7)	44.0 (38.6-50.2)	1.90-1.94	11.8 (9.6-14.4)	22.5 (18.5-27.3)	36.3 (30.8-42.9)
1.52-1.57	20.8 (15.0-28.9)	31.9 (23.0-44.3)	54.9 (38.7-77.9)	1.36-1.49	15.9 (9.8-25.8)	22.7 (15.0-43.3)	36.3 (29.4-44.8)
0.57-0.70	24.7 (20.6-29.7)	15.8 (12.7-19.6)	25.1 (19.6-32.1)	0.55-0.57	38.3 (27.2-53.8)	21.4 (15.4-29.7)	19.0 (15.8-23.0)
0.38-0.46	18.8 (9.8-35.8)	8.0 (4.2-15.3)	19.6 (16.0-23.9)	0.28-0.32	33.0 (17.8-61.2)	10.1 (6.0-17.1)	14.7 (10.6-20.4)
0.32-0.37	24.7 (17.8-34.3)	8.4 (5.8-12.0)	15.7 (13.4-18.3)	0.26-0.31	34.2 (23.9-49.0)	9.8 (7.2-13.3)	10.2 (8.1-12.7)

FERRIS-WHEEL 0.2rpm				GRID 20 str min^{-1}			
C	F	I	E	C	F	I	E
1.64-1.72	17.3 (9.5-31.5)	29.0 (16.3-51.7)	40.6 (33.0-50.0)	1.62-1.69	19.4 (4.9-76.1)	32.2 (8.6-121.1)	49.7 (39.1-63.1)
1.20-1.34	18.2 (13.2-25.1)	23.1 (17.0-31.4)	24.6 (21.1-28.6)	1.24-1.31	18.1 (13.1-25.0)	23.0 (16.4-32.3)	27.1 (18.4-40.1)
0.71-0.79	24.5 (11.7-51.5)	18.6 (7.9-43.9)	24.6 (16.6-36.4)	0.79-0.81	24.5 (10.9-55.1)	19.7 (8.9-43.8)	22.3 (18.1-24.4)
0.44-0.46	33.0 (19.7-55.4)	14.8 (9.1-24.1)	34.4 (26.0-45.7)	0.45-0.47	43.6 (31.3-60.6)	20.1 (14.7-27.7)	29.7 (26.9-32.7)
0.28-0.31	37.8 (28.7-49.8)	11.3 (8.5-15.2)	21.1 (17.7-25.3)	0.32-0.37	29.43 (16.5-52.5)	10.5 (6.0-18.4)	15.5 (10.4-23.2)
0.16-0.18	34.6 (27.8-43.1)	6.1 (5.1-7.1)	17.4 (34.5-58.1)	0.22-0.24	36.2 (28.7-45.6)	8.2 (6.3-10.9)	15.1 (11.6-19.5)

TABLE 3.4 - Mean values and range (in parenthesis) for the grazing efficiency index (G) of *A. grani* ♀ and *A. clausi* second series (conducted at 20 str min^{-1}).

ACARTIA GRANI ♀		ACARTIA CLAUSI 20 str min^{-1}	
FERRIS-WHEEL	GRID	FERRIS-WHEEL	GRID
32.2 (19.3-42.8)	32.9 (18.6-52.1)	26.4 (14.0-35.9)	27.8 (12.5-41.1)
26.6 (17.5-33.2)	25.3 (18.4-31.5)	26.6 (19.3-34.1)	22.5 (20.8-26.5)
37.3 (18.3-59.4)	52.2 (39.0-69.0)	25.5 (20.9-30.0)	21.1 (15.0-24.7)
22.9 (13.1-27.9)	50.8 (39.6-56.0)	42.9 (23.1-53.2)	48.7 (35.8-58.4)
41.6 (33.1-49.8)	54.7 (42.1-64.8)	50.9 (42.4-56.1)	37.4 (22.5-54.3)
33.9 (24.0-48.8)	51.8 (43.5-60.6)	45.3 (34.5-58.1)	42.3 (35.4-53.4)
50.5 (38.8-70.6)	67.5 (54.5-81.9)		
83.6 (71.3-106.)	130.0 (123.9-134.3)		
64.2 (56.2-73.7)	124.0 (114.0-137.9)		

In Tables 3.4 and 3.5 we represent mean values and ranges for grazing indexes. Grazing efficiency indexes for *A. tonsa* tended significantly to be higher under turbulence (Mann-Whitney two-tailed test, $P<0.017$). The same was observed for *A. grani* (males and females) in experiments run at food concentrations lower than 1.5 mm^{3}l^{-1} (respectively $P<0.005$ and $P<0.001$), but at food concentrations above this no difference was found on females' activity. Males (only one experiment) showed values that tended to be higher under turbulence even at high food concentration, although weakly significant (two-tailed test, $P<0.061$).

TABLE 3.5 - Mean values and range (in parenthesis) for the grazing efficiency index (G) of A. tonsa , A. grani ♂ and A. clausi first series (conducted at 9 str min^{-1}).

ACARTIA TONSA		ACARTIA CLAUSI 9 str min^{-1}		ACARTIA GRANI ♂	
FERRIS-WHEEL	GRID	FERRIS-WHEEL	GRID	FERRIS-WHEEL	GRID
45.0 (35.0-60.0)	39.3 (29.8-56.9)	10.5 (7.7-13.1)	9.6 (8.1-11.9)	6.6 (5.3-8.6)	10.4 (7.9-12.8)
40.8 (36.0-45.6)	82.8 (81.6-84.0)	13.6 (13.3-19.2)	16.2 (11.0-24.8)	24.2 (17.5-33.0)	38.1 (29.8-50.2)
55.4 (40.6-79.0)	130.9 (91.9-150.5)	29.8 (21.4-37.2)	47.3 (28.8-63.1)	25.1 (20.1-27.1)	35.7 (31.0-40.5)
53.6 (47.4-61.9)	70.6 (60.0-78.0)	22.1 (11.8-29.8)	38.7 (26.0-54.8)		
139.1 (128.1-156.0)	162.5 (156.2-176.2)	27.1 (20.3-35.6)	40.6 (28.0-49.7)		
141.6 (134.4-151.2)	181.8 (153.6-201.6)				

Regarding to *A. clausi* experiments, we differentiate between the two series conducted at different levels of turbulence. For the first series (Grid 9 str min^{-1}), the trend is similar to that observed for the other two species mentioned above. At food concentrations lower than 1-1.5 mm^{3}l^{-1} (the saturating ingestion point), turbulence did significantly tend to increase grazing efficiency (two-tailed test, $P < 0.006$), but this difference disappeared at higher concentrations. The experiments performed at 20 str min^{-1} for this species showed a different pattern of behaviour, with no significant differences throughout the range of food concentrations tested.

The quotients E/I (pooled data for all food concentrations tested) were significantly lower under turbulence for *A. clausi* (first series) and *A. grani* (Mann-Whitney two-tailed test, $P < 0.007$ and 0.002 respectively), but no difference was found for *A. tonsa* ($P < 0.523$). E/I values for the second series of experiments with *A. clausi* also tended to be lower, but significance was weak (Mann-Whitney one-tailed test $P < 0.050$). For this series, variability was much higher under calm conditions than under turbulence. As non-parametric tests are less sensitive to small differences, we also performed for this data a modified t-Student test for two samples with unequal variances (Sokal & Rohlf 1969). This test stressed more the statistical differences (one-tailed t-Student modified test, $0.025 < P < 0.027$).

The percentage of empty shells found also exhibited different trends. *A. tonsa* did not show any significant difference between turbulent and non-turbulent conditions. For *A. grani*, egg cannibalism tended to be lower under turbulence (Mann-Whitney two-tailed test $P < 0.032$). Regarding to *A. clausi*, egg cannibalism showed a remarkable different pattern in relation to the level of turbulence provided. For experiments at low turbulence (first series, 9 str min^{-1}), the percentage of empty shells tended to be higher under turbulence (two-tailed $P < 0.004$), reaching about 20% at low food ingestions. At the highest level of turbulence (second series, 20 str min^{-1}), egg cannibalism was significantly depressed in relation to non-turbulent conditions (two-tailed $P < 0.001$).

Discussion

Feeding on *T. weissflogii*

Rothschild & Osborn (1988) and Evans (1989) proposed the enhancement of ingestion rates of plankton in the field through the increase on encounter probability between predator and prey by small-scale turbulence. Recent videocinematographic observations by Costello et al. (1990) and Marrasé et al. (1990) provided first experimental evidence supporting this theory, but their work could not verify whether or not turbulence affects ingestion rates of copepods. Field work reported by Sundby & Fossum (1990) also provided indirect evidence of enhanced feeding as function of wind stress in cod larvae, but they could neither determine ingestion rates from their study.

Our experiments, performed over a wide range of food concentrations, indicate that the turbulence-induced enhancement of ingestion is food concentration-dependent, e.g. it is functional at food concentrations below the saturating ingestion point; afterwards any increment on encounter probability does not improve feeding efficiency of the zooplankter. Below the saturating-ingestion food level, the apparent increase by turbulence in food (prey) density for the zooplankter's environment perception induces a higher ingestion rate. This can produce a lack of correlation between ingestion rates and prey densities in field studies and (underestimated) rates determined in the laboratory (MacKenzie et al. 1990). At higher food concentrations, this apparent increase cannot be used efficiently by the zooplankter. However, our data on males of *A. grani*, showed increased ingestion under turbulence even at high food concentration. This could be due to a different feeding behaviour pattern in relation to food concentration, but the small number of experiments performed did not allow us to describe it. In that case, zooplankters with a non-saturating ingestion feeding behaviour pattern could be favoured by the effects of small-scale turbulence even at high food concentrations.

The different response of *A. clausi* fed on *T. weissflogii* to the two intensities of turbulence tested suggests two concomitant effects of small-scale turbulence does act upon the zooplankter: the increase on encounter probability that can enhance ingestion at moderate levels of turbulence, and on the other hand a detrimental effect on ingestion above a threshold turbulence intensity. This would explain why in the series performed at moderate intensities of turbulence (9 str min^{-1}) ingestion of *T. weissflogii* at low food concentrations was enhanced, while at higher intensities of turbulence this enhancing effect would be counteracted by the detrimental effect on feeding currents.

Egg cannibalism

Data on egg cannibalism show how predation on eggs can be sometimes considerable, even with abundant food. Differences among the species studied suggest a higher carnivorous behaviour by *A. grani* and *A. clausi* than *A. tonsa* in our experiments. However, the differences in egg cannibalism showed by the two populations of *A.*

clausi studied, suggest that feeding habits are quite variable and might depend on the copepods' feeding life history.

The egg cannibalism response of *A. clausi* to different levels of turbulence also reflexed the pattern exhibited when fed on *T. weissflogii*. While at 9 str min^{-1} egg predation was enhanced by turbulence in a similar way as herbivorous feeding behaviour does, at a higher intensity of turbulence (20 str min^{-1}) herbivorous feeding was not enhanced and, furthermore, egg cannibalism was depressed in comparison to the non-turbulence conditions. As suggested by Strickler (1985), the interference of turbulence motions on feeding currents would be more important for zooplankters with a long-distance perception feeding behaviour, e.g. egg cannibalism in our experiments probably would be more affected by turbulence than herbivorous feeding on small-sized food particles. Egg cannibalism exhibited by *A. grani* was also depressed under turbulence, while *A. tonsa* did not show any difference between conditions. These results indicate how small-scale turbulence can affect in different way feeding upon small-sized food (*T. weissflogii*) and large-sized food (eggs) in close related species, depending on the zooplankter performance.

Gross-growth efficiency

E/I quotients provide an estimator of gross-growth efficiency (efficiency in transforming ingested material into growth, Omori & Ikeda 1984). As we used the same cultured algae in our experiments, differences in E/I quotients between experimental conditions must be attributed to changes in metabolic requirements induced by turbulence. Thus, the lower values for *A. clausi* and *A. grani* under turbulent conditions suggest that a higher fraction of the energy budget went into metabolism. The second series of experiments performed on *A. clausi*, however, showed this difference less accentuated compared with the experiments performed at a lower turbulence intensity. We feel that this might be due to a saturation response of the zooplankter to turbulent motion, e.g. that increasing turbulence does not increase the response of the animal, as well as to the high variability on egg cannibalism found for this population under calm conditions, that could have led to an underestimation of egg production rates under calm conditions. Nevertheless, the results for these two species should be considered under the hypothesis proposed by Alcaraz et al. (1988, 1989) on mechanical stimulation of escape reactions under turbulence. The increased metabolism proposed by these authors would produce a lower gross-growth efficiency like that observed in our experiments.

The results for *A. tonsa* show a different behaviour under turbulence. In spite of having enhanced ingestion, E/I quotients under turbulence did not differ from those under calm conditions, even when intensity of turbulence in these experiments probably was higher than in all the other experiments performed due to the less coarse grid used. This suggests a weak behaviourial response of this copepod to the mechanical stimulation of small-scale turbulence (in the sense of Alcaraz et al. 1988). This could be in some way expectable when considering the tidal habitat for the population of *A. tonsa* studied, with a higher turbulent energy input than the Mediterranean semi-enclosed areas that inhabit the other two species studied.

Our study has shown some of the ways by which small-scale turbulence can affect copepod activity and behaviour. These results provide direct experimental evidence that small-scale turbulence can affect ingestion rates in zooplankton, and may support the mechanistic hypothesis of Rothschild & Osborn (1988) on encounter probability. But, as suggested previously by Strickler (1985) and Marrasé et al. (1990), feeding behaviour can also play an important role on its application. Moreover, changes in gross-growth efficiency as those observed in our experiments under turbulence could be responsible for part of the variability in structure and activity of copepod populations associated to hydrodynamical singularities in the field. Future laboratory work focused on other zooplankters coupled with "in situ" studies will confirm the relevance of small-scale turbulence in zooplankton communities. These studies will meet many of the recommendated future objectives for zooplankton ecology research in next decades (Marine Zooplankton Colloquium 1 1988).

RESUM

S'han estudiat el efectes de la turbulència de petita escala en les taxes d'ingestió i l'eficiència bruta de creixement (K_1) de copèpodes calanoides del grup congenèric *Acartia*. L'estudi s'ha endegat considerant la importància de la concentració de menjar i el propi hidrodinamisme de l'hàbitat com a moduladors de la resposta enfront de la turbulència de petita escala.

Les taxes d'ingestió d'algues (*Thalassiosira weissflogii*) en condicions de turbulència van augmentar respecte el control, sempre i quan la concentració de menjar fos menor que el punt de saturació de la ingestió. Això s'explica com a conseqüència per una banda d'un increment en la probabilitat d'encontre de partícules alimentícies, i per d'altra banda a l'efecte modulador del comportament de l'individu, amb resposta de saturació a la concentració de menjar.

Experiments amb *A. clausi* duts a terme a dos intensitats de turbulència, però, indiquen un canvi en aquesta resposta, afavoridora de la ingestió a intensitats baixes de turbulència i interferidora (negativament) a intensitats relativament més elevades.

L'eficiència bruta de creixement (quocient producció d'ous/ingestió) de les distintes espècies d'*Acartia* estudiades va exhibir diferentes pautes de resposta a la turbulència en relació a l'hidrodinamisme del seu hàbitat. *A. tonsa*, originària de zones estuàriques sotmeses a marees del Sud-Est dels USA, no va presentar canvis en el valor de K_1; *A. clausi* and *A. grani* provinents de zones semiconfinades de la Mediterrània Nord-Occidental tingueren una menor eficiència bruta de creixement en condicions de turbulència.

Les dades obtingudes relatives a canibalisme d'ous indiquen que la turbulència de petita escala afecta de mode diferent l'alimentació de tipus suspensívor (partícules de mida relativament petita) de l'alimentació de tipus depredador, essent aquesta darrera més sensible als efectes negatius.

CAPITOL IV

EFECTES DE LA TURBULENCIA EN EL COMPORTAMENT DE COPEPODES CALANOIDES

CAPITOL VI

EFECTES DE LA TURBULENCIA EN EL COMPORTAMENT DE COPEPODES CALANOIDES

4.1. Increased encounter rates between the calanoid copepod *Centropages hamatus* ♀ and the tintinnid *Favella spp.* induced by small-scale turbulence

4.2. Brief note on the effects of small-scale turbulence in the behaviour of *Centropages typicus* ♀

4.3. Free-swimming behaviour of *Acartia clausi* under turbulent water movement

4.1. INCREASED ENCOUNTER RATES BETWEEN THE CALANOID COPEPOD *CENTROPAGES HAMATUS* ♀ AND THE TINTINNID *FAVELLA SPP.* INDUCED BY SMALL-SCALE TURBULENCE.

Introduction

Recent theoretical work of Rothschild & Osborn (1988) and Evans (1989) proposed an increase of encounter rate between predator and prey through the effect of small-scale turbulent water motion. Experimental evidence from videocinematographic work (Costello et al. 1990, Marrasé et al. 1990) have confirmed this enhancing of encounter rates between calanoid copepods and small-sized algae under a quantified level of turbulence. Posterior experimental work (Saiz et al. submitted) have shown that this enhancement of encounters can be not always coupled with higher ingestion rates. This detrimental effect of turbulence on ingestion could be more important when copepods feed on large immobile preys (egg cannibalism). Here we use a similar set-up to that used by Costello et al. (1990) and Marrasé et al. (1990) to confirm the hypothesis of Rothschild & Osborn for calanoid copepods and large-sized, motile preys.

Material and methods

Copepods were collected from Buzzards Bay (Woods Hole, USA) by short horizontal surface net tows, diluted with "in situ" sea water and transported to the laboratory. *Centropages hamatus* ♀ were glued to a thin hair and kept in "in situ" water for an acclimatization period of about 6 hours. Two hours prior to the start of the experiment the individual was placed in a small aquarium filled with filtered sea water. Cultures of the loricated tintinnid *Favella spp.* (kindly supplied by Dr. D. Stoecker) were employed as food. The tintinnids were in a suspension of *Heterocapsa triquetra* as their own food. Temperature was 20±1°C. The experimental vessel had a volume of ca 100 ml. Turbulence was generated by a vibrating rod as described in Costello et al. (1990). The video equipment and set-up was the same as that described in Strickler (1985) and Costello et al. (1990).

The experimental design consisted of the video recording of the encounter rate corresponding to three consecutive experimental conditions: "No turbulence and low food concentration" (3.6 ciliates per ml), "No turbulence and high food concentration" (6.6 ciliates per ml), and "Turbulence and low food concentration" (2.8 ciliates per ml). Between the second and third period the zooplankter was kept in filtered sea water for 20 minutes. No food concentration acclimatization was conducted for any of the conditions.

Direct enumeration of encounter rate was based on the description of an encounter rate area (Strickler 1985, Costello et al. 1990) surrounding the feeding appendages of the tethered individual. *Favella* organisms entering the encounter area were tabulated in 1000 frame (33.3 seconds) bins. This resulted in the analysis of 114 1000-frame bins for "Calm, low concentration", 113 for "Turbulent, low concentration" and 108 for "Calm, high concentration".

Results and discussion

The average number of encounters in a 1000-frame period (33.3 seconds) were 0.5 for "Calm, low food concentration", 1.1±0.3 SE for "Turbulence, low food concentration" and 1.1±0.3 SE for "Calm, high food concentration". Counting error for "Calm, low food concentration" appeared to be null. Small-scale turbulence significantly increased encounter rates at low food concentration (Mann-Whitney two-tailed test, $P<0.001$). However, no significant difference was found between "Turbulence, low food" and

"Calm, high food" conditions. Data were classified according to the number of encounters accomplished for each 1000-frame period (0, 1, 2, 3, 4 and ≥5 encounters per period). The relative frequency of encounter events for each class and each experimental condition is represented in Figure 4.1.1. Events with low encounters are more frequent under "Calm, low food concentration", while the other two experimental conditions had the similar effect of increasing the frequency of encounter.

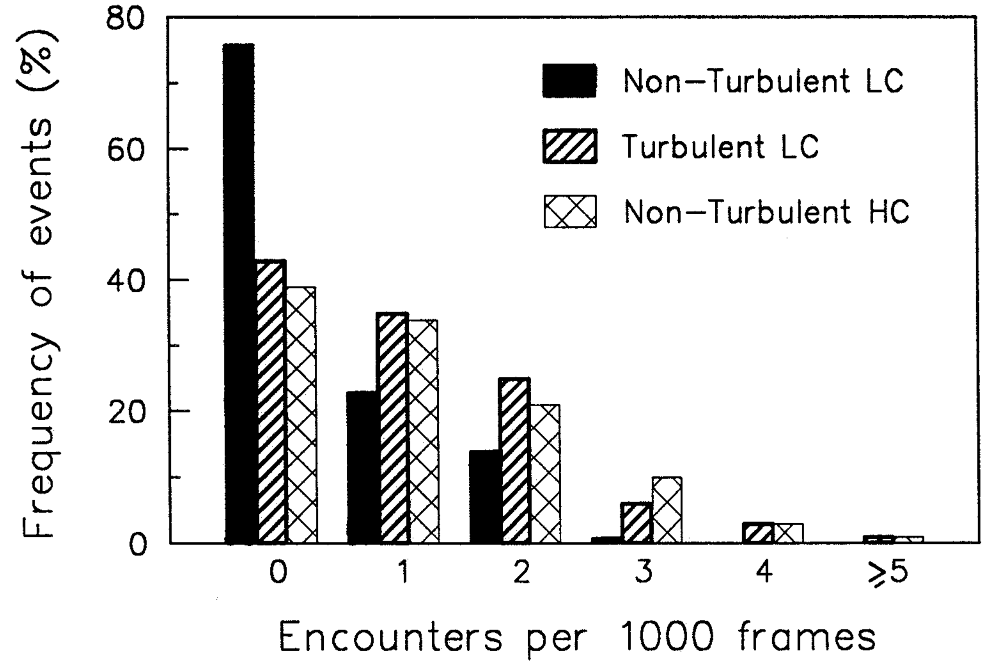


Fig. 4.1.1. Encounter rates for the different experimental conditions, expressed as frequency of events on 1000-frames bins.

Costello et al. (1990) and Marrasé et al. (1990) found that a low *Gymnodinium* concentration (70 cells ml^{-1}) under turbulence and a 5-times higher concentration (350 cells ml^{-1}) under non-turbulent conditions resulted in similar encounter rates at turbulent dissipation energy rates ranging from 0.15 to 0.05 cm^2 sec^{-3}. In our experiment prey concentration for the "Calm, high concentration" condition was only 2.4-times higher than for the "Turbulence, low concentration" one. Thus, it seems reasonable that to obtain a similar encounter rate in both conditions the intensity of turbulence in our experiments, although we did not quantify it, should be lower than in those reported in Marrasé et al. (1990). Differences in prey swimming velocity could theoretically account for this (Rothschild & Osborn 1988), although for the small velocities assumed for *Gymnodinium*-like dinoflagellates (i.e. *Gyrodinium* swim speed ranges from 30 to 360 μm sec^{-1}, Bauerfeind et al. 1986; *Gymnodinium nelsoni* swims at 1.0±0.07 SE, E. Saiz unpub. data) and *Favella* (about 800 μm sec^{-1}, Stoecker & Egloff 1987) these differences probably are overbalanced by turbulent motion in our experiment (Rothschild & Osborn 1988).

In any case, our data showed a significant increase in encounter rates between calanoid copepods and loricated ciliates, in a similar fashion to the experiments of Costello et al. (1990) and Marrasé et al. (1990) with copepods and algae. The restraint of the copepod certainly influenced the absolute encounter values, but comparisons for the different conditions are allowed. Feeding of *C. hamatus* on large-sized prey (*Favella*) probably induces a shift to raptorial foraging behavior (Tiselius & Jonsson 1990). In our experiments we did not consider either behavioral aspects of the feeding of *C. hamatus* or the efficacy of feeding currents under turbulence (Marrasé et al. 1990). Saiz et al. (submitted) reported changes in predatory behaviour (egg cannibalism) of *Acartia* under turbulence conditions, depending on species-specific performance and intensity of turbulence. These authors suggested that turbulent water motion could interfere with the mechanosensorial perception of large immobile preys. In the case of motile preys, such as ciliates, turbulence could also affect predator detection by preys, favouring prey capture. Further experiments should consider how turbulence affects differently the predatory behavior of copepods fed on large-sized prey compared to small-sized prey, and should contemplate also the influence of the motility of large preys in this response.

RESUM

S'estudia videocinematogràficament la taxa d'encontre entre copèpodes calanoides i ciliats tintínids. La taxa d'encontre en condicions de turbulència és unes 2.8 vegades superior respecte el control (condicions de calma). Aquest increment degut a la turbulència és comparable a l'increment en la taxa d'encontre observat en augmentar la concentració de preses en condicions de calma (no turbulència). Aquest resultat concorda amb estudis similars realitzats amb fitoplàncton (Costello et al. 1990, Marrasé et al. 1990) i amb estudis propis (Saiz et al. submitted) relatius a la ingestió d'ous en *Acartia*, confirmant la hipòtesi de Rothschild i Osborn (1988) relativa a probabilitat d'encontre i turbulència.

4.2. BRIEF NOTE ON THE EFFECTS OF SMALL-SCALE TURBULENCE IN THE BEHAVIOUR OF *CENTROPAGES TYPICUS* ♀

Introduction

The role that turbulent water motion plays in the behavior and activity of zooplankton is presently under reconsideration (Strickler 1985, Alcaraz et al. 1988, Marine Zooplankton Colloquium I 198 , Marrasé et al. 1990). Theoretical models (Rothschild & Osborn 1988, Evans 1989), new field data (Sundby & Fossum 1990) and experimental evidence (Oviatt 1981, Alcaraz et al. 1988, Alcaraz et al. 1989, Costello et al. 1990, Marrasé et al. 1990) confirm the importance of small-scale turbulence in increasing encounter rates between predator and prey, and the behaviourial response of the zooplankter to the mechanical stimulation of turbulent water motion.

Although the use of high-speed cinematography (Alcaraz et al. 1980, Rosenberg 1980, Koehl & Strickler 1981) and videocinematography (Buskey 1984, Strickler 1985, Tiselius & Jonsson 1990, Jonsson & Tiselius 1990) in the last decade have shown the complexity and plasticity of zooplankton behaviour, its application to study the effects of small-scale turbulence on copepods has just been approached very recently. The videocinematographic work of Costello et al. (1990) and Marrasé et al. (1990) showed that small-scale turbulence induces a shift in the behavior of *Centropages hamatus*, with an increase in the frequency of escape reactions and in the time spent in slow swimming. Here we study the response of a closely related species, *Centropages typicus*, to small-scale turbulence and address the possible differences in their behavioral response.

Material and methods

Zooplankters were collected from Barcelona Harbour (Western Mediterranean, Spain) by means of short horizontal tows, and transported to the laboratory in 10-l buckets diluted with "in situ" sea water. Once in the laboratory, suspensions of *Prorocentrum micans* cultures were added to ensure a food supply and to acclimatize the copepods to the algae to be offered in the experiment.

The experimental set-up was similar to that of Costello et al. (1990) and Marrasé et al. (1990), using a vibrating small grid (0.5 cm mesh size) placed vertically in the experimental vessel to generate turbulence. No quantification of the intensity of turbulence was performed. Adult females of *Centropages typicus* were tethered to a thin hair and allowed to acclimatize to restrainment for 7-8 hours. 2-3 hours prior to the start of filming, a single tethered individual which appeared to be in good shape was placed in the experimental aquarium (10 cm x 5 cm x 5cm) filled with ca 200 ml filtered sea water. Temperature was 19±1°C. The experiment was performed in dim red light. Video recording was conducted with a SONY domestic video camera attached to a horizontally mounted stereomicroscope. The experimental design comprised two consecutive series:

i) Series in filtered sea water. The behaviour of the individual was recorded in three conditions: the initial, pre-turbulent 35 minutes in which water was kept undisturbed, the following, turbulent 35 minutes in which turbulence was generated; and the final, post-turbulent 35 minutes in which turbulence was switched off.

ii) Series in low food concentration. A suspension of *Prorocentrum micans* was added to the aquarium to achieve a concentration of 0.2 mm^3l^{-1}. The zooplankter was allowed to acclimatize for one hour to food; afterwards a series similar to the previous one was recorded.

Analyses were performed for each 35 minutes period on three 5-minute intervals (spaced 10 minutes apart), on a frame by frame basis (Fig. 4.2.1).

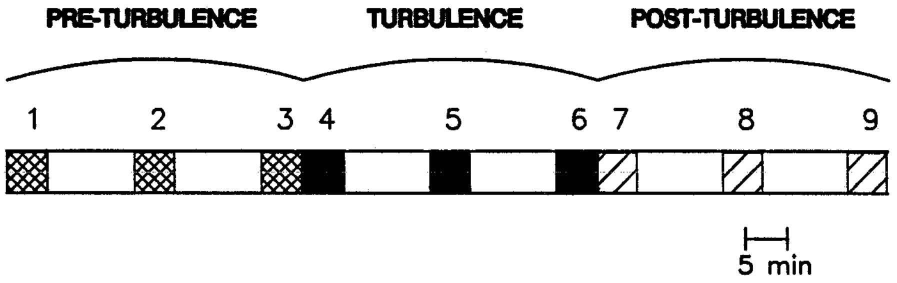


Figure 4.2.1. Time schedule of the experimental series performed. For each 35-minutes experimental period (Pre-turbulence, Turbulence and Post-turbulence), three 5-minute intervals (numbered in the figure) were analyzed.

We considered the behaviour of *Centropages typicus* according to the description by Cowles & Strickler 1983. Four main patterns of behaviour can be described :

- slow swimming or feeding bouts: it is the slow forward movement of the copepod while creating with its mouth parts a flow field to increase the amount of water passing through (feeding currents);

- grooming: quick movement of the first antennae between the mouth parts in order to clean them;

- fast swimming, escape reaction or jump: fast forward movement of the copepod driven by the first antennae and the thoracopods; and

- break: time spent with no movement.

Time spent in feeding bouts (slow swimming, SS), mean feeding bout length (duration of slow swimming events) and number of escape reactions (jumps) performed were counted for each interval analyzed. Error in determinations of time spent in SS and mean duration of SS events was low (variation coefficient of 4.9-6.9%).

Results and discussions

Table 4.2.1 shows time budgets and frequency of the behaviourial patterns considered. Our results agree well with the observations of Tiselius & Jonsson (1990) for free-swimming *C. typicus* individuals. In their experiments slow swimming accounted for about 58% of time, with a low frequency of jumping (0.8 per minute). In our study, during the preturbulent period *C. typicus* spent 34% of its time in slow swimming with a jump frequency of about 0.7 jumps per minute. There were no differences in time allocation for the series conducted in filtered sea water and low food concentration. This contrasts with the observations of Costello et al. (1990) for *C. hamatus*, in which filtered sea water reduced considerably the time allocated to feeding bouts (31% at low food concentration, 7% in filtered sea water). This could result from specific differences in feeding behavior at low food concentrations or to differences in short-time past feeding history (e.g. a hunger response of copepod in filtered sea water in our experiments).

In both series the frequency of escape reactions was higher during the turbulent period, especially during the first 20 minutes after the start of turbulence. This increase seems to be independent of the availability of food and be a consequence only of the stimulation due to turbulent motion. These results agree with the observations of Costello et al. (1990) and Marrasé et al. (1990) in *C. typicus*, and suggest that this increase in the frequency of escape reactions due to turbulent motion could be a general behavioral response in copepods. Alcaraz et al. (1988) proposed this mechanism to explain the higher concentration of ammonia in microcosms under turbulent motion, as escape reactions are supposed to require high metabolic expenditure (Strickler 1975, Morris et al. 1985, Alcaraz & Strickler 1988). However, our results

TABLE 4.2.1. Proportion of time spent in slow swimming (SS), average duration of each slow swimming event and number of escape reactions performed in each 5-minutes interval analyzed.

Filtered Sea Water

	Pre-Turbulence			Turbulence			Post-Turbulence		
Interval	1	2	3	4	5	6	7	8	9
% Time spent in SS	34	30	46	18	10	17	25	26	30
SS duration (sec)	1.7	1.2	2.9	0.7	0.4	0.5	0.8	1.1	1.5
Escape reactions	2	5	2	33	12	4	6	4	4

0.2 mm^3 l^{1} Prorocentrum micans

	Pre-Turbulence			Turbulence			Post-Turbulence		
Interval	1	2	3	4	5	6	7	8	9
% Time spent in SS	35	30	23	13	19	28	21	25	23
Average SS (sec)	1.6	1.3	1.2	0.7	0.8	1.5	0.9	1.0	1.1
Escape reactions	3	4	4	24	11	6	3	4	3

and those in *C. hamatus* indicate that under constant turbulent stimulation the behavioral response saturates. Thus, it seems that under natural conditions this pattern of behavior could be important only under successive turbulent energy inputs at the appropriate temporal and spatial scales. The intermittency and patchiness of small-scale turbulence could favour this (Spigel & Imberger 1987). The observations of Alcaraz et al. (1988) under constant turbulent input could also be explained by this behavioral response to turbulence (i.e. increased frequency of escape reactions) if the copepod species they worked with (*Acartia italica*) were more sensitive to small-scale turbulence. The higher proportion of antennal mechanorreceptors in copepods of the genus *Acartia* with respect to other genera (Barrientos 1980) would strengthen this hypothesis. Our data on *C. typicus* also showed a longer duration of fast swimming stimulation by turbulence with respect to the marked decrease after 3-4 minutes of the start of turbulence observed in *C. hamatus*.

The time spent in slow swimming tended to be lower during the turbulent period, but this trend was less conspicuous in the series performed at low food concentration (the last interval analyzed). The average duration of each slow swimming event (Table 4.2.1) was also lower during the turbulent period, although the series conducted at low food concentration also showed lesser differences.

These results contrast with those reported for *C. hamatus*, in which turbulence increased the time allocated to slow swimming, even after switching off turbulence. This suggests that turbulence could have negative advantages for the feeding of *C. typicus*. Tiselius & Jonsson (1990) reported feeding behaviour differences in free-swimming *C. typicus* and *C. hamatus* that might explain their differential response to turbulence. They both allocate to suspension feeding a similar proportion of time (58 and 41% respectively), but feeding bouts are shorter in *C. hamatus* (0.6 and 4.0 seconds respectively). *C. typicus* swims more slowly (1.9 and 7.2 mm per second respectively), so that flow velocities in its feeding currents are half the value for *C. hamatus* (4 and 8 mm per second respectively). Thus, it seems reasonable that the weaker feeding currents created by *C. typicus* would be more affected by turbulent water motion than those of *C. hamatus* (as suggested by Strickler 1985). Moreover, Marrasé et al. (1990) observed that turbulence decreased the efficacy of feeding currents to increase encounter rate in *C. hamatus*, but the higher time allocated to slow swimming resulted in higher effective encounter rates under turbulence at low food concentrations, while at higher food concentration no improvement was evident. This resulted in a 3 times increase in effective encounters under turbulence at low food levels. Although we don't have data about encounter rates, a presumably lower efficacy of feeding currents of *C. typicus* under turbulence in our experiments could explain why the copepod did not allocate more time (or even spent less time) to feeding bouts. This suggests a decreasing foraging when encounters and/or captures are low, similar to the functional response to food concentration described for copepods.

During the post-turbulent period the frequency of escape reactions was similar to the pre-turbulent period. With regarding to the slow swimming behaviour, no conspicuous differences were found during the pre- and post-turbulent period. This indicates a short-time adaptation of *C. typicus* to changes in the surrounding environment, in contrast with the behavior of *C. hamatus* which exhibited an enhanced foraging after the cessation of turbulence (Costello et al. 1990), that was attributed to a hysteresis-like effect with a residual encounter expectation level.

Any comparison of our results with those of Costello et al. (1990) must be considered cautiously, as dissimilar turbulent intensities between their experiment and ours could have induced a different behavioral response in the zooplankter (Saiz et al. submitted). Furthermore, our work, as that of Costello et al. (1990), lacked replication to take into account individual variability, although general patterns can be outlined. We must conclude that although some widespread responses of zooplankton to turbulence can be outlined (e.g. increase in the jump frequency), the influence of turbulent water motion in the predator-prey interaction can be more difficult to summarize, and specific behavior probably will account for most of the variability observed.

R E S U M

S'estudia videocinematogràficament el comportament del copèpode *Centropages typicus* en relació a la turbulència. L'anàlisi en condicions de restricció de moviments (fixació del copèpode en l'àrea en focus) indica canvis en la proporció de temps esmerçada fent corrents d'alimentació i llur durada en condicions de turbulència. La freqüència de reaccions d'escapada també augmenta en condicions de turbulència, però s'observa un esmorteïment en la resposta al llarg del temps.

Finalment es discuteixen aquests resultats en comparació amb l'estudi similar en *C. hamatus* dut a terme per Costello et al. (1990) i Marrasé et al. (1990).

4.3 FREE-SWIMMING BEHAVIOUR OF *ACARTIA CLAUSI* UNDER TURBULENT WATER MOVEMENT

Introduction

The importance of small-scale turbulence on zooplankton activity and dynamics has acquired new interest from recent results obtained by microcosm experiments (Perez et al. 1977, Nixon et al. 1979, Oviatt 1981, Alcaraz et al. 1988, 1989, Saiz & Alcaraz 1991), theoretical models (Rothschild & Osborn 1988, Evans 1989, Granata & Dickey 1991), videocinematographic observations (Costello et al. 1990, Marrasé et al. 1990) and field evidence (Kiφrboe et al. 1990, Sundby & Fossum 1990).

The study of Costello et al. (1990) and Marrasé et al. (1990) on restrained copepods of the species *Centropages hamatus* confirmed previous hypotheses derived from theoretical models (e.g. increase in encounter rates under turbulent motion, Strickler 1985, Rothschild & Osborn 1988, Evans 1989) and from microcosm evidence (e.g. increase of escape reaction frequency under turbulence, Alcaraz et al. 1988, 1989). But many questions arose from their study: what happens to copepods which are not tethered? how do the changes in feeding performance (i.e. time spent doing feeding appendage movements and efficacy of feeding currents) translate into ingestion rates? Does the increase in the frequency of escape reactions raise metabolism?

Very recent evidence from laboratory experiments have partially answered these questions. Experiments using incubation techniques (Saiz et al. submitted) have demonstrated how small-scale turbulence can affect the ingestion rates of copepods of the genus *Acartia*, depending on food concentration and its specific feeding behaviour. Predatory feeding behaviour has also been shown to be more sensitive to turbulence (Saiz et al. submitted), in agreement with the higher importance of mechanoreceptors in its performance (Paffenhöfer & Stearns 1988, Jonsson & Tiselius 1990). Direct measurements of excretion rates from incubation experiments have also confirmed the direct effect of small-scale turbulence on copepod metabolism (Saiz & Alcaraz submitted). However, we lack visual confirmation of the behaviourial performances (i.e. escape reactions, feeding bouts) responsible for the enhanced metabolic and feeding rates observed under turbulence in *Acartia*.

Furthermore, when studying the effects of turbulence on copepod behaviour, tethering (as in Costello et al. 1990 and Marrasé et al. 1990) could induce artifacts in the patterns exhibited (for example, tethering can induce an increase in the flow past a copepod, Tiselius & Jonsson 1990). So observations on free-swimming individuals are required to be able to compare our observations with experimental evidence and translate them into the field, especially in copepods as *Acartia* whose swimming behaviour is not associated to the generation of feeding currents and consists mainly of a high jumping frequency to keep the body in position.

The goal of this paper is to study the behaviour of free-swimming individuals of the copepod species *Acartia clausi* under non-turbulent (standing, calm) and turbulent conditions in relation to the reported evidence on the effects of small-scale turbulence in metabolism and feeding obtained by incubation experiments and microcosm approach. The experiments consisted of the video recording of free-swimming behaviourial response of copepods under turbulent and non-turbulent conditions, and further description of behaviour patterns and their frequency.

Methods

Experimental procedure

Copepods were captured by means of short oblique net tows (200 μm mesh size) in Barcelona Harbour and transported to the laboratory in buckets filled with in situ sea water. Once in the laboratory copepods were kept in the buckets for at least 36 hours to acclimatize to laboratory conditions. After this period, copepods were sorted and placed in 2l-jars filled with the "in situ" water. The jars were fixed on a Ferris-Wheel rotating at 0.2 rpm to keep algae in homogenous suspension. Every day suspensions of cultures of the algae *Thalassiosira weissflogii* and *Gymnodinium nelsoni* were added in excess (until the water became coloured) to ensure an "ad libitum" food supply.

Experiments began after the copepods were on the Ferris-Wheel for at least 24 hours, and were conducted during four consecutive days (one or two experiments each day). For each experiment, 90 *A. clausi* ♀ were placed in a 1-liter aquarium (9 cm x 9 cm x 12 cm) filled with 900 ml of a 0.7 $mm^3\ l^{-1}$ suspension of *G. nelsoni*. Experiments were conducted under two conditions: non-turbulence (standing, undisturbed or calm conditions) and turbulence. Picture 4.3.1 shows the experimental set-up. Turbulence was generated by a small Netlon grid (0.5 cm mesh size) placed vertically in the aquarium and attached to a vibrating rod. Five experiments were performed, two in calm conditions (Calm1 and Calm2) and three under turbulence (Turb1, Turb2 and Turb3). Experiments were conducted on alternating days (respectively Calm1, Turb1, Calm2,...), except for the experiments Calm2 and Turb2 that were conducted consecutively the same day with the same organisms. We switched the vibrating rod in the experiment Turb3 for a different one which provided a slower movement of water in comparison to the previous ones (see Observations). Video recording was performed with a SONY AVC-D5CE CCD video camera attached to a dissecting microscope mounted horizontally. Illumination was provided with a cold light source fitted with a infrared Kodak gelatine filter (Ref. 88A). The video camera used was highly sensitive to infrared light and allowed the experiment to be performed at dark. Temperature during experiment was 20±1°C. After being placed in the experimental vessel, the copepods were allowed to acclimatize for 60-90 minutes before recording started. Filming in all experiments began at approximately local sunset time. After the experiments, copepods exhibited normal behaviour and no damage.

Picture 4.3.1. Experimental set-up used for the experiments.

Data analysis

Only the first 15-20 minutes of each video tape were analyzed for experiments Calm1, Turb1, Turb2 and Turb3, on a frame by frame basis. For experiment Calm2 we extended the period to the first 55 minutes to get an analyzed time similar to that of Calm1. This was done to compensate for the fact that at the beginning of experiment Calm1 on several occasions copepods were tracked with the dissecting microscope and they appeared in focus more frequently.

The magnification (14X) and temporal resolution (25 frames s^{-1}, i.e 40 ms between frames) allowed us to distinguish three different patterns of behaviour:

1. Passive behaviour, with no movements. Corresponded to sinking periods under calm conditions or to a passive displacement under turbulence.

2. Feeding bouts, with movements of the feeding appendages and thoracopods, associated or not to a small jump (tilt) and reorientation of the body.

3. Jumps, escape reactions or fast swimming, about 2 body lengths long.

Only pictures in focus good enough to recognize these patterns were used. We realized, however, than in experiment Turb1 sometimes movement was so fast that feeding bouts not associated to tilts could have been underestimated in some pictures. To avoid the increased probability of observing passive behaviour under turbulence due to the mechanical advection of individuals, we considered for all experiments only sequences in which the copepod made at least one active pattern.

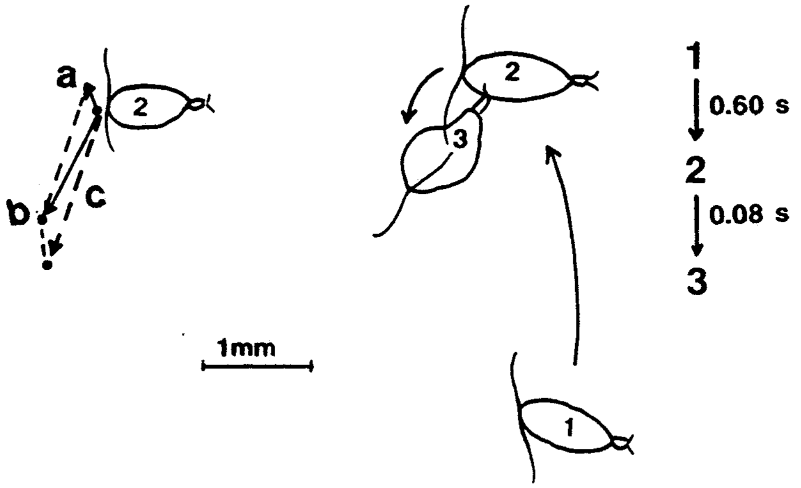


Fig. 4.3.1. Velocity correction for jumping behaviour under turbulence. "a" is the fluid advection component, "b" is the observed copepod velocity, and "c" is the corrected jumping speed.

Frequency of feeding bouts and jumps was counted for the sequences analyzed. Tracking successive copepod position on plastic sheets frame by frame, velocities for passive sinking and jumps were determined. Due to the advection component in the measured velocity under turbulent conditions, velocity vectors were drawn on the sheets assuming constant speed and the copepod jumping velocity was calculated (Figure 4.3.1). This forced us to consider for this analysis only sequences in which advection could be determined accurately (i.e. good focus). Although passive sinking provided a very small velocity component, velocities for calm conditions were also corrected.

Turbulence was quantified using the approach of Batchelor (1950) reported in Nixon et al. (1979), based on the relative motion of pairs of particles to estimate the rate of turbulent energy dissipation (ϵ). About 30 pairs of particles (algae) in focus were traced on a plastic sheet for 3-frame (120 ms) periods, and initial and final scalar distance between each pair, as well as their x and z components, were computed. ϵ was estimated using the relationship

$$\epsilon_i = [\ (|L_{i2}{}^2 - L_{i2}{}^2|/t)\ /\ (2t * (1+((1/3)*(L_{i1}{}^2/L_o{}^2))) * L_o{}^{2/3})\ ]^{3/2}$$

where L_o is the initial scalar distance between the pair of particles, L_{i1} is the initial distance between the particles projected on the i axis, L_{i2} is the distance between the floats after some time, t (120 ms), projected on the i axis.

Observations

In Table 4.3.1 the estimated ϵ values for each turbulence experiments are represented. No differences for x and z components were found (Wilcoxon rank test), confirming the isotropic turbulent field. Variability was large, probably due in part to the small number of pairs accounted and accuracy in measurements.

Table 4.3.1. Estimated turbulent energy dissipation rate (ϵ) for the experiments Turb1 and Turb3. X and Z components, as well as pooled data, are represented. ϵ is expressed in $mm^2\ s^{-3}$.

	Turb1			Turb3		
	ϵ_x	ϵ_z	Pooled ϵ	ϵ_x	ϵ_z	Pooled ϵ
n	33	33	66	33	33	66
geom. mean	$8.7\ 10^{-4}$	$9.6\ 10^{-4}$	$9.1\ 10^{-4}$	$3.2\ 10^{-4}$	$1.1\ 10^{-3}$	$5.9\ 10^{-4}$
95% CI (10^{-4})	21.4-3.5	23.8-3.9	17.0-4.9	8.0-1.3	27.2-4.4	11.3-3.1
min. value	$6.2\ 10^{-7}$	$7.5\ 10^{-7}$	$6.2\ 10^{-7}$	$2.1\ 10^{-6}$	$7.5\ 10^{-7}$	$7.5\ 10^{-7}$
max. value	0.031	0.046	0.046	0.019	0.046	0.046

No significant differences in dissipation rates between experiments Turb1 and Turb3 were found when comparing pooled data for both components (Mann-Whitney test).

In Table 4.3.2 we show the frequency of jumps and feeding bouts for each experiment, as well as the total effective time analyzed. Pooled data for experiments under calm and turbulent conditions is also shown. Comparison of the frequency of jumps in pooled data suggests a higher frequency under turbulent conditions, but when considering the variability between experiments for each condition the differences were not significant.

There were marked differences in the frequency of feeding bouts between experimental conditions (Table 4.3.2). Copepods under turbulence significantly increased the frequency of feeding bouts by about 2-3 times (two-tailed t-Student test $P<0.004$). Mean durations of suspension feeding bouts were similar under calm and turbulent conditions (Calm: 168±20 SE ms; Turbulence: 136±8 SE ms). Raptorial feeding events (small jumps or tilts) were shorter, although sometimes they were associated to suspension feeding-like movements and extended to longer durations (ranged from 80 to 280 ms).

Velocities for sinking, turbulent advection and jumps (after correction) are represented in Table 4.3.3. Sinking velocity was on average 1.2 mm s^{-1}. Water movement on turbulence experiments increased the velocity of displacement in passive behaviour (advection). Although there were no significant differences between Turb1 and Turb3 experiments for ϵ, advection velocity almost doubled in Turb1.

Table 4.3.2. Frequency of jumps and feeding bouts for the experiments conducted. Total effective time for the sequences analyzed and pooled data for both conditions are also represented.

Experiment	Effective time	Jumps min^{-1}	Feeding bouts min^{-1}
Calm1	95.4 sec	41	14
Turb1	47.6 sec	59	42
Calm2	77.3 sec	21	13
Turb2	76.7 sec	70	34
Turb3	78.4 sec	41	39
Pooled Calm	172.7 sec	32	14
Pooled Turb	202.7 sec	56	38

Table 4.3.3. Velocities (mm s^{-1}) for sinking, jumping and flow advection of *Acartia clausi* in experiments Calm1, Turb1 and Turb3.

	Calm1	Calm1	Turb1	Turb1	Turb3	Turb3
	Sinking	Jump	Flow	Jump	Flow	Jump
n	28	20	33	6	37	23
average	1.2	15.5	10.0	36.2	5.4	21.6
std error	0.1	0.8	0.8	4.2	0.3	1.7
min value	0.3	11.0	3.8	27.0	2.6	10.8
max value	2.3	23.0	19.3	54.0	8.7	45.5

Jump velocity under turbulent conditions was significantly higher than under calm conditions (two-tailed Mann-Whitney test $P < 0.008$). In experiment Turb3 mean jump velocity was ca 37% higher than in Calm1. Despite the small number of effective events recorded in Turb1, jump velocities were significantly higher than those for Turb3 (two-tailed test $P < 0.005$).

Conclusions

Turbulence estimates

Our values fell in the range of ϵ reported for natural systems (Table 4.3.4), especially for areas characterized by low turbulence (oceanic areas).

Table 4.3.4. Literature values for turbulent energy dissipation rates in different areas of the world (from Granata & Dickey 1990)

Region	ϵ (mm^2 s^{-3})
North Pacific	0.0001 to 1
Sargasso Sea	0.001 to 1
Scotia Shelf	0.1 to 1
Seymour Narrows	0.1 to 100

If we compare the estimated ϵ with the advection velocity of passive copepods under turbulence, we observe that the stirring mechanism in experiment Turb1 increased ca two times advection velocity with respect to Turb3, while this velocity difference had no significant effect on ϵ. This seems to be a consequence of the low accuracy in our measurements, especially in experiment Turb1 where the faster movement of particles difficulted to find sequences of pairs of particles in good focus. The velocity of the particles used in our estimates did not differ between conditions (Turb1: 2.6 mm s^{-1} ± 0.2 SE; Turb3: 2.7 mm s^{-1} ± 0.2 SE), but were considerably lower that the estimates of copepod advection velocity determined (see Table 4.3.3). This indicates that our determinations were probably biassed because only the slowest pairs of particles were plausibly taken into account.

Furthermore, our determinations must be interpreted as only partially representative of the turbulence conditions in the experiments, as copepods were free-swimming in 1l-vessel and the vibrating net was placed in one of the upper corners of the vessel. Our measurements comprised only a small square area (92.1 mm^2) in the center of the aquarium, and consequently spatial differences could be considerable. Marrasé et al. (1990), with a comparable set-up, reported one order of magnitude changes in ϵ throughout a small area of 63 mm^2.

We must conclude that our ϵ estimates are probably weak representative of the turbulence input in our experiments. Future studies will require to take into account the spatial variation in dissipation rates throughout the experimental vessel as well as the use of higher shutter-speed video cameras in order to obtain meaningful estimates.

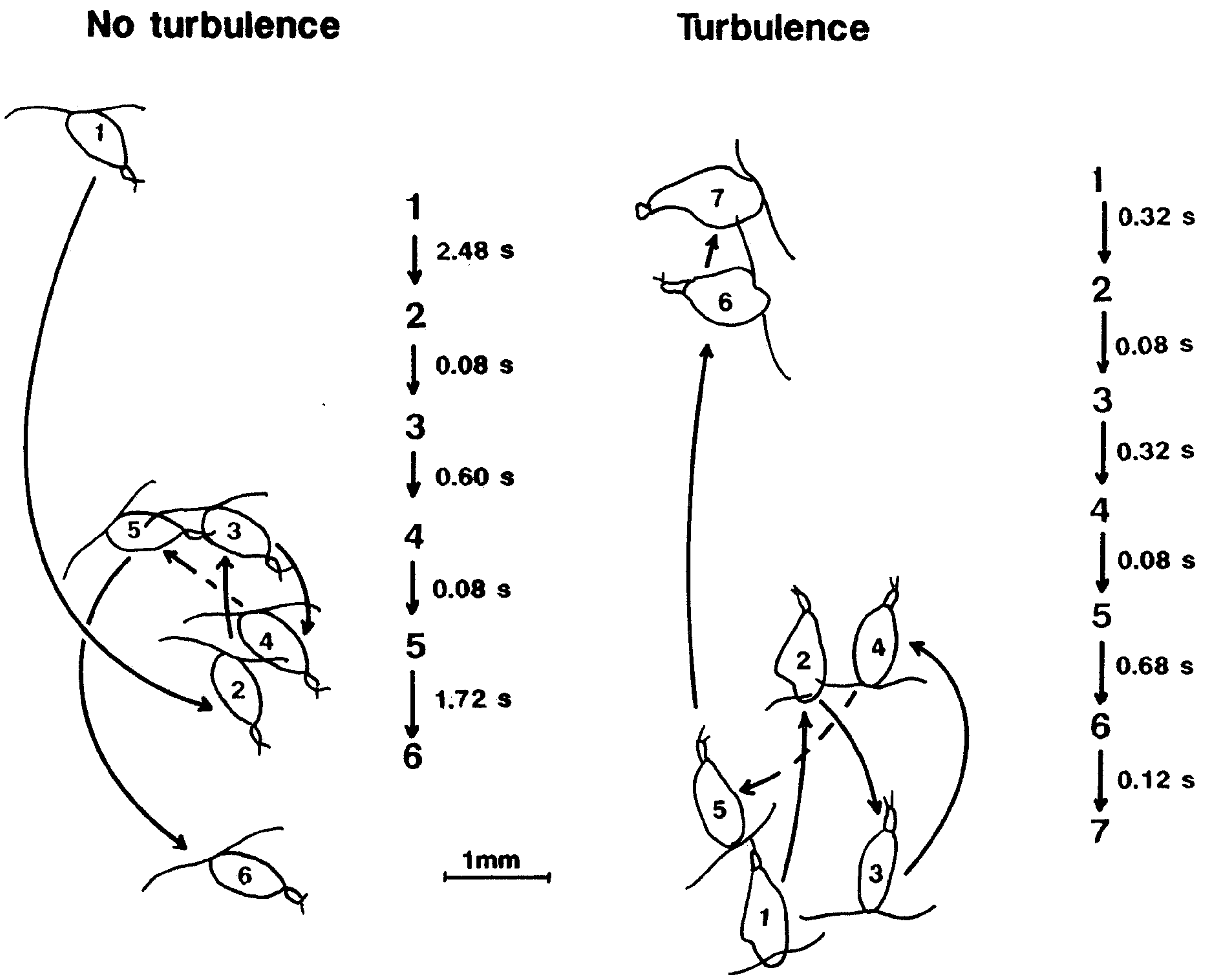
Acartia clausi behaviour under calm conditions

Figure 4.3.2 shows two representative drawings of free-swimming behaviour patterns of *A. clausi* under turbulence and calm conditions. The behaviour exhibited by *A. clausi* under calm conditions in our experiments agreed with previous reports for this and related species (Rosenberg 1980, Paffenhöfer & Stearns 1988, Jonsson & Tiselius 1990, Tiselius & Jonsson 1990). Instead of showing a slow swimming pattern (i.e. creation of feeding currents associated to a slow forward motion), *A. clausi* sinks passively through the water and displays frequent rapid upward bursts of swimming (99±4 SE ms of duration, which represented a distance covered of 1.5±0.06 SE mm) to maintain its depth position. This behaviour has been related to the search for motile relatively large preys (Paffenhofer & Stearns 1988, Jonsson & Tiselius 1990) according to the high abundance of first antenna mechanoreceptors owned by this genus (Barrientos 1980) and to the structure and performance of its mouthparts (Paffenhöfer & Stearns

19880. Passively sinking provokes a low rate of fluid deformation, probably below the critical value for prey avoidance (Haury et al. 1980, Tiselius & Jonsson 1990).

Mean sinking velocities were slightly higher than those reported for *A. clausi* (0.3 mm s^{-1}, Tiselius & Jonsson 1990) and A. tonsa (0.8 mm s^{-1}, Jonsson & Tiselius 1990). As described by Jonsson & Tiselius (1990), copepods usually started sinking with a horizontal body orientation but a torque tended to align the copepod along the vertical axis. We frequently observed individuals passively sinking head down, who jumped downward too. The frequency of jumps observed was very similar for those reported by the authors mentioned (*A. tonsa*: ca 60 min^{-1}; *A. clausi*: in low light 54 jumps min^{-1}, in high light 19 jumps min^{-1}). However, the low jump frequencies reported by Tiselius & Jonsson (1990) in their experiments performed at high light intensity are difficult to explain, as light induces an increase in metabolic activity associated with a higher swimming activity in copepods (Fernández 1977).

Copepods displayed two different patterns of feeding activity in our experiments. Suspension feeding-like behaviour involved short feeding bouts (168±20 SE ms of duration) with movements of mouthparts and thoracopods (Rosenberg 1980, Paffenhöfer & Stearns 1988). This motion generates a ventrally directed flow field (feeding currents) used by the copepod to gather food. Due to the magnification used in our experiments (14X) this flow field could not be discerned in our observations. The other pattern of behaviour exhibited was raptorial feeding; it was associated to reorientations of the body and short jumps (tilts) and movement of the mouthparts and thoracopods. There is obvious evidence that *Acartia* does not behave as a true suspension-feeder. It spends little time creating feeding currents (<30% time compared to 50-90% in true suspension-feeding calanoid copepods) (Gill 1987, Jonsson & Tiselius 1990, Tiselius & Jonsson 1990). *Acartia* can rapidly switch from one feeding behaviour to the other when food conditions (i.e. food size) change. From our observations we conclude that the size of *G. nelsoni* (ca 37 μm ESD) and its speed (1.0±0.05 SE mm s^{-1}) can induce both the suspension-like feeding and the switch to raptorial patterns.


No turbulence

Turbulence

Fig. 4.3.2. Two representative sequences of Acartia clausi free swimming behaviour under calm (left) and turbulence (right) conditions. Movements are sequentally numbered, and time intervals between them (in seconds) are represented in the vertical axis.

Behaviour under turbulence

Our results confirm the different behaviour exhibited by *Acartia* under turbulence. The increase in the frequency of feeding bouts suggests a higher feeding activity, although ingestion cannot be inferred from our experiments. So, our results must be interpreted according to available data on ingestion under turbulence for this species (Saiz et al. submitted). At food concentrations lower than the saturating ingestion point (between 1-1.5 $mm^3\ l^{-1}$), relatively low turbulence increased ingestion rates on small sized algae; higher intensities could produce a negative effect. Although turbulence also increases the encounter rates of copepods with motile large preys (Saiz, unpub. data), experimental evidence indicates that turbulence can affect negatively raptorial predation (lower egg cannibalism under turbulence, Saiz et al. submitted), probably in relation to the importance of mechanoperception in large prey detection. In our experiments, performed at food concentrations below the saturating ingestion point, *Acartia clausi* exhibited both behaviours, a suspension-feeding like and the raptorial one (small jumps or tilts). Consequently, the raptorial events observed under turbulence probably resulted in a reduced capture; the efficacy of ingestion for the suspension-feeding behaviour in our experiments cannot be presumed as the work of Saiz et al. (submitted) was qualitative and did not quantify turbulence intensity.

The frequency of jumps under turbulence tended to be higher, although differences were not significant. However, jump velocity was significantly higher under turbulence. This indicates that the proposed direct effects of turbulence on escape reactions could affect not only its frequency (Alcaraz et al. 1988, 1989, Costello et al. 1990, Marrasé et al. 1990) but also its strength, especially in copepods such as *Acartia* that ordinarily display a high frequency of jumps to keep in position. The increase in jumping velocity under turbulence is considerable (ca 37% in Turb2, ca 130% in Turb1). Its metabolic cost must be significantly high and, coupled with the increase in jumping frequency, would agree with the higher excretion rates reported previously for *Acartia* under turbulence (Saiz & Alcaraz, submitted). The videocinematographic study of Costello et al. (1990) and Marrasé et al. (1990) reported an increase in the frequency of escape reactions in tethered *Centropages hamatus* after the switch to turbulence, although a saturation effect was manifested after a few minutes. We did not consider changes in time in our experiments. However, the higher excretion rates of *Acartia* under turbulence in 24 hours incubations (Saiz & Alcaraz submitted) as well as the importance of its antennal mechanosensorial system suggest that this effect of turbulence in jumping should last longer.

The differences in jump speed between experiments Turb1 and Turb3 should be considered in relation to differences in the intensity of turbulence generated in both experiments. The higher fluid motion in Turb1 seems to increase the strength of jump events. Unfortunately, we failed to obtain good estimates of ϵ in our experiments to confirm this hypothesis.

The conclusions derived from our experiments are two-fold. First, our results confirm the influence of small-scale turbulence on copepod activity and behaviour. Feeding activity was modified in agreement with previous results from incubation techniques. Furthermore, turbulence seems to affect not only changes in the frequency of escape reactions (Alcaraz et al. 1988,1989, Costello et al. 1990, Marrasé et al. 1990) but also their strength. The metabolic expenditure that would represent this shift in behaviour would agree with previous hypotheses related to accelerated development in *Acartia* populations grown in microcosms with turbulence, as well as enhanced excretion rates reported under turbulence (Saiz & Alcaraz, submitted).

On the other hand, the difficulties in generating turbulence in laboratory experimental set-ups become evident in our experiments. Problems in achieving a homogeneous level of turbulence throughout all the experimental vessel make the comparison and extrapolation of results difficult. The use of video cameras with higher shutter speed would facilitate the accuracy of turbulence estimates.

Higher activity of zooplankton (feeding, excretion, fecundity) have frequently been reported in relation to hydrodynamic singularities (Kiφrboe & Johansen 1986, Peterson & Bellantoni 1986, Harris & Malej 1986, Kiφrboe et al. 1988, 1990), but most of variability observed has usually been attributed to indirect effects of turbulence in phytoplankton (i.e. changes in food size and quality, see Peterson & Bellantoni 1986, Kiφrboe et al. 1990). Direct effects are difficult to discern in the field and only the study of Sundby & Fossum (1990) has described a direct effect of turbulence relating feeding of cod larvae (gut contents) with wind stress. Our results, coupled with the other experimental evidence mentioned above, indicate that the importance of small-scale turbulence in activity and behaviour of copepods can be considerable. Through changes in their feeding activity and metabolism, small-scale turbulence can influence both biomass and structure of zooplankton communities, as well as their interaction with phytoplankton (Alcaraz et al. 1988, 1989, Saiz & Alcaraz 1991). The importance of copepods as a link between producers and higher trophic levels, specially in pelagic systems suitable to human exploitation (Cushing 1989), emphasizes the relevance of these studies. Future direct evidence from the field and experimental work will confirm the important role of small-scale turbulence on zooplankton activity and dynamics, as a decisive modulating factor of ecological relationships in pelagic ecosystems.

RESUM

S'ha estudiat el comportament en natació lliure del copèpode calanoide *Acartia clausi* en condicions de moviment turbulent de l'aigua. L'anàlisi videocinematogràfica mostrà diferències significatives en les pautes de comportament estudiades.

La freqüència de reaccions de salt (o d'escapada) va tendir a ser més alta en condicions de turbulència. Semblantment, la velocitat del salts també va ser significativament més alta en condicions de turbulència. L'activitat alimentícia (entesa com aquelles pautes de comportaments relacionades amb l'alimentació, però que no comporten necessàriament la ingestió) també presentà diferències significatives entre tractaments, essent més alta en condicions de turbulència.

Aquests resultats es discuteixen en funció dels estudis previs relatius a desenvolupament, metabolisme i alimentació de copèpodes calanoides. Encara que s'observa un augment en l'activitat alimentícia (pautes de comportament) en condicions de turbulència, l'evidència prèvia amb la mateixa espècie (Saiz et al. submitted) ens indica que la taxa d'ingestió dependrà de la intensitat de turbulència i que a nivells relativament alts podria inhibir-se la ingestió. En conseqüència, no pot inferir-se que la major activitat alimentícia observada comporti un augment en la ingestió en els nostres experiments. Pel que fa a l'augment en la velocitat de les reaccions d'escapada i a la tendència a augmentar la seva freqüència en condicions de turbulència, amb el conseqüent augment en la despesa energètica que representen, s'integrarien dins de la hipòtesi metabòlica descrita per Alcaraz et al. (1988, 1989), i corroboren les taxes d'excreció de N i P inorgànics més altes observades en copèpodes sotmesos a turbulència.

D'altra banda, s'ha assajat la quantificació dels coeficients de dissipació d'energia turbulenta en el sistema experimental emprat. Es discuteixen els problemes en les estimacions realitzades i la seva importància per a futurs experiments.

SINTESI
I
CONCLUSIONS

SINTESI

Al llarg d'aquest estudi s'ha demostrat la importància que la turbulència de petita escala pot tenir en l'activitat i comportament del zooplàncton marí, en la seva interacció amb el fitoplàncton i conseqüentment en l'estructura i dinàmica dels ecosistemes pelàgics. S'ha comprovat la validesa de les hipòtesis de treball inicials, i n'han sorgit de noves. L'estudi ha pretés observar des d'un punt de vista múltiple les possibles vies per les quals la turbulència pot afectar el zooplàncton, amb la finalitat de donar una visió general i complementària més que no pas de realitzar un estudi conscienciós sobre un sol d'aquests aspectes. La Fig. 1 completa les hipòtesis de treballs inicials amb els resultats presentats en aquesta Memòria, junt amb els d'altres autors fortament citats al llarg dels diversos capítols.

La recerca duta a terme amb microcosmos evidencia el paper modulador de la turbulència en la interacció entre consumidors i productors (Capítol I). Els nostres resultats demostren un accelerament de la dinàmica de les poblacions de copèpodes en condicions de turbulència, escurçant-se el temps de desenvolupament i produint-se canvis en les taxes de creixement. Aquest accelerament es podria interpretar, en la línia descrita per Alcaraz et al. (1989), com a conseqüència d'un increment general en el metabolisme, que comportaria una acceleració dels processos vitals i d'envelliment. Aquests efectes es tradueixen en canvis en la quantitat de biomassa suportada pel sistema. Mentre que en els primers experiments realitzats en microcosmos la biomassa de copèpodes (*A. italica*) i l'eficiència tròfica del sistema (quocient biomassa de consumidors/biomassa de productors) va ser menor en condicions de turbulència, l'experiment dut a terme amb *A. grani* donà el resultat oposat. Apart de la possible influència de diferències en el disseny experimental (p.e. aports periòdics de nutrients), els resultats són difícils de comparar donat que la intensitat de la turbulència generada possiblement va ésser més elevada en l'experiment realitzat amb *A. grani*. En qualsevol cas, la discrepància en la resposta indica tant possibles diferències específiques com possibles efectes distints depenents de la intensitat de turbulència.

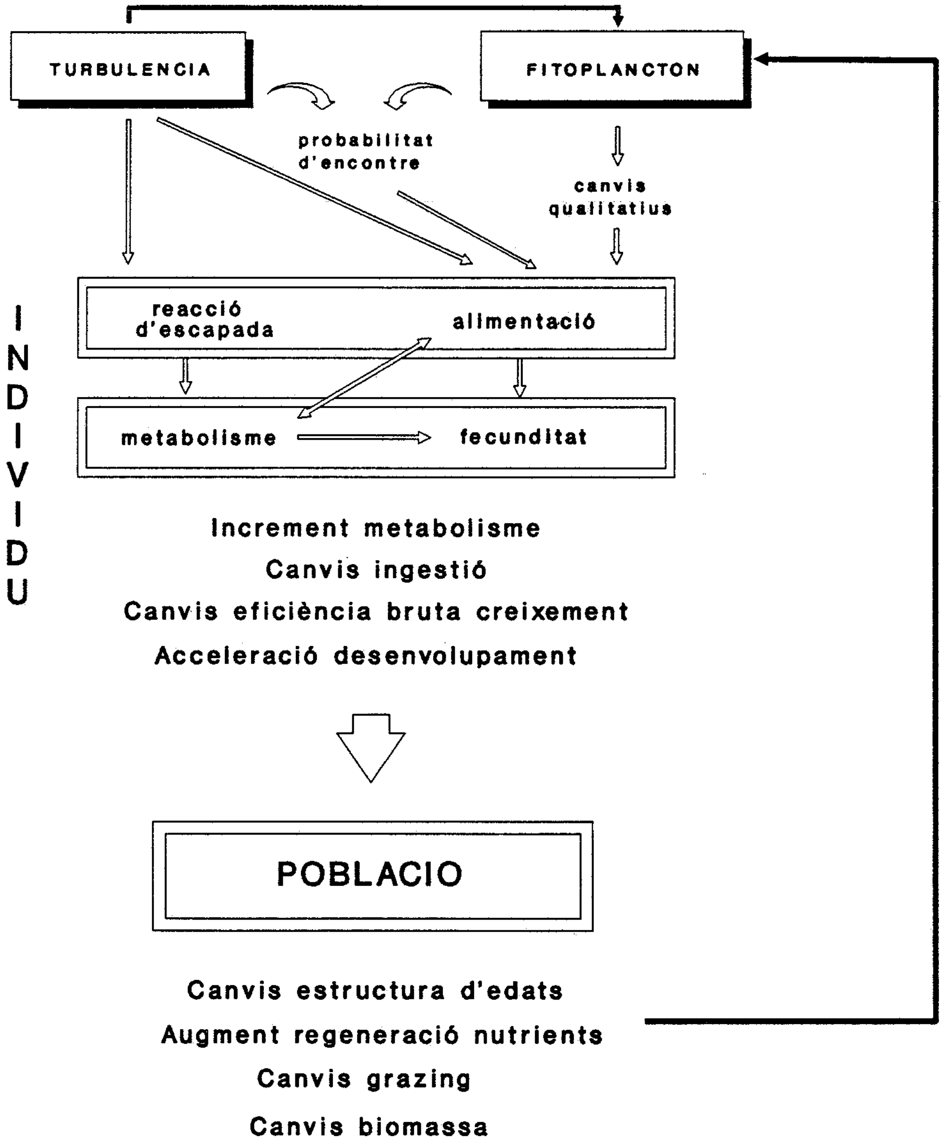


Fig. 1. Principals efectes de la turbulència en el zooplàncton i la seva interacció amb el fitoplàncton.

D'altra banda, en els estudis amb microcosmos es va evidenciar un augment en les taxes de regeneració de nutrients (Capítol I), posteriorment verificat per mesures directes d'excreció mitjançant incubacions (Capítol II), la qual cosa podria comportar un augment de la importància de la producció reciclada en el sistema a través del mesozooplàncton.

Aquests resultats, però, reflecteixen la interacció de la turbulència tant amb el zooplàncton com amb el fitoplàncton, és a dir, tant efectes directes com indirectes (recordeu la Introducció) de la turbulència. Això es va fer palès en els estudis descrits en el segon apartat del Capítol I, en els quals en lloc d'emprar la clorofil.la com a estimador de la biomassa fitoplànctònica vam considerar també el volum de matèria particulada i el seu espectre de mides. Encara que la clorofil.la va presentar una mateixa pauta ens els microcosmos amb i sense turbulència (A i Q respectivament), la quantitat de matèria particulada (biovolum) i el seu espectre de mides van divergir fortament a partir de la meitat de l'experiment. En conseqüència, mentre que els efectes directes s'evidencien a la primera part de l'experiment, a la segona no poden discernir-se dels deguts a canvis en la qualitat del menjar. Això ens indica que els resultats obtinguts amb poblacions naturals s'han d'interpretar amb cautela, i que els canvis qualitatius en el fitoplàncton a causa de la turbulència poden ser rel.levants, com s'ha observat en el medi natural (p.e. Peterson i Bellantoni 1987, Kiϕrboe et al. 1990).

Un aspecte important relatiu a l'existència d'efectes directes i indirectes és la diferència en l'escala de temps en la qual actuen. Els efectes directes actuen en el moment en què s'origina l'entrada d'energia mecànica turbulenta (p.e. ventades), i són de resposta gairebé immediata; els efectes indirectes són conseqüència de l'acció més o menys continuada de l'hidrodinamisme en les comunitats, que permet a curt termini la substitució de les poblacions de fitoplàncton. Així, aquests darrers es manifesten en zones amb singularitats hidrodinàmiques establertes (p.e. zones frontals, afloraments, cicles de barreja-estratificació) i són de més fàcil estudi.

Partint doncs de l'evidència obtinguda amb els microcosmos que la turbulència pot induir efectes directes en l'activitat i metabolisme del zooplàncton, el següent pas del nostre estudi fora esbrinar per quins mecanismes es podien desenvolupar aquests efectes directes.

El nostre estudi confirma la validesa de les hipòtesis proposades inicialment per les quals la turbulència de petita escala podria actuar directament en l'activitat del zooplàncton marí:

i) la turbulència de petita escala pot provocar un increment metabòlic com a conseqüència directa de l'estimulació mecànica (Alcaraz et al. 1989),

ii) la turbulència augmenta la probabilitat d'encontre entre depredador i presa (Rothschild i Osborn 1988), acoplat a

iii) canvis en l'eficiència alimentícia (Strickler 1985, Perez et al. 1977) per acció hidrodinàmica de la turbulència en els mecanismes i comportament d'alimentació.

Respecte a la primera, la verificació experimental de l'existència de taxes d'excreció més altes (Capítol II) conjuntament amb l'anàlisi videocinematogràfica del comportament (Capítol IV) confirmen clarament la hipòtesi. La importància d'aquest mecanisme en el medi natural, però, no és gens òbvia. Sota condicions constants de turbulència al laboratori, sembla que només organismes amb un aparell mecanosensorial força desenvolupat podrien ser els més afectats, mentre que pels altres els efectes serien més efímers. El caràcter intermitent de la turbulència de petita escala al medi natural, però, podria afavorir el funcionament d'aquests mecanismes de forma més generalitzada. Lògicament aquesta resposta dependrà de la intensitat de turbulència present. El fort increment metabòlic en condicions de turbulència detectat en els nostres experiments (en promig del 60% per les taxes d'excreció d'amoni i fòsfor) suposa una considerable despesa energètica per l'individu que haurà d'intentar compensar amb la ingestió d'aliment. Conseqùencies evidents són una previsible menor eficiència bruta de creixement (producció) i possiblement una menor vida mitjana de l'individu (esperança de vida) sota aquestes condicions d'estrés metabòlic. Si això fos cert, possiblement indicadors de envelliment com la concentració de lipofucsina en els teixits donarien resposta a la presència de moviment turbulent en el medi.

Així, els efectes de la turbulència sobre els processos biològics dels copèpodes (l'increment en les taxes metabòliques i en la velocitat de desenvolupament, i potser una tendència en la reducció de mida corporal en adults) semblen anàlegs als efectes d'un augment en la temperatura ambiental, la variable física que es considera que exerceix el control més rígid del metabolisme i desenvolupament del zooplàncton (Landry 1975, 1983, Miller et al. 1977, Ikeda 1985). En aquest sentit, Brooks (1947) descriu un efecte de la turbulència en la ciclomorfosi de cladòcers comparable a l'efecte de la temperatura. La similitud entre les conseqüències biològiques de la turbulència de petita escala i l'increment de la temperatura ambiental són comparables a la semblança en la naturalesa física d'ambdós factors (desordre molecular en el cas de la temperatura, desordre hidrodinàmic en el cas de la turbulència de petita escala).

Pel que fa a la probabilitat d'encontre en un medi turbulent, Costello et al. (1990) i Marrasé et al. (1990) van proporcionar la primera evidència directa de la hipòtesi de Rothschild i Osborn (1988). Les nostres observacions videocinematogràfiques verifiquen també aquesta hipòtesi en el cas de comportament depredador dels copèpodes envers ciliats. L'augment en la probabilitat d'encontre és un efecte purament mecànic que depèn de les velocitats absolutes del depredador i presa, és a dir, de la seva capacitat de natació respecte el flux turbulent. Per tant, és evident la seva aplicació a tots els casos en què la velocitat dels organismes sigui petita en relació a la velocitat de difusió turbulenta.

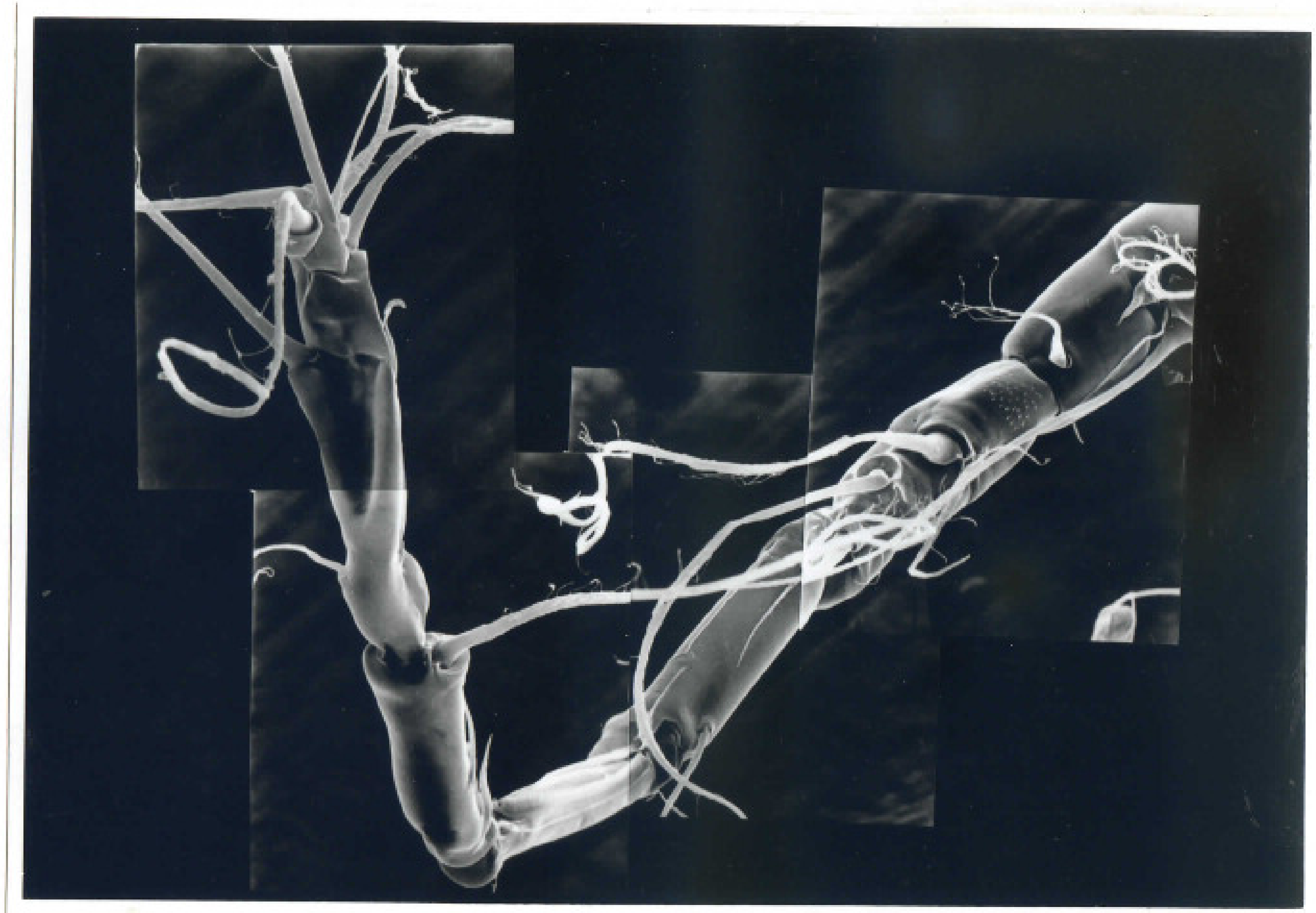
Com Marrasé et al. (1990) van suggerir, la hipòtesi de Rothschild i Osborn no té en compte el propi comportament de l'individu. Les nostres observacions videocinematogràfiques amb individus lliures i amb individus amb natació restringida (Capítol IV) indiquen com la turbulència pot afectar l'activitat (comportament) alimentícia. A més, probabilitat d'encontre no és sinònim d'ingestió. El nostre estudi de l'alimentació (ingestió) i producció (eficiència bruta de creixement) de diferents espècies del gènere *Acartia* en condicions de turbulència proporciona les primeres dades sobre aquests aspectes i confirma moltes de les hipòtesis esmentades (Capítol III). Hem demostrat que la turbulència pot afectar les taxes d'ingestió de copèpodes envers microalgues i com aquest efecte depèn de la concentració de menjar. Per concentracions saturants de la ingestió, la turbulència no produeix cap increment. Dels nostres resultats amb mascles d'*Acartia grani* podria deduir-se que si no es produeix saturació en la ingestió la turbulència podria incrementar les taxes d'ingestió inclús a concentracions d'aliment força elevades. Els experiments realitzats amb dues intensitats de turbulència indiquen com aquest efecte positiu (afavoridor de la ingestió) pot tornar-se negatiu (perjudicial) a intensitats més elevades. També hem comprovat com la turbulència afecta diferencialment l'alimentació sobre organismes de mida petita (fitoplàncton de 12-14 micres de diàmetre) i sobre organismes més grans (ous). Com proposara Strickler (1985), els nostres experiments indiquen com l'alimentació sobre preses més grans (canvi en el comportament alimentici de pautes suspensívores a pautes depredadores), basada principalment en la capacitat mecanosensorial del copèpode, és més afectada per la turbulència, emmascarant els estímuls mecanosensorials produïts per la natació de la presa.

En condicions d'estrés metabòlic una major part de l'energia disponible (ingerida) per l'individu s'esmerçaria en mantenir les funcions vitals bàsiques, mentre que la proporció d'energia destinada al creixement o produccio (és a dir, fecunditat en famelles adultes de copèpode) seria menor. Els nostres resultats sobre fecunditat i eficiència bruta de creixement (K_1, el quocient nombre d'ous produits per quantitat de menjar ingerit) en condicions de turbulència confirmen aquest estrés metabòlic i, conseqüentment, donen suport a la hipòtesi metabòlica proposada per Alcaraz et al. (1989) i a les nostres observacions d'augment en les taxes metabòliques i d'increment en la freqüència i intensitat de les reaccions d'escapada.

Així mateix, el nostre estudi demostra com espècies filogenèticament molt properes (congenèriques) poden tenir respostes diferents a la turbulència, i com les característiques hidrodinàmiques del seu hàbitat poden determinar la capacitat de resposta. Les poblacions d'*A. clausi* i *A. grani*, provinents de zones semiconfinades de la costa catalana, són sensibles a l'estímul hidromecànic de la turbulència i presenten menor eficiència de creixement; la població d'*A. tonsa* estudiada, provinent d'una zona sotmesa a marees, no va presentar aquesta resposta (K_1 no diferents). Independentment d'això, però, s'observa l'increment en la taxa d'ingestió abans mencionat.

L'extrapolació d'aquests resultats a d'altres espècies de copèpodes dependrà en part de les característiques del seu comportament alimentici i sistema sensorial. Ja hem esmentat l'abundància de mecanorreceptors (pèls sensorials tipus "e") en les antenes primeres d'*Acartia* (Fotografia 1). El mecanisme d'alimentació d'*Acartia* també és exclusiu a causa de l'ús de l'antena 2 (A2), la maxil.la 2 (Mx2) i els toracòpodes com a principals apèndixs en la captació d'aliment (Rosenberg 1980, Paffenhöfer i Stearns 1988), mentre que a la majoria de copèpodes herbívors (suspensívors) la generació de corrents d'alimentació depèn principalment del moviment de l'antena 2 (A2), la maxil.la 1 (Mx1) i el maxilípede (Mxp). Això fa que *Acartia* tingui uns corrents d'alimentació relativament forts, reduïts en extensió i de caràcter intermitent respecte d'altres copèpodes de mida similar i de comportament típicament suspensívor, com p.e. *Paracalanus*. Així, mentre un copèpode herbívor típic (suspensívor) empra al voltant del 80% del seu temps en la generació de corrents d'alimentació, *Acartia* no utilitza més del 20% (Paffenhöfer i Stearns 1988, Jonsson i Tiselius 1990).

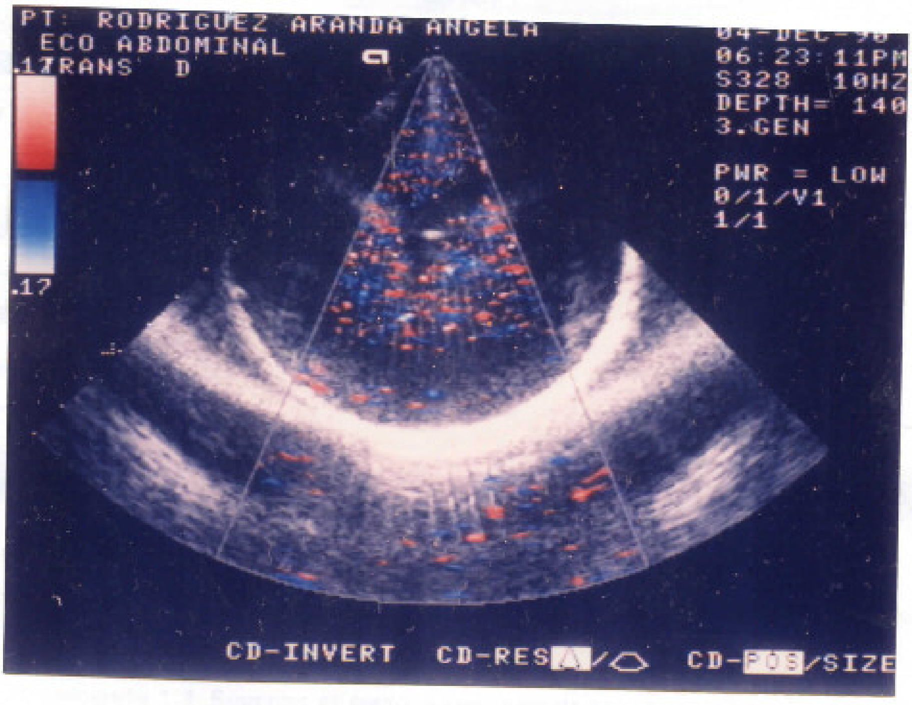
Tot això fa pensar que, inclús a petites intensitats, la turbulència pot tenir efectes negatius en d'altres copèpodes amb un comportament típicament suspensívor. P.e. les nostres observacions en *Centropages typicus* (Capítol IV) suggereixen un comportament



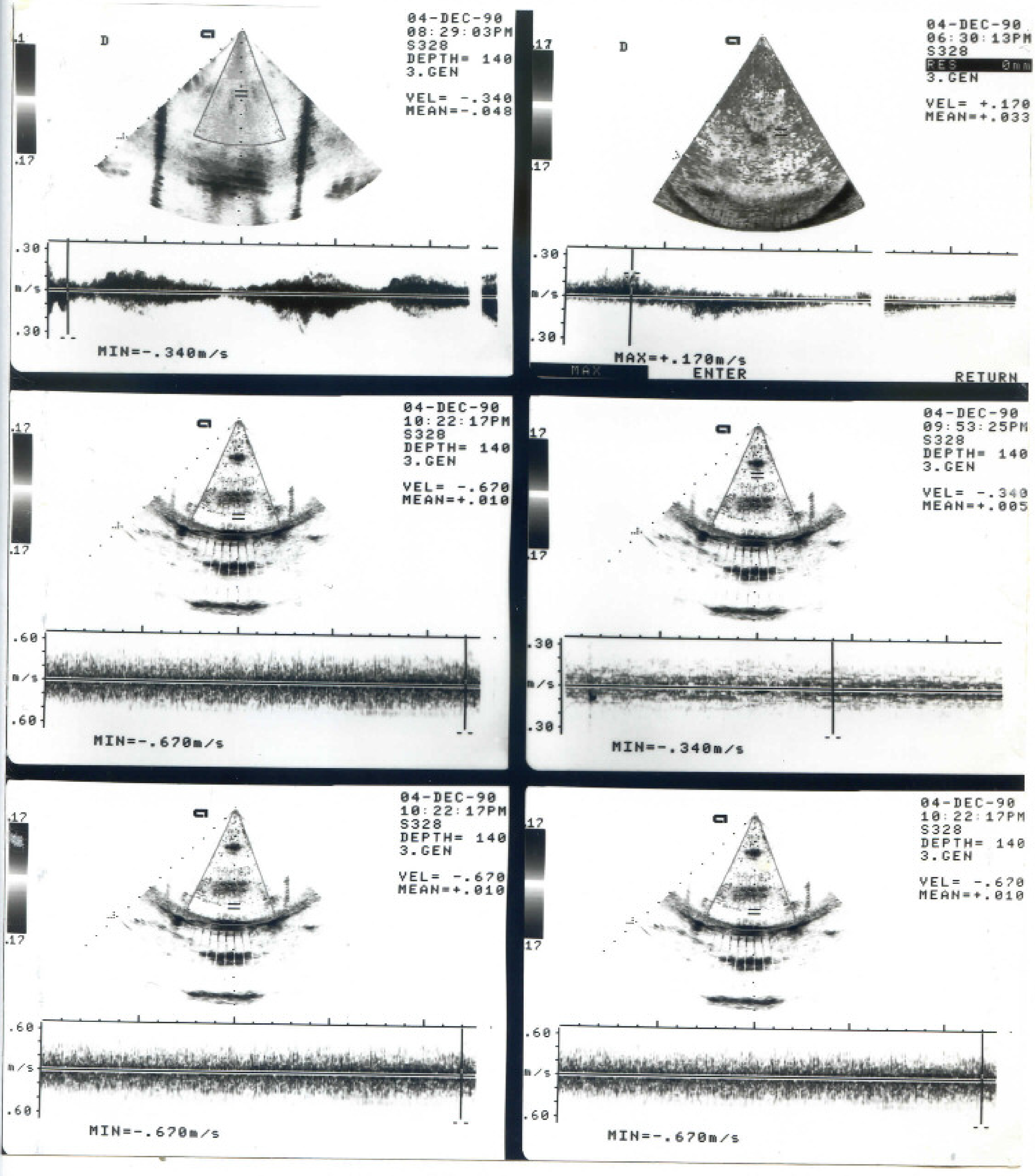
Fotografia 1.1. Detall al microscopi electrònic d'escombrada d'una antena de copèpode mascle del gènere Acartia, on es manifesten clarament els pèls sensorials de tipus "e", de funció suposadament mecanorreceptora.

diferent enfront de la turbulència de l'observat en *C. hamatus* (Costello et al. 1990, Marrasé et al. 1990), encara que en cap cas no s'ha avaluat la ingestió. La turbulència de petita escala podria tenir dos efectes negatius en els mecanismes d'alimentació: limitar la capacitat de detecció mecanosensorial de preses, per a partícules alimentícies relativament grans, i d'altra banda un efecte interferidor en els corrents d'alimentació, el qual dependria de la intensitat (velocitat de fluxe) d'aquests. El nostre coneixement actual sobre els mecanismes que intervenen en la percepció mecanosensorial dels copèpodes és encara escàs i actualment el seu estudi està adquirint molta importància (Marine Zooplankton Colloquium 1 1989). Mentre que per partícules alimentícies relativament petites (comportament suspensívor, p.e. algues de mida <20 μm) la seva importància està descartada (hi intervenen principalment processos de quimiorecepció), per partícules majors (comportament depredador) sembla ser el mecanisme principal, en relació als moviments de natació de la presa. Així, s'ha observat que partícules inerts no eliciten cap resposta en *Acartia*, inclús si topen amb les antenes, mentre que un ciliat en moviment és ràpidament detectat (Jonsson i Tiselius 1990). Prova també de la importància dels sistemes de detecció mecanosensorial en copèpodes com *Acartia* és el seu comportament enfront de possibles preses: l'animal roman immòbil, enfonsant-se lentament amb les antenes desplagades i creant la menor perturbació a l'aigua. Quan una presa és a l'abast, s'hi aboca ràpidament (Jonsson i Tiselius 1990). Perturbacions hidrodinàmiques (turbulència) de no gaire intensitat probablement contribuiran a augmentar el soroll de fons hidromecànic. La interferència en els corrents d'alimentació possiblement requerirà intensitats més elevades de turbulència. Les velocitats màximes del corrent d'alimentació varien amb l'espècie: 4 mm sec^{-1} a *Paracalanus*, 8 mm sec^{-1} a *Temora*, 8 mm sec^{-1} a *Centropages typicus*, 10 mm sec^{-1} a *C. hamatus*, 8 mm sec^{-1} a *Acartia tonsa* (Tiselius i Jonsson 1990). En els nostres estudis videocinematogràfics en condicions de natació lliure (Capítol IV) la velocitat de flux en condicions de turbulència era del mateix ordre, la qual cosa indica que podria començar a interferir-hi.

Un aspecte que ha quedat sense resoldre en aquest estudi és la quantificació de l'energia turbulenta introduïda en els dissenys experimentals emprats. Les dificultats metodològiques de simulació i quantificació al laboratori són grans (Nixon et al. 1979, Caldwell 1983, Price et al. 1988). Teòricament, a petita escala (menor del cm) totes són comparables qualsevulga sigui el mecanisme generador emprat. Mentre que mesures de difusió turbulenta en el temps són relativament fàcils d'obtenir, realment no són una mesura directa d'energia turbulenta a escales petites. Els treballs experimentals d'ecofisiologia del plàncton en els quals s'ha quantificat la dissipació d'energia turbulenta indiquen valors raonables independentment del mecanisme generador. El rang de valors present al medi natural també és vastament extens, de l'ordre de 10^{-6} a 1 cm^2 sec^{-3}, en zones oceàniques i costaneres respectivament. Malauradament, els mètodes emprats són de difícil aplicació per l'estudi rutinari de l'activitat i el metabolisme de zooplàncton. P.e., l'anàlisi videocimetogràfica de Marrasé et al. (1990) es basa en el seguiment d'un nombre molt elevat de partícules i el càlcul de les fluctuacions en les seves velocitats. La turbulència, originada des de nivells superficials, creava en el seu disseny experimental un fort gradient de dissipació d'energia turbulenta, evident per les dades que presenta al seu treball en les quals al llarg d'una superfície de 9 x 7 mm^2, el coeficient de dissipació (ϵ) variava un ordre de magnitud. Per tant, al llarg de l'aquari de 4.7 litres de capacitat emprat probablement hi trobaríem tot un ventall de valors de ϵ, la qual cosa dificultaria l'experimentació amb animals lliures sota condicions controlades (un rang estret) de turbulència. Els mateixos problemes ha tingut el nostre assaig de mesura (Capítol IV). El disseny de Pasiack i Gavis (1975) i Thomas i Gibson (1990) consisteix en dos cilindres inscrits deixant un petit espai lliure entre ells; la rotació a diferents velocitats origina un esforç fàcil de quantificar en funció de les velocitats angulars i la viscositat cinemàtica. El petit volum experimental lliure, però, fa de difícil aplicació rutinària aquest disseny per al zooplàncton. L'ús de reixetes oscil.lants també té els seus problemes, especialment pel que fa a l'efecte intrusiu de la reixeta. L'ús d'agitadors de laboratori orbitals o recíprocs requereixen altes velocitats de funcionament si no es vol obtenir una simple rotació del líquid. Sembla evident que posteriors estudis sobre l'efecte de la turbulència de petita escala en el zooplàncton (i també en el fitoplàncton) requeriran una quantificació acurada i rigurosa de la intensitat de turbulència subministrada i, si és possible, el seu espectre. També caldrà tenir en compte quin tipus de turbulència es vol estudiar i com interacciona amb les pautes de comportament de zooplàncton, fent especial èmfasi en l'acoplament de les característiques hidrodinàmiques d'un hàbitat i les espècies que l'habiten (p.e. distingir entre poblacions sotmeses a un règim de marees, que es podria considerar com una aplicació continua o periòdica d'energia cinètica turbulenta, i poblacions d'aigües somes sotmeses a ventades (polsos de major magnitud i baixa freqüència)).



Fotografia 1.2. Aspecte del monitor d'un Doppler acústic ACUSON 128 en realitzar una mesura.



Fotografia 1.3. Exemples de mesures contínues de velocitat mitjançant un Doppler acústic en algunds dels sistemes experimentals emprats.

Totes aquestes respostes requeriran un estri de mesura de turbulència de fàcil ús i aplicació en diferents tipus de models experimentals. En el moment actual sembla que la mesura més senzilla i efectiva es fonamentarà en l'ús de tècniques òptiques i acústiques basades en l'efecte Doppler (Price et al. 1988). L'anemometria per efecte Doppler permet quantificar les velocitats d'un fluid i processar un gran nombre de dades en pocs minuts de lectura. La seva utilització en Medicina Cardiovascular ha originat l'aparició d'aparells on la miniaturització i senzillesa en el funcionament faciliten el seu ús al laboratori. El nostre equip de treball ha realitzat molt recentment uns estudis preliminars d'aplicació d'aquests aparells en la quantificació de turbulència en les nostres investigacions. A la Fotografia 1.2 s'hi representa l'aspecte del monitor d'un Doppler acústic ACUSON 128. Els punts vermells i blaus indiquen fluxes d'aigua en direccions oposades. La imatge inferior representa l'espectre de velocitats en el punt de lectura al llarg del temps i llur magnituds. La digitalització d'aquests espectres proporciona en pocs minuts el que caldrien moltes hores d'analisi videocinematogràfica. A la Fotografia 1.3 s'observen els espectres de velocitats al llarg del temps i l'espai originats per alguns dels mecanismes emprats en els nostres experiments d'ecofisiologia. L'ús de reixetes oscil.lants origina ones que es desplacen al llarg del temps per a un mateix punt i al llarg de l'espai en moure's la reixeta. L'us d'una reixeta vibrant a nivell superficial origina un nivell constant al llarg del temps per un determinat punt, però amb intensitats ràpidament minvants en l'espai. Malauradament, però, el caràcter preliminar d'aquestes dades no ha permés una posterior quantificació de la turbulència. Sembla factible que l'aplicació d'algoritmes similars als emprats per Marrasé et al. (1990) permetrà a curt termini una immediata quantificació de turbulència i la posterior aplicabilitat d'aquesta tècnica a l'experimentació en el laboratori.

Al llarg de les investigacions dutes a terme en aquesta Tesi hem comprovat com la turbulència de petita escala influeix en l'activitat, comportament i desenvolupament dels copèpodes calanoides marins, tant per efectes directes com indirectes, comportant globalment un increment en les taxes dels processos fisiològics (metabolisme, alimentació, desenvolupament), la qual cosa es traduiria a mig termini en canvis en l'estructura demogràfica i biomassa de les poblacions de copèpodes i en la seva interacció amb el fitoplàncton (grazing i regeneració de nutrients) (Figura 1.1). El paper del zooplàncton (copèpodes) com a nexe entre els productors primaris i els consumidors superiors es fonamental en gran part dels ecosistemes pelàgics, especialment en aquells sotmesos a explotació (Cushing 1989). La relevància d'aquests estudis, doncs, és ben palesa. Des d'un punt de vista ecològic, podem concloure que la turbulència de petita escala modula l'activitat del zooplàncton, afectant la transferència d'energia biològica entre productors i consumidors i, conseqüentment, l'estructura general de l'ecosistema.

L'estudi dels efectes de la turbulència sobre l'activitat i comportament del zooplàncton, però, ha demostrat ésser força complex, tant pel propi caràcter de la turbulència com per la variabilitat dels processos del zooplàncton que afecta. En aquesta Tesi, doncs, només s'ha pretès contribuir en el coneixement dels mecanismes pels quals es donen aquestes relacions, encara poc conegudes, i avaluar la seva importància en funció de les característiques tant del zooplàncton com del medi. Estudis posteriors hauran de confirmar els resultats obtinguts en d'altres espècies de copèpodes i facilitar, amb l'ajut de mesures conjuntes de turbulència i dades biològiques (Haury et al. 1990), l'extrapolació al medi natural en les escales espacio-temporals adients.

CONCLUSIONS

1. La turbulència de petita escala afecta el desenvolupament de poblacions de copèpodes calanoides confinats en microcosmos.

2. Els nostres estudis indiquen que l'accelerament en el desenvolupament observat en condicions de turbulència és conseqüència d'efectes directes i indirectes.

3. Els efectes indirectes es concreten en un canvi qualitatiu en les comunitats de fitoplàncton sotmeses a turbulència, amb una tendència a la selecció d'espècies de major mida.

4. Els efectes directes es relacionen amb les pautes de comportament de l'individu i amb la probabilitat d'encontre entre depredador i presa.

5. La probabilitat d'encontre entre el zooplàncton i el seu menjar (algues, ciliats, etc.) es veu augmentada en condicions de turbulència per un efecte purament mecànic.

6. Els estímuls hidromecànics de la turbulència afecten la reacció d'escapada del zooplàncton, tant en la seva freqüència com en la seva intensitat, fet que comporta un increment considerable en el metabolisme (60% en *Acartia*).

7. La turbulència de petita escala també afecta els processos d'alimentació del zooplàncton.

8. L'augment de la probabilitat d'encontre origina un increment aparent en la densitat de preses, la qual cosa comporta un augment en les taxes d'ingestió sempre que les condicions d'aliment no siguin saturants.

9. Quan l'alimentació és de tipus depredador (envers preses relativament grans), els efectes de la turbulència poden ser més importants i inhibir les taxes d'ingestió.

10. Les característiques del comportament de cada espècie, l'hidrodinamisme del seu hàbitat i la intensitat de la turbulència modulen fortament les pautes generals esmentades.

11. L'efecte global de la turbulència és accelerar l'activitat del zooplàncton, afectant el metabolisme, l'alimentació, el comportament i el desenvolupament i, conseqüentment, l'eficiència bruta de creixement. Aquests efectes es tradueixen en canvis en la biomassa suportada pel sistema, en el reciclat de nutrients per excreció i en la pressió de depredació (grazing).

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